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THE PHYLOGEOGRAPHY OF AMAZONIA REVISITED: NEW EVIDENCE FROM RIODINID BUTTERFLIES

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Abstract.—A fully resolved cladogram for 19 species in the *Charis cleonus* group of riodinid butterflies, which have closely parapatric ranges throughout the Amazon basin, is used to derive an area cladogram for the region. This represents the first comprehensive species-level analysis using insects and results in a hypothesis of Amazonian area relationships that is the most detailed to date. The *Charis* area cladogram is interpreted as supporting an historical vicariant split between the Guianas and the remainder of the Amazon and then between the upper and lower Amazon. The latter two clades can be further divided into the six most widely recognized areas of endemism and even smaller endemic centers within these, some of which, especially along the Madeira and lower Amazon Rivers, have never been previously hypothesized for butterflies. The overall pattern of historical interrelationships indicated is Guiana + ((Rondônia + (Pará + Belém)) + (Imeri + (Napo + Inambari))). The area relationships for riodinid butterflies show substantial congruence with those presented from the literature for amphibians, reptiles, birds, primates, rodents, and marsupials, suggesting a common vicariant history for these organisms. A summary area cladogram generated by combining area cladograms for all the aforementioned groups of organisms indicated the pattern of historical interrelationships to be (Guiana + (Rondônia + (Pará + Belém))) + (Imeri + (Napo + Inambari)). *Charis cleonus* group species distributions are noticeably larger around the upland periphery of Amazonia and smaller in the central and lower regions. A significant positive correlation between the proportion of range area above 100 m and total range size for each species is used to suggest that past sea-level rises may explain smaller range sizes in low-lying regions and that riverine barriers have been important in shaping the current distribution of *C. cleonus* group species.

Key words.—Amazon, area cladograms, biogeography, *Charis*, endemism, phylogeny, Riodinidae.

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The Amazon basin supports the Earth's highest concentration of terrestrial biodiversity (Myers 1988; McNeely et al. 1990; Wilson 1992; Myers et al. 2000), and its history, including the mechanisms that have generated this diversity, has thus long fascinated biologists, conservationists, and geologists alike. The search for historical speciation mechanisms to explain this diversity has led to the discovery of striking and often congruent faunal discontinuities within the seemingly uniform rainforest environment of Amazonia in a wide array of organisms, including plants (Prance 1973, 1982a), mammals (Kinzey 1982; Patton et al. 1994, 1997, 2000; da Silva and Oren 1996; Patton and da Silva 1998), birds (Haffer 1969, 1987; Cracraft and Prum 1988; Capparella 1988, 1991; Prum 1988; Bates et al. 1998), amphibians (Lynch 1979; Duellman 1982, 1988; Heyer and Maxson 1982; Heyer 1988; Gascon et al. 1998; Ron 2000), reptiles (Vanzolini and Williams 1970; Vanzolini 1988; Ávila-Pires 1995), and insects (Brown et al. 1974; Brown 1982, 1987; Erwin and Pogue 1988; Erwin 1998; Hall and Harvey 2001). Hypotheses that have been developed to explain these patterns differ in treating speciation as having occurred in sympatry, parapatry, or allopatry and in their emphasis on which physical or ecological barriers were most important in controlling interbreeding and dispersal. They include the gradient hypothesis (steep environmental gradients; Endler 1977, 1982; Mallet 1993), palaeogeography hypothesis (tectonic movements and sea-level rises; Chapman 1917; Emsley 1965; Frailey et al. 1988; Räsänen et al. 1995; Webb 1995; Nores 1999), river hypothesis (rivers and their floodplains; Wallace 1852; Capparella 1988, 1991; Ayres and Clutton-Brock 1992), disturbance-vicariance hypothesis (climatic cooling causing ecologically unsuitable habitat; Colinvaux 1993, 1996; Colinvaux et al. 1996), and refuge hypothesis (reduced precipitation causing forest fragmentation; Haffer 1969; Simpson and Haffer 1978; Prance 1982a; Whitmore and Prance 1987). The last is probably the most frequently championed, especially by its original proponent (e.g., Haffer 1997). Controversy as to which of these processes might have been the most important in diversification continues in part because of the difficulty in devising tests to distinguish between them and the relative paucity of often-conflicting spatial and temporal geoscientific evidence (Colinvaux 1996).

