

A Preliminary Zoogeographical Division of Peru, Based on Butterfly Distributions (Lepidoptera, Papilionoidea)

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ABSTRACT Examination of the geographical ranges of a large number of butterfly species and subspecies in Peru, has indicated the presence of at least 48 biogeographical units, each of which contains a significant number of endemic taxa.

The areas of study include forested (closed) and nonforested (open) vegetation. The closed formations have been subdivided into lowland, montane, and upper montane forests. The open formations have been classified as lowland, montane, upper montane, and páramo-puna regions.

Many colleagues and friends, too numerous to be named individually, have contributed, in several ways, to the development of the ideas presented herein. Among them, special thanks are due to Hernando de Macedo and Antonio Brack, and Manuel Plenge, Pedro Hocking, and Gustavo del Solar, all from Peru, for sharing with me their expertise on Peruvian ornithology and geography. For a most profitable collaboration and generous advice, I want to express my gratitude to Keith S. Brown and Jürgen Haffer. Any virtues this paper may have, I owe to the teachings and guidance of Professor Paulo E. Vanzolini who introduced me to the delights of biogeographic research.

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It is considered that such regions could include endemism centers which may have been shaped by Quaternary climatic and vegetational changes.

THE GEOGRAPHICAL TERRITORY of Peru may well be considered to have the richest biological diversity on earth. Out of 103 ecological "life zones" proposed by Holdridge for the world, 84 have been identified in this country (ONERN, 1976). My conservative estimate, is that there are approximately 4,000 butterfly species in Peru (Lamas 1978; Legg 1978). About 1,640 species of birds are currently known for the country, out of 2,965 species listed by de Schauensee (1966) for South America.

Several authors have previously attempted to classify the rich biological diversity of Peru into biogeographical units. Ceballos (1976, 1977) gives a summary of such attempts, and proposes a more elaborate version. However, most of those authors have used the "regional concept" (Darlington 1957), which is rather arbitrary, as it is based on the geographical ranges of families and genera (Müller 1973). In contrast, the chorological analysis method employed by de Lattin (1967), based on the study of so-called dispersal centers of species and subspecies of organisms, seems to be a more satisfactory approach to delimit such units.

Centers of Origin and Related Concepts

Under this title, Croizat, Nelson and Rosen (1974) present a paper criticizing the Darwinian concept of "center of origin," and its corollary, dispersal of species, as being inconsistent in certain respects with the principles of common ancestry and vicariance (allopatry). Instead, they use the concept of "tracks" to define the distribution of a species, or of a monophyletic group of organisms. Individual tracks are distributions of species, or monophyletic groups; generalized tracks include the coincident individual tracks of several species, or groups.

On the other hand, Müller (1973) indicates that "every species possesses, or used to possess, at least one dispersal centre that was its centre of origin. During the evolution of a taxon, however, the centre of origin and the centre of dispersal can become widely separated from each other."

Brown (1977a) established the differences between the terms "evolutionary center" and "refuge." The first concept indicates a geographical region showing a high degree of endemism of species or subspecies, of plants and animals, whose populations are mostly monomorphic. An ecological refuge is a region where continuity of favorable conditions makes the preservation rather than the extinction of organisms associated with these conditions statistically more probable, and is represented by a restricted area inside an evolutionary center.

In my opinion, Croizat's "tracks," Müller's "dispersal centres," and Brown's "evolutionary centers" roughly define the same concept, which is here called an "endemism center." An endemism center denotes a common biogeographic unit, shared by several monotypic species or subspecies, which have a strongly coincident spatial

distribution, and similar environmental requirements (cf. also Brown & Ab'Sáber 1979.)

My paper is both descriptive and predictive in nature. I indicate what we presently know about the geographical distribution patterns of the butterflies found in Peru. The main body of the paper is dedicated to a description of 48 areas that show coincident geographic distributions of differentiated butterfly populations (species and subspecies).

Material and Methods

I have mapped the distribution ranges of a large number of selected species and subspecies of butterflies, with which I am personally familiar, either through recent revisionary work performed by myself, field experience, or both. The species studied belong to families Papilionidae, Pieridae, and Nymphalidae (*sensu lato*). No species of the less-known Lycaenidae and Hesperidae has been considered herein.

In spite of what is commonly thought, the systematics of Neotropical butterflies is not very well known. Although possibly well over 95 percent of the South American Papilionidae, Pieridae, and Nymphalidae species have already been described, an enormous number of unrecognized subspecies remain. Also, many species currently regarded as monotypic are nothing more than subspecies. For example, out of 509 species listed by Bryk (1937) in the last published catalogue for the Ithomiinae (Nymphalidae), it is considered now that less than 300 full species belong in the subfamily (Lamas, unpublished), notwithstanding that many "new" species were described during the last 40 years. However, recent work, mostly unpublished, done by Dr. Keith S. Brown and myself, on the heliconiine and ithomiine nymphalids, and

the dimorphiine pierids, has resulted in a much better understanding of those groups.

Besides the problems posed by poor systematic knowledge of the Neotropical butterflies, a serious drawback for chorological analysis is that many species preserved in collections have unreliable distribution data. This is especially true for old material, or material purchased or received from private collections. A large number of records in the literature are unreliable, not only because of faulty labeling, or misplacing of the collecting stations (especially common for Latin American countries, where many places bear the same, or similar names), but also because of misidentification of species and subspecies.

To overcome these difficulties, I have relied mostly on material I have personally examined, or collected, keeping literature records to a minimum. This means that most of this paper is based on unpublished studies.

With the exception of the works by Müller (1973), Schreiber (1978), and F. Vuilleumier (1969), most recent work on Neotropical endemism centers and refuges has been made on lowland and lower montane tropical rain forest areas (*sensu* Richards 1966). The present paper tries to offer a broader picture, including the two main types of terrestrial environments, forested (arboreal), and nonforested (eremial), and ranging from sea level to the permanent snow line.

Butterflies are exclusively terrestrial organisms, and their species usually can be divided into those favoring forested (closed) environments, and others preferring nonforested (open) areas. Of course, the ecological requirements vary from species to species, showing all possible gradations—from species that never leave the interior of the deep forest, to those that never enter the forest. Also, many species show a vertical zonation on mountains, which corre-

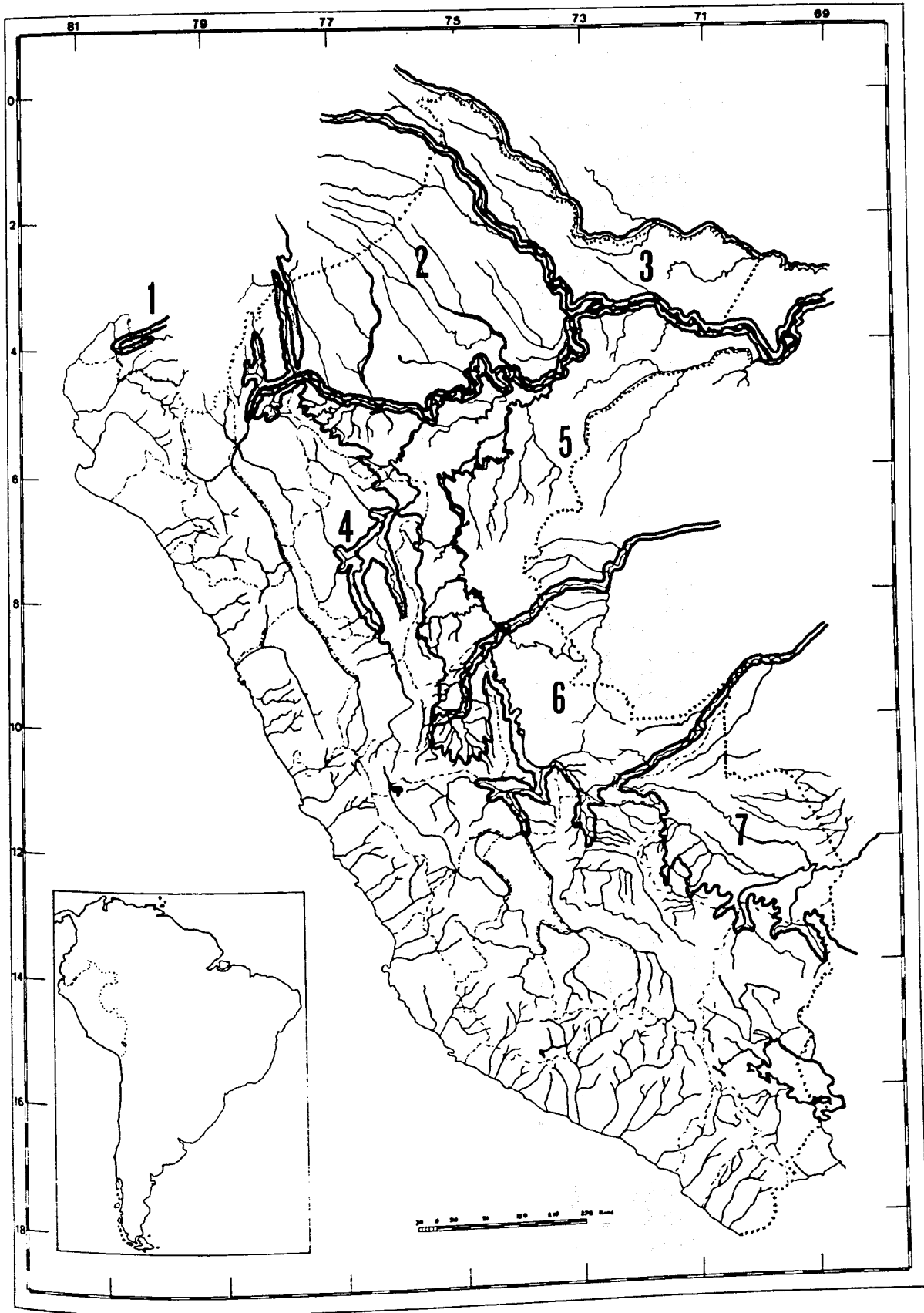
sponds quite closely with the main vegetational levels.

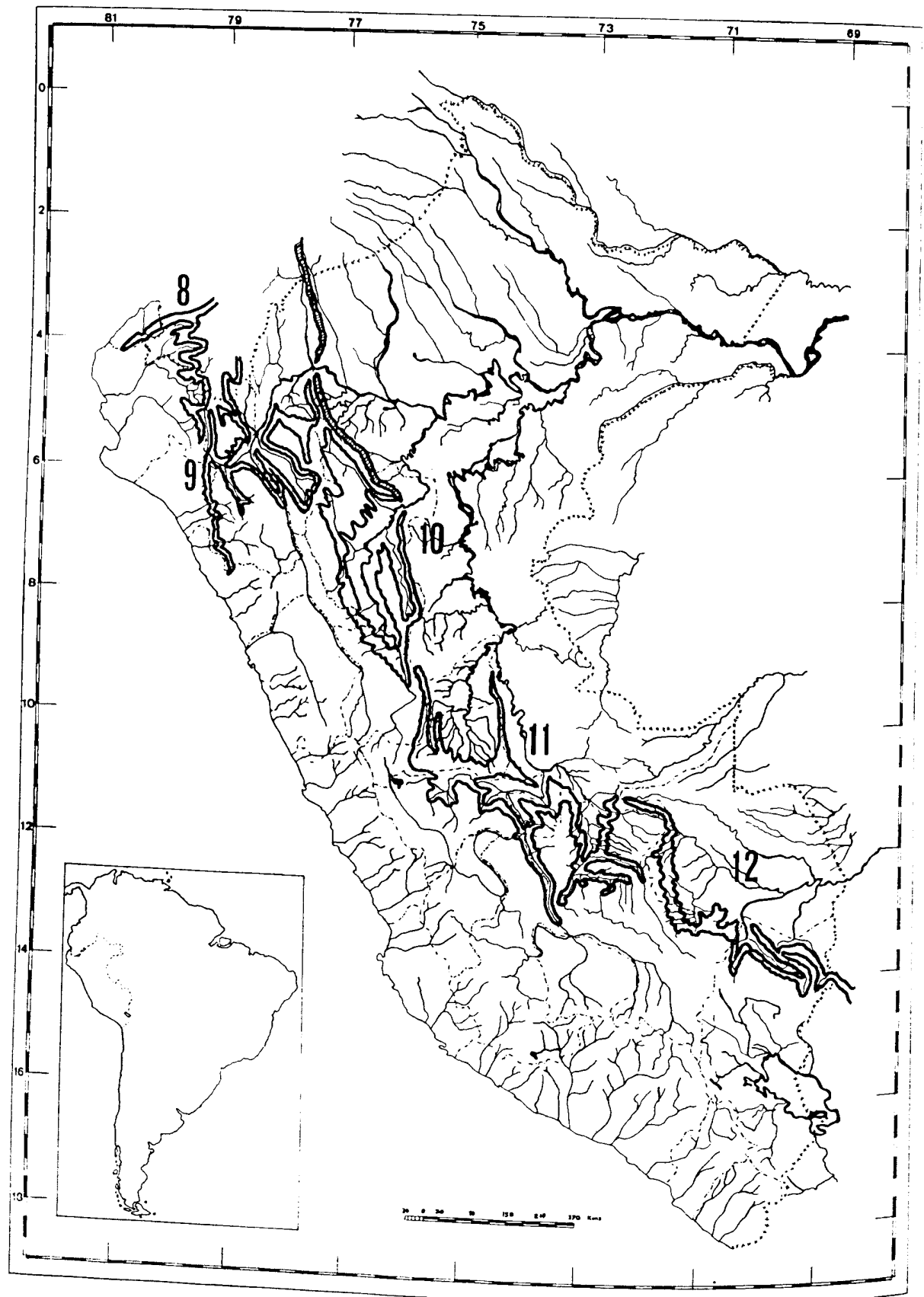
I have divided the forested areas into three levels of vertical zonation: 1) *lowland forest*, below 500 m elevation; 2) *lower montane forest*, between 500 and 1,500 m; and 3) *upper montane forest*, from 1,500 m to timber line (about 3500 m). The nonforested areas show four levels: 1) *lowlands*, below 500 m on the east side of the Andes, but reaching somewhat over 1,000 m on the western side; 2) *lower montane*, between 500 and 2,000 m on the east side, but between 1,000 and 2,700 m on the west side; 3) *upper montane*, between 2,000 (2,700) and 3,500 (3,800) m; and 4) *Páramo-Puna*, above 3,500 (3,800) m, up to the snow line (about 5,000 m). The upper montane forest level includes both cloud and elfin forest, which may be separated in the future, when the dominant species found in the elfin forests (e.g., Satyrinae), are better known (the Ithomiinae are dominant in the cloud forests, from about 1,500 to 2,500 m). This vertical zonation is somewhat arbitrary, and represents an average of observations made in several areas of Peru, as there are places where marked displacement of vegetational zones is found (Terborgh & Weske 1975).

Figures 18.1–18.3 (forested areas), and 18.4–18.7 (nonforested areas) below show the approximate limits of the biogeographical units suggested by the present research. Each area harbors several endemic, monotypic species or subspecies of butterflies, which so far have been found to occur nowhere else but inside the proposed limits of those biogeographic units. There are some exceptions, as occasional specimens may sometimes be found outside the distributional limits of their species or subspecies ranges, but never too far outside (unless an obvious locality mislabeling has occurred).

It has not been possible yet to trans-

Figure 18.1 Lowland forest (0–500 m) biogeographical units. 1. El Caucho; 2. Napo; 3. Pebas; 4. Tocache; 5. Yurimaguas; 6. Atalaya; 7. Inambari.





form those distributional data into a quantitative map of isolines for endemism (Brown & Ab'Sáber 1979), as not enough information is available for most areas treated herein. For that reason, I am not in a position to consider the biogeographic units described in this paper as centers of endemism, although only supposedly endemic populations of butterflies have been listed as examples for each area.

The areas drawn on the maps of figures 18.1-18.7 represent the theoretical maximum extent of the distributional ranges of selected monotypic species and subspecies of butterflies in Peru (no attempt has been made to figure the limits of units that extend outside the Peruvian territory). This does not necessarily mean, however, that every one of the endemic populations found within an area will have that maximum range, as some populations, possibly due to various ecological reasons, may have significantly smaller ranges. The limits drawn indicate the main, present-day barriers which, supposedly, are effectively reducing, or altogether stopping, dispersal and/or gene flow between populations on opposite sides of the barrier.

In the case of montane and inter-Andean areas, the limits have been given, rather arbitrarily, as contour lines indicating the elevations at which marked changes in species compositions apparently occur (roughly, at the 500, 1,500 and 3,500 m levels in forested environments, and at the 500 (1,000), 2,000 (2,700), 3,500 (3,800) and 5,000 m levels in open areas).

Large rivers or deserts have usually been selected as indicating the limits between biogeographic units in lowland areas. In several instances, narrow hybridization zones between subspecies have been detected on opposite banks of a large river. Admittedly, however, several smaller tributaries have been arbitrarily chosen as rep-

resenting distributional limits, because not enough information is available on the true limits in certain poorly collected areas. This does not necessarily indicate that wide rivers represent effective barriers against gene flow for all, or even most, butterfly populations. Indeed, several species or subspecies, which are considered here as "nonendemic," may be found in two or more biogeographic units, without differentiation, as they are able to cross wide rivers, which could represent strong barriers against dispersal for other butterflies (cf. Haffer 1978, for a discussion on large rivers and mountains as barriers).

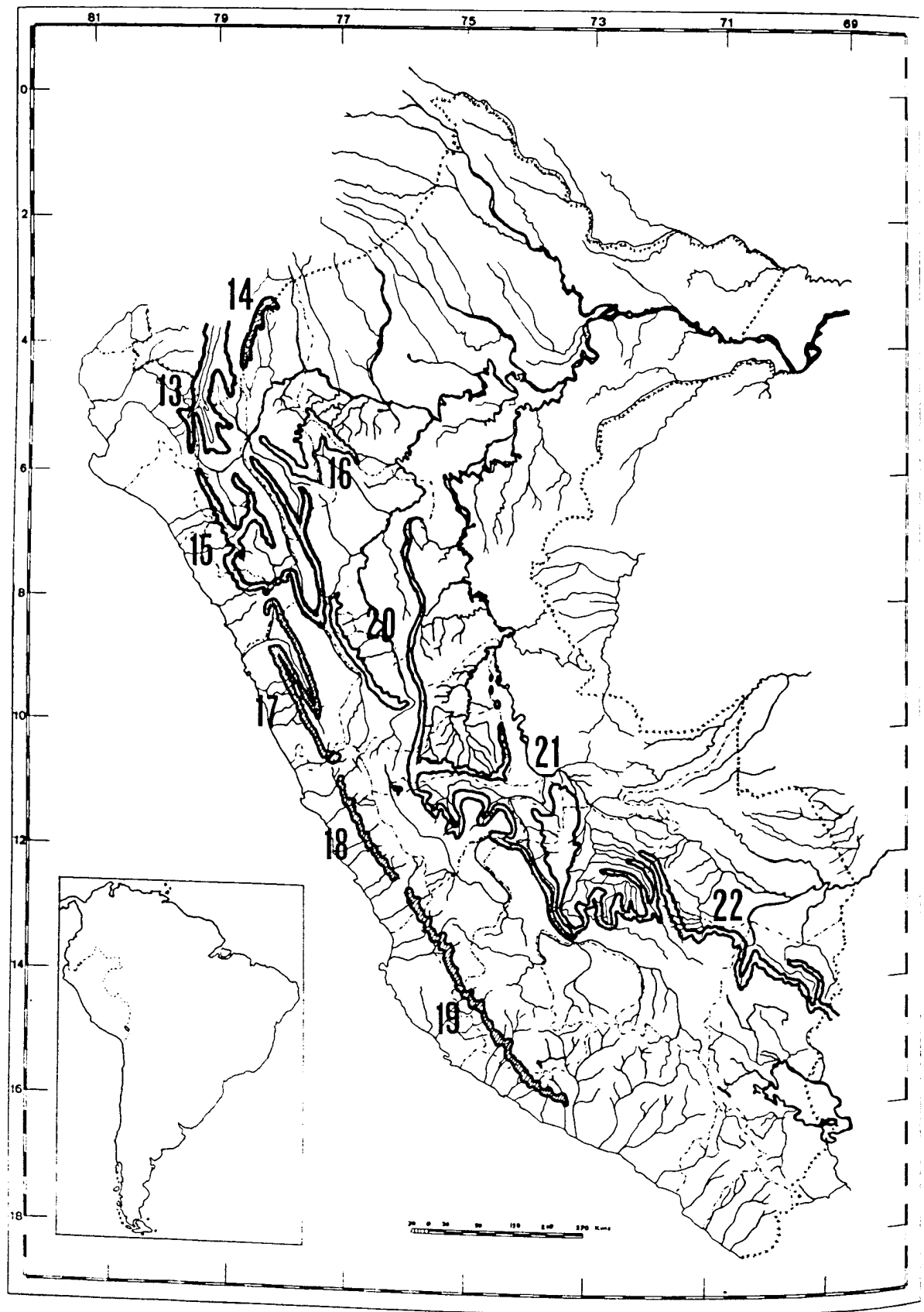
For instance, a species X may include three subspecies (a, b, and c), a being found in at least part of the area covered by units 2 and 3, b in unit 4, and c in units 5 to 7 (Fig. 18.1). Of such a species, only subspecies b would be considered as representing an endemic of area 4, while a and c would be regarded as nonendemics.

The biogeographic units 1-48 (figs. 18.1-18.7) in this paper, are defined either on the basis of the presence of endemic monotypic species or subspecies of butterflies, or on the prediction that such endemics may occur in certain areas.

Biogeographic Units

The following abbreviations will be used for butterfly families and subfamilies: A, Apaturinae; B, Brassolinae; D, Danainae; H, Heliconiinae; I, Ithomiinae; M, Morphinae; N, Nymphalinae; Pa, Papilionidae; Pi, Pieridae; S, Satyrinae.

Figure 18.2 Lower montane forest (500-1,500 m) biogeographical units. 8. Amotape; 9. Marañón; 10. Hualaga; 11. Chanchamayo; 12. Quincemil. The hatched area indicates the assumed corridor connecting the Huallaga unit with southeastern Ecuador.



Forested Areas

Lowland Forest (fig. 18.1)

1. *EL CAUCHO Unit*: The only place in western Peru where lowland tropical rain forest has been found, is in a narrow belt in the interior of Tumbes department, around the Amotape mountains, north and west of the Tumbes river. This area has been described in part by H.-W. Koepcke (1961: 150), and by Lamas (1976b). It is the southernmost extension of the lowland forests of western Ecuador (Chimborazo refuge of Brown 1977b, in part), and has as its center the settlement of El Caucho.

As characteristic species (faunal elements, *sensu* Müller, 1973), the following may be mentioned: *Itaballia marana* (Pi), *Perrhybris pamela* ssp. n. (Pi), *Scada zemira* (I), *Ithomia iphianassa cleora* (I), *Morpho achilles maculata* (M), *Heliconius erato cyrbia* (H), *H. melpomene cythera* (H), *Siproeta stelenes sophene* (N), and *Anaea ecuadoralis* (A).

2. *NAPO Unit*: Includes the area between the Cordillera de Campanquiz to the west, the lower Napo river to the east, and the lower Marañón river to the south. Its faunal elements are also found in eastern Ecuador, and some reach the lower portion of the Cenepa and Santiago valleys (Amazonas department, Peru).

Characteristic species are: *Dismorphia theucharila leuconoe* (Pi), *Tithorea harmonia hermius* (I), *Napeogenes achaea quadrilis* (I), *Hypothyris moebiusi moebiusi* (I), *Callithea batesii degandii* (N), *C. leprieurii depuiseti* (N), and *Agrias phalcidon beatifica* (A).

This is equivalent to Brown's (1977b) Napo refuge, and is perhaps the least-known lowland forest area in Peru.

3. *PEBAS Unit*: Covers the area east of

the lower Napo, and north of the upper Amazonas; its northern limit may lie on the Putumayo river, or further north.

It is characterized by the following species: *Dismorphia theucharila erythroae* (Pi), *Napeogenes achaea curvilutea* (I), *Hypothyris anastasia porsenna* (I), *H. ninonia apollinis* (I), *H. semifulva soror* (I), *Heliconius hecale humboldti* (H), *H. numata aurora* (H), *H. ethilla adela* (H), *Callithea batesii srnkai* (N), *C. leprieurii fassli* (N), and *Agrias phalcidon stuarti* (A).

This is called the Loreto refuge by Brown (1977b), although he places it in a different position, between the Amazonas and Yavari rivers, but this view is corrected in Brown and Ab'Sáber (1979: fig. 7).

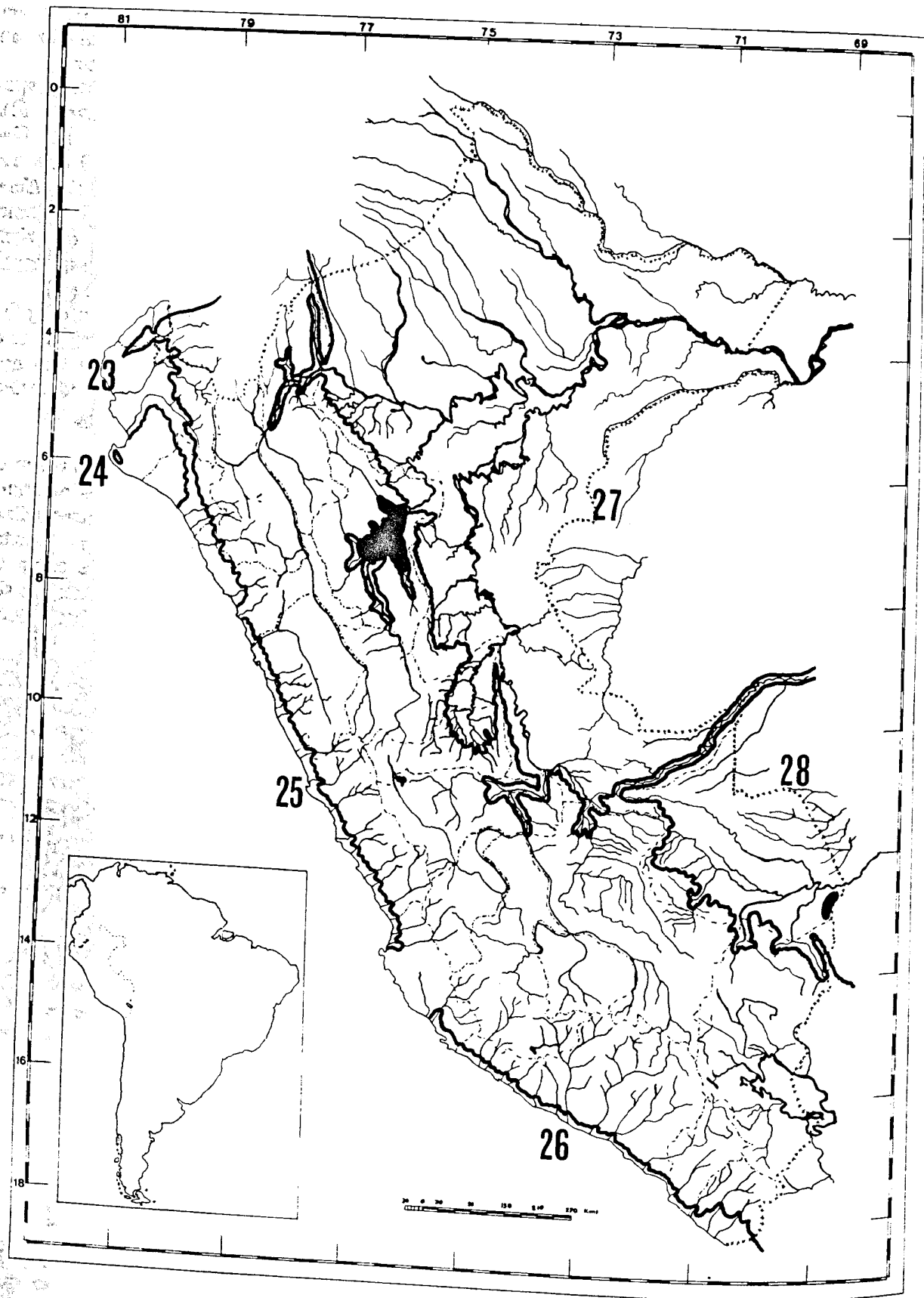
4. *TOCACHE Unit*: Located on the middle Huallaga valley, it has as its northern limit the Pongo (Canyon) de Aguirre (where the Huallaga crosses the eastern Cordillera), and reaches at least the town of Uchiza on the south. Also, it includes the lower Mayo, Abiseo, and Huayabamba rivers, as well as the Biabo valley.

Characteristic elements are: *Dismorphia laja lysianax* (Pi), *D. theucharila* ssp. n. (Pi), *Melinaea ethra tarapotensis* (I), *Hypothyris fluonia uchiza* (I), *Ceratinia neso tarapotis* (I), *Heliconius ethilla arotome* (H), *H. hecale felix* (H), *H. pardalinus sergestus* (H), *Callithea leprieurii* ssp. n. (N), *Batesia hypochlora hypochlora* (N), and *Agrias phalcidon pherenice* (A).

This is Brown's (1976b) Huallaga refuge (in part).

5. *YURIMAGUAS Unit*: Its northern limit is given by the lower Marañón and upper Amazonas, while the southern limit is about the Pachitea river to the west, and the Jurúa to the east. The western limit is given by the easternmost chain of the Andes (Cordillera Oriental). Some species may extend their range west into the middle Mara-

Figure 18.3 Upper montane forest (1,500-3,500 m) biogeographical units. 13. Huancabamba; 14. El Cóndor; 15. Cutervo; 16. Chachapoyas; 17. Ancash; 18. Lima; 19. Chuquibamba; 20. Carpish; 21. Oxapampa; 22. Marcapata. The hatched areas indicate presumed units.



ñón, up to the lower Nieva and Chiriaco rivers.

Characteristic faunal elements are: *Dismorphia amphiona* ssp. n. (Pi), *D. theucharila melanoë* (Pi), *Moschoneura pinthous* ssp. n. (Pi), *Tithorea harmonia* ssp. n. (I), *Melinaea ethra cydon* (I), *Mechanitis polymnia dorissides* (I), *Sais rosalia zitella* (I), *Hypothyris anastasia anastasina* (I), *H. fluonia pardalina* (I), *Heliconius ethilla clarus* (H), *H. pardalinus dilatus* (H), *Callithea batesii bartletti* (N), *C. buckleyi staudingeri* (N), *C. leprieurii optima* (N), and *Agrias phalcidon olivencia* (A).

6. **ATALAYA Unit:** Its presumed northern limit is given by the Pachitea river to the west, and the Juruá to the east, while it is bound to the south by the lower Uribamba to the west, and the Purús river to the east. Species belonging to this area are found on the lower Palcazu and Pichis rivers to the northwest, and the lower Perené, Satipo, and Apurímac rivers to the southwest. Although very incompletely known, especially east of the upper Ucayali, it is rich in endemics. Some of them have been figured by Papageorgis (1975), and the most characteristic are: *Dismorphia laja koenigi* (Pi), *Tithorea harmonia melanina* (I), *Hypothyris moebiusi unicolora* (I), *H. ninonia latipennis* (I), *H. semifulva angelina* (I), *Hyposcada anchiala interrupta* (I), *Ceratinia neso peruensis* (I), *Heliconius pardalinus tithoreides* (H), *Callithea batesii adamsi* (N), *C. leprieurii philotima* (N), and *Agrias phalcidon beata* (A).

Brown (1977b) called this the Ucayali refuge (in part).

7. **INAMBARI Unit:** Possibly bound to the north by the Purús, and to the west and south by the eastern chain of the Andes, it extends east into southwestern Brazil, and northwestern Bolivia. Only recently have

significant collections been made in this area (cf. Lamas 1976a).

Endemic butterflies are: *Parides echemon empistocles* (Pa), *Perrhybris pamela* ssp. n. (Pi), *Tithorea harmonia brunnea* (I), *Melinaea ethra lamasi* (I), *M. marsaeus clara* (I), *Hypothyris fluonia seminigra* (I), *H. ninonia* ssp. n. (I), *H. semifulva virgilini* (I), *Heliconius ethilla nebulosa* (H), *H. pardalinus maeon* (H), *Callithea batesii frigga* (N), *C. leprieurii eminens* (N), and *C. sapphira tirapatensis* (N).

This corresponds, in part, to Brown's (1977b) Inambari refuge.

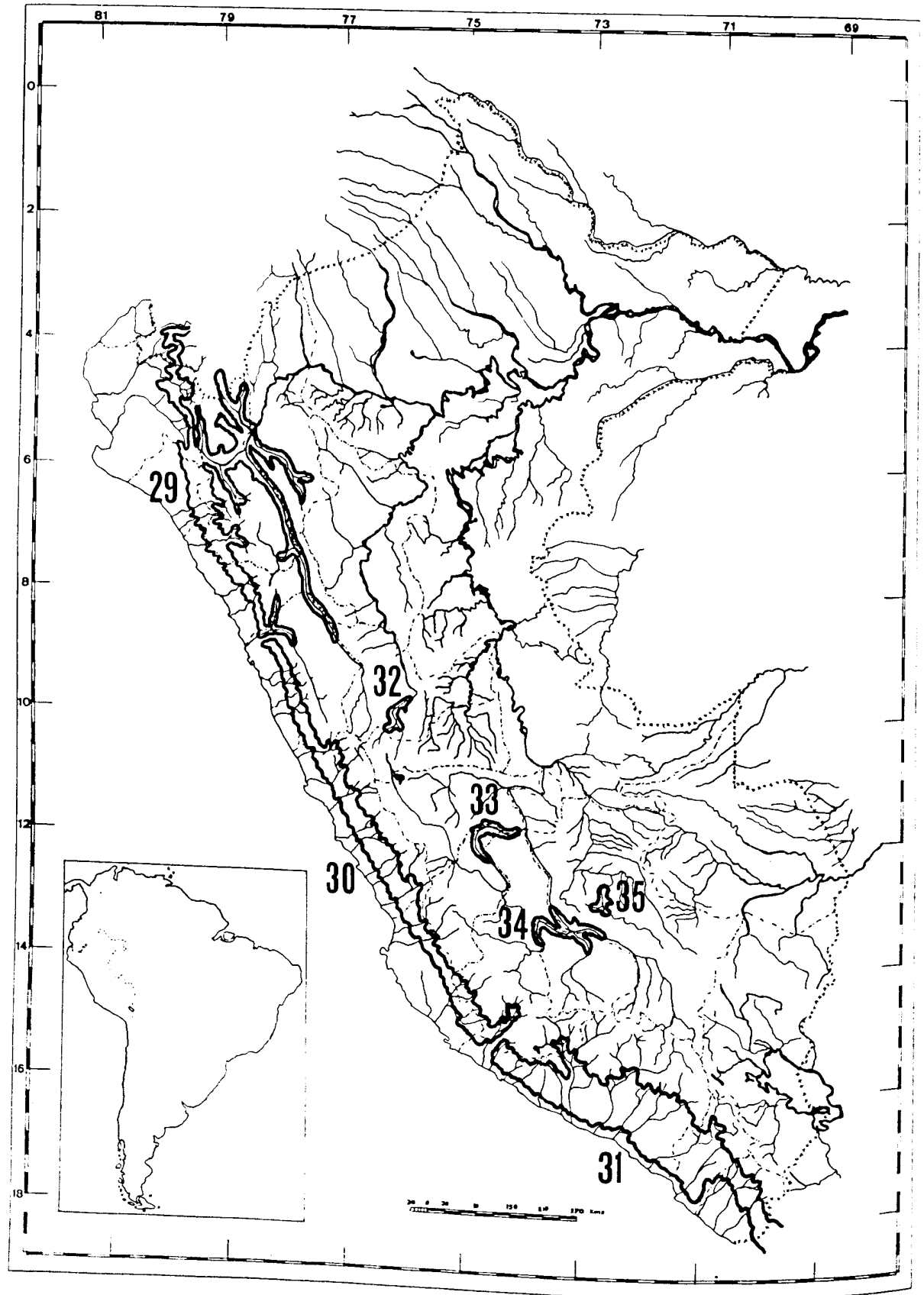
Lower Montane Forest (fig. 18.2)

8. **AMOTAPE Unit:** Includes the Amotape mountains in Tumbes and northern Piura, and the upper portions of the Quiroz and Piura rivers, possibly going as far south as the Porculla Pass in southeastern Piura (the lowest pass between the upper Marañón valley, and the western slopes of the Cordillera Occidental).

Although well documented for birds (cf. H.-W. Koepcke, 1961: 150ff.), this is one of the least-known regions for butterflies. I can list only two species, *Dismorphia crisia* ssp. n. (Pi), and *Diaethria ceryx* (N), and possibly also *Heliconius clysonymus hygiana* (H), which I have collected in the upper Puyango river in Ecuador, close to the Peruvian border.

9. **MARAÑÓN Unit:** This is a complex area, which may really include several units, but present data are still too scant to confirm this assumption. As defined here, it includes: (i) the lower montane forests found in the Huancabamba, Tabaconas and Chinchipe rivers, in northern Cajamarca; (ii) the Chotano, Cutervo and Llangas rivers, in southern Cajamarca; (iii) the Utcubamba, upper Chiriaco and upper

Figure 18.4 Open lowland (0-500 m in the east; 0-1,000 in the west) biogeographical units. 23. Piura; 24. Illescas; 25. Callao; 26. Mollendo; 27. Loreto (the black area indicates the drier area of the Huallaga valley); 28. Madre de Dios (the black area shows location of the Pampas del Heath).



Nieva rivers, in Amazonas; and (iv) a narrow strip of relict forest islands on the western side of the Andes, from the Porculla pass in the north, to about the Moche river (La Libertad), in the south.

This unit has a large number of endemics, some of which are: *Eurytides agesilau montanum* (Pa), *E. harmodius tabaconas* (Pa), *Parides erlaces chinchipensis* (Pa), *Dismorphia crisia* ssp. n. (Pi), *Tithorea harmonia gilberti* (I), *Mechanitis polymnia* ssp. n. (I), *Scada kusa kusa* (I), *S. reckia* ssp. n. (I), *Hyaliris coeno latilimbata* (I), *Ithomia agnosia* ssp. n. (I), *Greta andromica* ssp. n. (I), *Episcada apuleia* ssp. n. (I), *Opsiphanes cassiae* ssp. n. (B), *Morpho achilles charapensis* (M), *Heliconius clysonymus tabaconas* (H), *H. erato himera* (H), and *H. numata talboti* (H).

Each of the four areas forming the Marañón unit may harbor endemic populations. The least-known area is that found on the western side of the Andes, which also lacks many species found on the eastern slopes. Apparently, a number of species are unable to cross the low (2,145 m) Porculla Pass.

Most examples of Brown's (1977b) Marañón refuge belong to this unit.

10. HUALLAGA Unit: Includes the upper Mayo, Sisa, Saposoa and Huayabamba valleys in northwestern San Martín, and the upper Huallaga and its tributaries in southwestern San Martín and northwestern Huánuco. It is bound to the east by the Cordillera Oriental (Azul), and to the west by the eastern slopes of the Cordillera Central. Two well-known hybridization areas with faunal elements of the Yurimaguas unit (5 above), are on the upper Cainarache river (on the road from Tarapoto to Yurimaguas), and on the Boquerón del Padre Abad (on the road from Tingo María to Pucallpa) (Lamas 1976a).

Although many collections have been made in this region during the last 100

years, especially on the upper Mayo, a large number of characteristic subspecies have not been named yet. This is one of the richest areas of Peru, and corresponds (in part) to Brown's (1977b) Huallaga refuge.

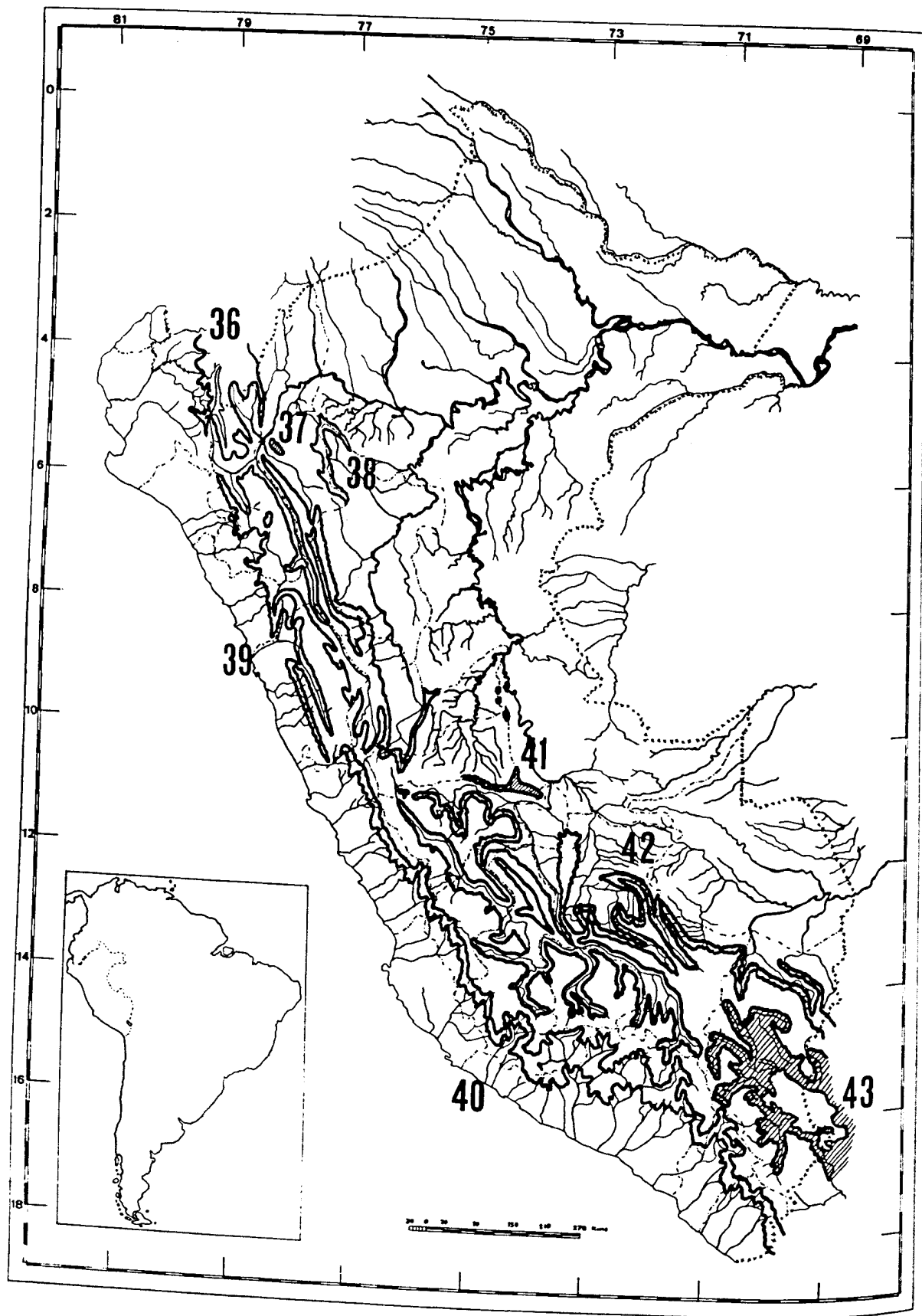
Among its many endemics, the following may be mentioned: *Parides drucei* ssp. n. (Pa), *P. erlaces xanthias* (Pa), *Pseudopieris nehemia* ssp. n. (Pi), *Dismorphia theucharila* ssp. n. (Pi), *Tithorea harmonia martina* (I), *Mechanitis polymnia proceriformis* (I), *Napeogenes apulia palmasensis* (I), *N. stella incas* (I), *N. sylphis rindgei* (I), *Hypothyris euclea* ssp. n. (I), *H. semifulva pallisteri* (I), *Hyaliris coeno schlingeri* (I), *Ceratinia tutia onoma* (I), *Opsiphanes invirae cassina* (B), *Morpho achilles orestes* (M), *M. adonis huallaga* (M), *M. menelaus occidentalis* (M), *M. aurora* ssp. n. (M), and *M. rhetenor helena* (M).

Both Brown (1977b) and I (Lamas 1979) have indicated the possible existence of two "subrefuges," or subareas, for the Huallaga region, one including the Mayo river, the other the upper Huallaga. I believe this can now be explained by the fact that one is a lowland forest unit (Tocache), the other a lower montane forest unit. Most samples of the characteristic Tocache-unit butterflies have been collected in the Mayo area ("Tarapoto" being the generalized locality), while only recently has the lowland part of the upper Huallaga been accessible for collectors. Classical "Tarapoto" species are now being collected from as far south as Uchiza.

Some species of wider distribution seem to use a narrow corridor, partly connecting the Huallaga unit with southeastern Ecuador, along the eastern slopes of the Cordillera del Otanau (northeastern San Martín), and the Cordillera de Campanquiz (northeastern Amazonas).

11. CHANCHAMAYO Unit: This is another well-known area, rich in endemics, although its true limits are poorly under-

Figure 18.5 Open lower montane (500-2,000 m in the east; 1,000-2,700 m in the west) biogeographical units. 29. Porculla; 30. Surco; 31. Arequipa; 32. Huánuco; 33. Mantaro; 34. Pampas; 35. Santa Ana.



stood. As defined here, it has its nucleus in the Chanchamayo valley, Junín department. To the northeast, it extends at least to the Pozuzo valley (in the border between Huánuco and San Martín); also includes the mountains separating the Pozuzo and Palcazu rivers (Cordillera de Yanachaga), and the Cerros del Sira, between the Pachitea and Ucayali (for a description of the latter mountains see Terborgh & Weske 1975). To the southwest, it extends to the lower Apurimac river (up to the Pampaconas river), and to the southeast, the middle Urubamba, and its tributaries, the Yavero, Yanatili, and Concebidayoc. Its easternmost limit seems to lie on the border between Cuzco and Madre de Dios.

Characteristic faunal elements are the following: *Pseudopieris viridula* ssp. n. (Pi), *Dismorphia medorilla* ssp. n. (Pi), *Moschoneura pinthous amelina* (Pi), *Tithorea harmonia neitha* (I), *Mechanitis polymnia eurydice* (I), *Napeogenes apulia woytkowskii* (I), *Hypothyris euclea peruviana* (I), *Hyaliris juninensis* (I), *H. oulita metella* (I), *Ceratinia tutia chanchamaya* (I), *Godyris mantura honrathi* (I), *Morpho achilles papirius* (M), *M. adonis major* (M), *M. rhetenor cacica* (M), *M. menelaus didius* (M), and *M. aurora aureola* (M).

The unit corresponds quite closely with Brown's (1977b) Chanchamayo refuge.

12. **QUINCEMIL Unit:** Its western limit could be on the Pantiacolla range, in the border between Cuzco and Madre de Dios, while its eastern boundary lies in Bolivia. It includes the Pantiacolla, Cosñipata, Marcapata, San Gabán, upper Inambari and upper Tambopata valleys. This unit is also extremely rich in endemics (perhaps the richest area in Peru). Some of its diagnostic butterflies are: *Pseudopieris viridula* ssp. n. (Pi), *Dismorphia medorilla* ssp. n. (Pi), *Hypothyris euclea callanga* (I), *Hyaliris coeno* ssp. n. (I), *H. oulita lurida* (I),

Ceratinia tutia fuscens (I), *Godyris mantura mantura* (I), *Morpho achilles peripherica* (M), *M. aurora aurora* (M), and *M. menelaus alexandrowna* (M).

Upper Montane Forest

13. **HUANCABAMBA Unit:** This is located on the western chain of the northern Andes, and includes both its western and eastern slopes, from southern Ecuador down to the Huancabamba Depression (Porculla Pass) in the south.

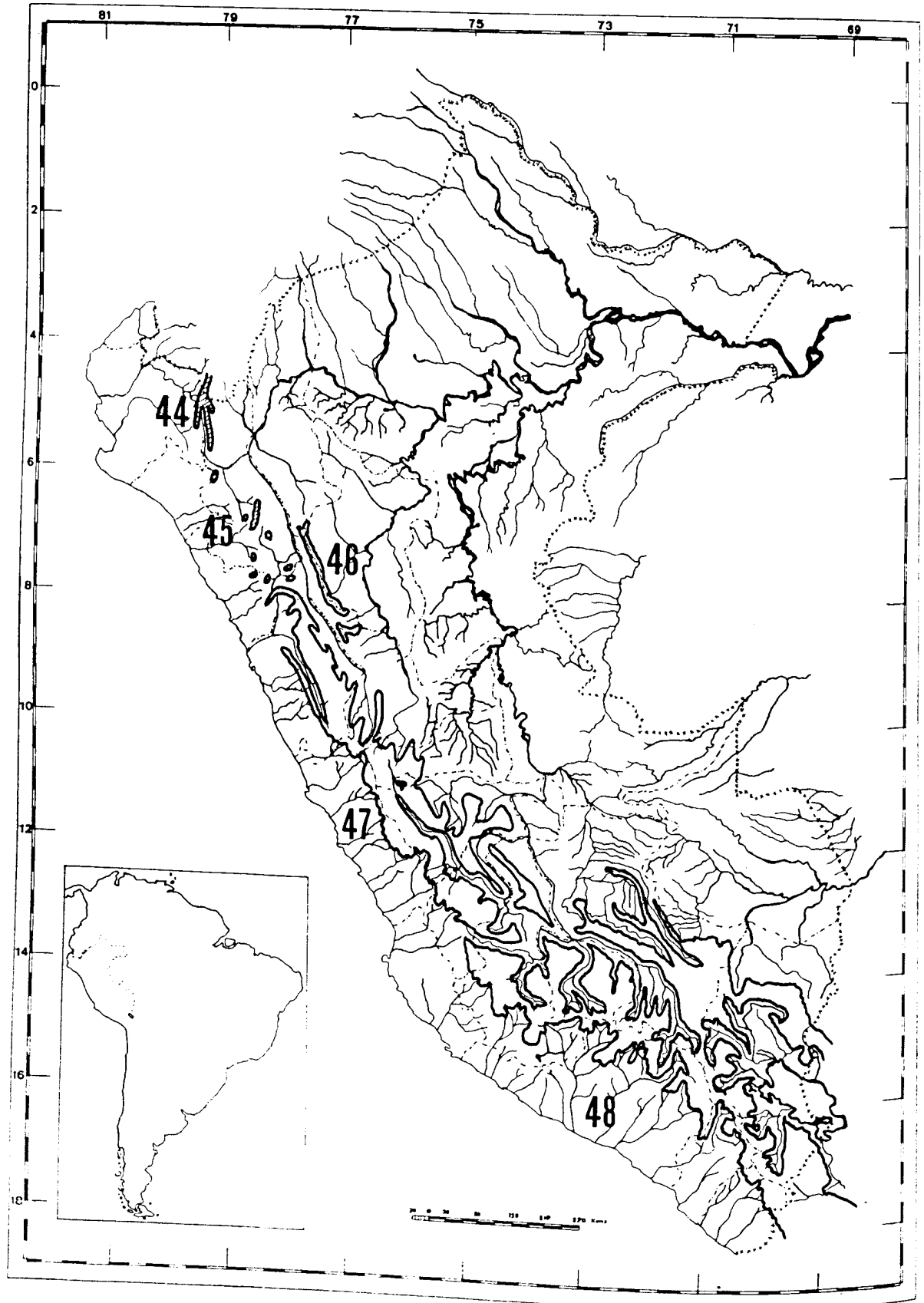
The following are among its known endemics: *Battus philetas magnimacula* (Pa), *Dismorphia arcadia lucilla* (Pi), *D. medora* ssp. n. (Pi), *Pagyris ulla* ssp. n. (I), *Hyposcada cyrene* ssp. n. (I), *Godyris hewitsonii* ssp. n. (I), *Veladyris pardalis totumbra* (I), and *Corderopedaliodes corderoi* (S).

14. **EL CÓNDOR Unit:** It is predicted that some endemic butterflies may be found in the isolated Cordillera El Cóndor, in the border between northern Amazonas and Ecuador. Recent collections of birds indicate that the area harbors a few endemics (Brack, pers. comm.; Plenge, pers. comm.). As far as I know, no butterfly collections have ever been made in this region.

15. **CUTERVO Unit:** Includes areas in Cajamarca, south of the Huancabamba Depression, the mountains between the upper Marañón and the Utcubamba in southern Amazonas, and relict forests in La Libertad and northeastern Ancash. The southwestern limit seems to lie in the Otuzco area, while the southeastern one should be in Pataz, around the sources of the Abiseo river. A description of the area of southwestern Cajamarca may be found in H.-W. Koepcke (1961: 154ff.).

Some of its endemics are: *Napeogenes*

Figure 18.6 Open upper montane (2,000–3,500 m in the east; 2,700–3,800 m in the west) biogeographical units. 36. Ayabaca; 37. La Peca; 38. Molinopampa; 39. Huamachuco; 40. Parinacochas; 41. Unini; 42. Apurímac; 43. Titicaca. The hatched areas indicate presumed units.



harbona forsteri (I), *Greta cyrcilla* ssp. n. (I), *Pteronymia zerlina* ssp. n. (I), *P. veia* ssp. n. (I), *Corades cistene* ssp. n. (S), *C. iduna* ssp. n. (S), *Pronophila assarrhaddon* ssp. n. (S) and *Heliconius telesiphe cretacea* (H).

16. **CHACHAPOYAS Unit:** This consists of the mountains between the Utcubamba and Chiriaco rivers, and the Chachapoyas area (Amazonas), as well as the mountains in the northern tip of San Martín. This region has only very recently been recognized as an important endemism area.

Some of its most characteristic species are: *Napeogenes harbona* ssp. n. (I), *N. glycera eunomia* (I), *Pagyris ulla* ssp. n. (I), *Velamysta peninna* ssp. n. (I), *Greta cyrcilla* ssp. n. (I), *G. hermana* ssp. n. (I), *G. esula* ssp. n. (I), *Veladyris pardalis* ssp. n. (I), *Pteronymia serrata* ssp. n. (I), *P. zerlina* ssp. n. (I), *P. veia* ssp. n. (I), *Corades ulema tripunctata* (S), *Lasiophila phalaesia* ssp. n. (S), and *Pronophila assarrhaddon* ssp. n. (S).

17. **ANCASH Unit:** I do not have enough data yet to confirm the existence of this unit for butterflies, although it has been recognized for birds (H.-W. Koepcke 1958; M. Koepcke 1961; Paynter 1972). Apparently, it is restricted to small patches of relict forest, which extend from southern La Libertad to northern Lima, on the western slopes of the Cordillera Occidental.

18. **LIMA Unit:** Also not confirmed yet for butterflies, this area has been recognized by ornithologists (M. Koepcke 1954, 1958, 1961; H.-W. Koepcke 1958; Paynter 1972). It comprises forest relicts in the Lima department, along the western slopes of the Andes. The best-known relict is the Zárate forest, described by M. Koepcke (1958), H.-W. Koepcke (1961:165ff.), and Ferreyra (1978).

19. **CHUQUIBAMBA Unit:** This is another area inhabited by endemic forest birds, but for which no data on butterfly fauna are available; it comprises a chain of relict forest islands which extend from southern Lima to northern Arequipa, apparently reaching its southernmost limit in the Chuquibamba area (H.-W. Koepcke 1961: fig. 55).

20. **CARPISH Unit:** Surprisingly little is known about this area, in spite of being traversed by an important road, linking Huánuco and Tingo María, at the southern extremity of its range (the Carpish-Chinchao area). Its northern limit is presumably located on the Abiseo headwaters, and the Tayabamba area of La Libertad.

I can only mention two endemics that have been positively identified: *Dismorphia lygdamis doris* (Pi), and *Patricia dercyllidas* ssp. n. (I); many apparently endemic Satyrinae and Ithomiinae have not yet been identified. Reissinger (1972) describes a number of new species and subspecies of *Catasticta* (Pieridae) from this area, which could represent endemic populations. Several endemic birds have been discovered in the Carpish area during the last few years (Hocking, pers. comm.; Plenge, pers. comm.).

21. **OXAPAMPA Unit:** This unit is quite well known, and includes a rather large area. Its northern limit must lie somewhere on the Cordillera Azul (the border between southern San Martín and Loreto), perhaps on the Cushabatay and Chipurana sources (I have records from as far north as La Divisoria, on the Tingo María-Pucallpa road). It includes the sources of the Pachitea in Pasco department, and probably the highest areas of the Cerros del Sira as well. The area around the Chanchamayo valley is the best known, whereas those portions lying in Ayacucho and Cuzco are almost unex-

Figure 18.7 Páramo-Puna (3,500-5,000 m in the east; 3,800-5,000 m in the west) biogeographical units. 44. Shimbe; 45. Cajamarca; 46. Huancaspata; 47. Pasco; 48. Vilcanota. The hatched areas indicate presumed centers.

plored, as regards butterflies. The easternmost limit should lie on the western slopes of the Pantiacolla range.

The following endemics are diagnostic: *Papilio warscewiczii mercedes* (Pa), *Dismorphia hyposticta* ssp. n. (Pi), *D. lua* ssp. n. (Pi), *D. medora* ssp. n. (Pi), *D. medorilla* ssp. n. (Pi), *Napeogenes glycera anteella* (I), *N. harbona domiduca* (I), *Hyaliris praxilla* ssp. n. (I), *Pagyris ulla* ssp. n. (I), *Hyoscada cyrene taliata* (I), *Dircenna paradoxa catenata* (I), *Velamysta phengites* ssp. n. (I), *V. pupilla* ssp. n. (I), *Corades argentata albomaculata* (S), *Lasiophila ciria diducta* (S), *Oressinoma sorata* ssp. n. (S), and *Morpho sulkowskyi selenaris* (M).

22. **MARCAPATA Unit:** Its northwestern limit should be on the eastern slopes of the Pantiacolla range, then extending south-eastwards to western Bolivia.

It is also quite well known, and this unit has many endemics, some of which are: *Papilio warscewiczii warscewiczii* (Pa), *Battus madyes crispus* (Pa), *Dismorphia lewyi boliviensis* (Pi), *D. lycosura* ssp. n. (Pi), *D. medorilla buchtieni* (Pi), *Patricia oligyrtis nebulosa* (I), *Napeogenes glycera olyrina* (I), *Hyaliris frater atagalpa* (I), *H. praxilla fassli* (I), *Hyoscada cyrene attilodes* (I), *Velamysta pupilla* ssp. n. (I), *Greta ortygia gardneri* (I), *G. esula* ssp. n. (I), *G. hermana* ssp. n. (I), *Oressinoma sorata sorata* (S), *Corades argentata argentata* (S), *C. iduna iduna* (S), *C. sareba fuscipalpa* (S), *Pronophila orchus lucumo* (S), *Pseudomaniola zerlinda zerlinda* (S), and *Morpho sulkowskyi lympharis* (M).

Nonforested Areas

In general, only a few species of nonforest butterflies can be assigned with confidence to each unit, mainly for three reasons: (i) most species are widespread in the Neo-

tropics, and do not show geographical differentiation, perhaps as a result of recent range expansions; (ii) most collectors neglect obtaining good samples of many nonforest butterflies, as they are considered "too common"; and (iii) the dominant group of nonforest butterflies, Lycaenidae and Hesperidae, have not been studied in the present paper.

Open Lowlands

23. **PIURA Unit:** Includes the southern part of Chapman's (1926) "Arid Tropical Zone." As defined here, it covers most of Tumbes, Piura, and Lambayeque departments, being extended to the north as far as Esmeraldas (Ecuador), and reaching to the south at least to the Chicama and Moche valleys in La Libertad and southwestern Cajamarca.

Among its diagnostic endemics, the following may be noted: *Phoebis argentea* ssp. n. (Pi), *P. bourkei* (Pi), *Eurema eudora* (Pi), *E. elathea ella* (Pi), *E. albata* ssp. n. (Pi), *E. nise sulla* (Pi), *E. daira cogenia* (Pi), *Dione junonia andicola* (H), *Junonia evarete basifusca* (N), *Phyciodes simois pratti* (N), and *P. flavida* (N).

24. **ILLESCAS Unit:** A few endemic birds have been found in the Cerro Illescas region of southwestern Piura, on the western border of the Sechura desert (M. Koepcke, 1963). I know of no butterfly collections made in that area; it would be surprising not to find some differentiated butterfly populations in those isolated hills.

25. **CALLAO Unit:** This consists of a rather narrow strip at the foot of the western Andes, presumably reaching from southern La Libertad in the north, to about the Pisco valley (Ica) in the south. It has an impoverished fauna, which includes the following three endemics: *Phoebis argentea chinchana* (Pi), *Eurema nise stygma* (Pi), and *Junonia evarete lima* (N).

26. **MOLLENDO Unit:** The butterflies of this area, which extends from about the Rio Grande (Ica) in the north, to the northern limit of the Atacama desert in Chile, are very poorly known, and I can list only one doubtful endemic, *Danaus plexippus erippus* (D), which, however, also occurs in the Madre de Dios unit (see below, number 28), and seems to be a rather recent introduction into southwestern Peru (Lamas, in prep.). Several bird species have endemic populations in this area (M. Koepcke 1965).

27. **LORETO Unit:** Covers almost the whole of Loreto department; its elements are usually also found on the lower Santiago and middle Marañón valleys (Amazonas), the middle Huallaga (San Martín), the upper Pachitea (Huánuco-Pasco), the lower Perené, Ene and Tambo (Junín), and the lower Urubamba (Cuzco). Apparently, its southern limit lies on the upper Purús.

Butterflies belonging to this unit fly over the forest canopy, on natural and man-made forest clearings, and along the rivers.

Most of the region is covered with lowland rainforest, but at least in one important area in the middle Huallaga, between Tarapoto and Juanjui (black area on the map), a tropical dry forest predominates, including many xerophytic plants, and some savannalike formations (ONERN 1976: 72ff.).

In this, and the next unit, it is difficult to talk about "endemic" butterflies as most of the species found here have a widespread distribution in South America. However, for several species, there is a consistent distribution pattern, in that one subspecies is usually found in the Loreto area, and a different one in the Madre de Dios region. The following two species may be listed among the Loreto elements: *Battus belus varus* (Pa), and *Danaus plexippus nigripus* (D).

28. **MADRE DE DIOS Unit:** Includes the Madre de Dios department, and the lower Inambari and Tambopata rivers in northern Puno. West of the Heath River

(Madre de Dios) lie the important "Pampas del Heath," two patches of savanna covering about 85 km² (ONERN 1972; Denevan, unpublished). This is the only place in eastern Peru where significant areas covered with natural savanna vegetation have been found. Recent collections of birds made in the Heath savannas (marked in black on the map), have resulted in several additional species for the Peruvian list (Plenge, pers. comm.; Macedo, pers. comm.).

The following three elements may be regarded as characteristic: *Battus belus cochabamba* (Pa), *Danaus gilippus gilippus* (D), and *D. plexippus erippus* (D).

Open Lower Montane Areas

29. **PORCULLA Unit:** Includes the western slopes of the northern Andes, from southwestern Ecuador to the Santa valley in Ancash, and is connected, through the Porculla Pass and other low passes in Cajamarca, to the upper Marañón, and its main tributaries. Its eastern border lies at approximately the Pongo de Rentema, while its southern extremity should lie in the Pomabamba valley, Ancash.

The following are some of its faunal elements: *Battus polydamas streckerianus* (Pa), *Eurema nigrocincta nigrocincta* (Pi), *Teriocolias zelia mathani* (Pi), *Danaus gilippus nivosus* (D), *Parapedaliodes parepa parepa* (S), and *Junonia evarete fuscescens* (N).

30. **SURCO Unit:** Formed by a narrow strip along the western slopes of the Cordillera Occidental, it should have its northern limit somewhere in western Ancash, while possibly extending as far south as southwestern Ayacucho. Characteristic butterflies are: *Eurema nigrocincta* ssp. n. (Pi), *Teriocolias zelia andina* (Pi), and *Parapedaliodes parepa milvia* (S).

31. **AREQUIPA Unit:** This consists of the area along the western Andes of Arequipa, Moquegua and Tacna, extending

south into northern Chile. It has a very poor butterfly fauna, and I can list only one endemic, *Teriocolias zelia kuscheli* (Pi).

32. **HUÁNUCO Unit:** The upper Hualaga valley, between the cities of Ambo and Huánuco, has a characteristic xerophytic vegetation cover (cf. Weberbauer 1945:429-30). I have seen only a few Lycaenidae and Hesperidae collected there, but I have no doubt that some endemic butterflies will be found in the area.

In extreme northeastern Junín, where the Tambo river joins the upper Ucayali, lies a region known as the Gran Pajonal, which consists of a mosaic of small savannas, which were formerly regarded as natural. However, it is now acknowledged that those savannas are anthropogenic (Scott 1977), and they probably do not constitute a biogeographic unit. Some butterflies collected at Obenteni, in the heart of the Gran Pajonal, were either forest species, belonging to the Chanchamayo unit (11, above), or widespread, nonforest species.

33. **MANTARO Unit:** Includes the lower Mantaro and its tributaries, down to its junction with the Apurímac, in the border between Junín, Huancavelica, and Ayacucho. The savannalike vegetation of this region has been described by Weberbauer (1945:422-24). Of this poorly collected area, I only know one endemic, *Battus polydamas* ssp. n. (Pa).

34. **PAMPAS Unit:** Formed by the lower Pampas and the upper Apurímac, in the border between Ayacucho, Apurímac, and Cuzco. Its vegetation has been described by Weberbauer (1945:408-13), and Goodspeed and Stork (1955:122, pl. 10).

Some of its endemics are: *Battus polydamas peruanus* (Pa), *Danaus gilippus candidus* (D), *Hamadryas februa* ssp. n. (N), *Hypanartia bella* ssp. n. (N), and *Junonia evarete* ssp. n. (N).

35. **SANTA ANA Unit:** The arid inter-Andean part of the Urubamba valley, be-

tween Huadquiña and Echarate, has been described several times (Chapman 1921; Weberbauer 1945:605-7; Hughes 1959). Its most characteristic endemic is *Battus polydamas* ssp. n. (Pa.).

The presence of endemic taxa in this area would indicate that its xerophytic vegetation is natural, and not anthropogenic, as assumed by Ceballos (1976:31).

Open Upper Montane Areas

36. **AYABACA Unit:** Found in the northwestern Andes, on the sources of the Chira, Piura, Huancabamba, Tabaconas, Chinchipe and Chirinos rivers, extending north into Ecuador.

Some of its characteristic elements are: *Colias euxanthe alticola* (Pi), *C. lesbia dinora* (Pi), and *Tatochila sterodice arctodice* (Pi).

37. **LA PECA Unit:** This is a presumed unit, as no butterfly collections are available from the summit of the rather isolated mountains separating the lower Utcubamba from the lower Chiriaco, in Amazonas department. Recent collections of birds made in the area indicate that it may represent a biogeographic unit (del Solar, pers. comm.; Plenge, pers. comm.).

38. **MOLINOPAMPA Unit:** Includes the sources of the Nieva, Chiriaco, Utcubamba and Huayabamba rivers in Amazonas, the Mayo river in San Martín, and some tributaries of the lower Marañón in Loreto. *Colias euxanthe hermina* (Pi), and *C. lesbia* ssp. n. (Pi), are its only known endemics, up to the present.

39. **HUAMACHUCO Unit:** Formed by the Andes chains on both sides of the upper Marañón, in the departments of Cajamarca, La Libertad, Amazonas, Ancash and Huánuco, and parts of the Cordilleras Blanca and Negra in Ancash. Its southeastern limit lies in Pasco department, where the Cordilleras Central and Occidental merge, forming the Pasco knot.

As diagnostic elements, we may consider the following: *Colias euxanthe stuebeli* (Pi), *C. flaveola mossi* (Pi), *C. lesbia* ssp. n. (Pi), *Tatochila homoeodice* (Pi), *T. sagittata sagittata* (Pi), *T. xanthodice pyrrhomma* (Pi), and *Euptoieta claudia* ssp. n. (N).

40. **PARINACOCHAS Unit:** Extended along the western side of the Cordillera Occidental, from northern Lima, south into northern Chile. Only two endemics are known for the area: *Pierphulia rosea maria* (Pi), and *Tatochila sagittata* ssp. n. (Pi).

41. **UNINI Unit:** The mountain chains (Cerro de la Sal, Cerros Kitchungari and Cerros del Sira), that fringe the Gran Pajonal in Pasco, rising over 2,000 m, may represent another unit, although no data are available (see Scott 1977, and Terborgh & Weske 1975, for descriptions of different parts of the area).

42. **APURÍMAC Unit:** Includes the eastern Andes of Junín, Huancavelica, Ayacucho, Apurímac, Cuzco and Puno; the northwestern limit lies south of the Pasco knot, whereas the southeastern end is found in Bolivia.

Some of its endemics are: *Colias flaveola weberbaueri* (Pi), *Pierphulia rosea annamariae* (Pi), *Tatochila orthodice carabaya* (Pi), and *T. xanthodice* ssp. n. (Pi).

43. **TITICACA Unit:** The Titicaca lake basin may eventually represent a separate unit, but the available data are not yet conclusive. Weberbauer (1945:324) noted the mixed character of its flora, pointing out that its "mesothermic" elements are related to the western Andes.

Páramo-Puna

44. **SHIMBE Unit:** According to Brack (1976:109), the southernmost extension of the Ecuadorean páramo occurs on the border between Piura and northern Cajamarca, where the mountains rise over 3,500 m. Un-

fortunately, nothing is known about its butterfly fauna, but it will possibly contain some of the endemic páramo butterflies found in Ecuador.

45. **CAJAMARCA Unit:** In southern Cajamarca, between the Huancabamba Depression to the north, the upper Marañón to the east, and the Cordillera Pelagatos (La Libertad) to the south, lies an area, known as the Jalca, or Peruvian páramo (Weberbauer 1945:437). It is restricted to somewhat isolated patches in the highest mountains, and may have an endemic butterfly fauna, but enough data are lacking.

46. **HUANCASPATA Unit:** Between the upper Marañón and the upper Huallaga lies a chain of high mountains, which are very poorly known, and which I tentatively regard as a biogeographic unit. Its northern limit should lie in the border between Amazonas and La Libertad, while its southern end could be in northwestern Huánuco. The only species which I can refer to this center is a striking acraeine, *Actinote rubrocellulata*, known only from the Huancaspata area, where it flies above 3,500 m.

47. **PASCO Unit:** This includes the Puna formation of La Libertad, Ancash, Lima, Pasco, Junín, Huancavelica, and northern Ayacucho. Its northern extension may reach the Cordillera Pelagatos (Weberbauer 1945:440), while its southern limit appears to be at the border between Huancavelica and Ayacucho, the source of the Grande and Pampas rivers.

Its main endemics are: *Phulia garleppi* (Pi), *P. nannophyes* ssp. n. (Pi), *Punargentus lamna lamna* (S), and *Yramea cora* (N).

48. **VILCANOTA Unit:** This is formed by the Puna of southern Ayacucho, Apurímac, Arequipa, Moquegua, Tacna, Cuzco and Puno, and extends south into Chile and Bolivia.

Known endemics are: *Phulia nannophyes nannophyes* (Pi), *Piercolias coronae* (Pi), *Punargentus lamna angusta* (S), and *Yramea sobrina* (N).

Discussion and Conclusions

The biogeographic units 1-12 in this paper correspond quite well with Brown's (1977b) presumed tropical forest refuge areas for Peru. Although I believe that most, if not all, forest units listed herein may be expressions of evolutionary divergence during Pleistocene forest regressive phases (Brown & Ab'Sáber 1979), I also think it is still too early to pinpoint specific locations for forest refuges in Peru, especially as we lack basic geoscientific information.

Conversely, several nonforest units, notably those found in the lower montane level of the inter-Andean valleys (fig. 18.5), may represent endemism centers, and are possibly acting today as refuges (nonforest

islands); further elaboration on them will be presented elsewhere (Lamas, in prep.).

Although few data are yet available, it seems that among forest butterflies, the most primitive species of a genus, or the most primitive genera of a tribe or subfamily, are found mainly either in montane or in upper montane forests, in contrast with most advanced members, which occupy lowland forests (Lamas 1973 and unpubl.). No comparable studies have been attempted yet on nonforest butterflies.

It is concluded that there are at least 48 different biogeographic units for butterflies in Peru, although confirmation is required for several of them by adequate sampling of their butterfly faunas. It is believed that those units may include centers of endemism, which could have been shaped in ecological refuges during Pleistocene regressive climatic periods.

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