Although the mapping of Amazonian biota to determine the existence and distribution of endemic centers or refugia has been done for numerous taxa (e.g., Prance 1982b; Whitmore and Prance 1987), very few studies (Prum 1988; Cracraft and Prum 1988) have attempted to produce comprehensive species-level phylogenetic hypotheses for a diverse group of organisms and in turn address relationships between the areas they occupy. Here we report results for the first such study using an insect group and compare the Amazonian area cladogram for this group with those in the literature for other organisms.

The study organisms used are a monophyletic group of riodinid butterflies in the *Charis cleonus* group, whose taxonomy has recently been revised by Harvey and Hall (2002). The family Riodinidae is almost exclusively confined to the Neotropics, where it is the second most diverse true butterfly family after the Nymphalidae (Heppner 1991;

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Robbins 1993). The family is conspicuous not only for its species diversity, but also for its great phenotypic, morphological and ecological diversity (Stichel 1910–1911; Callaghan 1983; DeVries 1990, 1991, 1997; d'Abrera 1994; Hall 1999), yet remains perhaps the most poorly studied butterfly group. The genus *Charis* is a medium-sized group of small, inconspicuous species in the tribe Riodinini (sensu Harvey 1987) that are common in primary and secondary growth habitats throughout the Neotropics. The *cleonus* group of *Charis* ranges throughout the Guianas and Amazon basin and as far south as southeastern Brazil, but the species range sizes exhibit substantial variation. We discuss possible reasons for an apparent correlation between large range sizes and their position on higher ground around the periphery of the Amazon basin.

Because the broad applicability of conclusions drawn from any biogeographic study are dependent on the type of study organism analyzed, it is important to ask how suitable the *C. cleonus* group of riodinid butterflies is for studying Amazonian area relationships. We believe they are a well-suited study group for several reasons. First, all species are distributed parapatrically across a wide area of South America east of the Andes, creating a fragmented pattern of species distributions that is not known elsewhere in the Lepidoptera in a continuous lowland habitat. Four instances of apparent sympatry at the periphery of ranges (from more than 1000 specimens) are based on historical label data and that of commercial dealers and are believed to be mislabeled (Harvey and Hall 2002). The methodological problems inherent in delineating a priori areas of endemism are thus circumvented (e.g., Morrone 1994). Each species occupies effectively its own potential area of endemism. Although an area of endemism must by definition contain multiple taxa, the use of the phrase throughout this paper in connection with the individual ranges of *C. cleonus* group species is meant to highlight the potential the range of that species has for delineating a more broadly applicable area of endemism. In fact, the ranges of most species are already known to coincide with those of unrelated endemic butterflies and other organisms (see discussion). Second, because each species represents a discrete 100% diagnosable unit characterized by substantial qualitative morphological differences, whose distribution points have been sampled in an unbiased manner from entomological collections worldwide, the problem of subjectivity in the recognition or description of taxa (typically mimetic subspecific taxa) from potentially preconceived areas of endemism is avoided. Third, because of the two reasons outlined above, the effect of historical collector bias in determining the location of areas of endemism (Nelson et al. 1991) is also minimized. Further collecting will enlarge the *Charis* areas of endemism but not significantly change their position. Fourth, *C. cleonus* group species are relatively well represented in collections from a diverse array of Amazonian localities, and thus also have the ability to highlight the potential existence of previously unrecognized or poorly known areas of endemism. Finally, *C. cleonus* group species are all sedentary inhabitants of primary and predominantly wet forest understory, and the larvae are detritivores (Harvey and Hall 2002). It is just such organisms—those dependent on intact forest understory habitats—that would be expected to exhibit prolific speciation under fluctuating palaeoclimatic, physical, and ecological conditions leading to habitat disturbance and fragmentation.

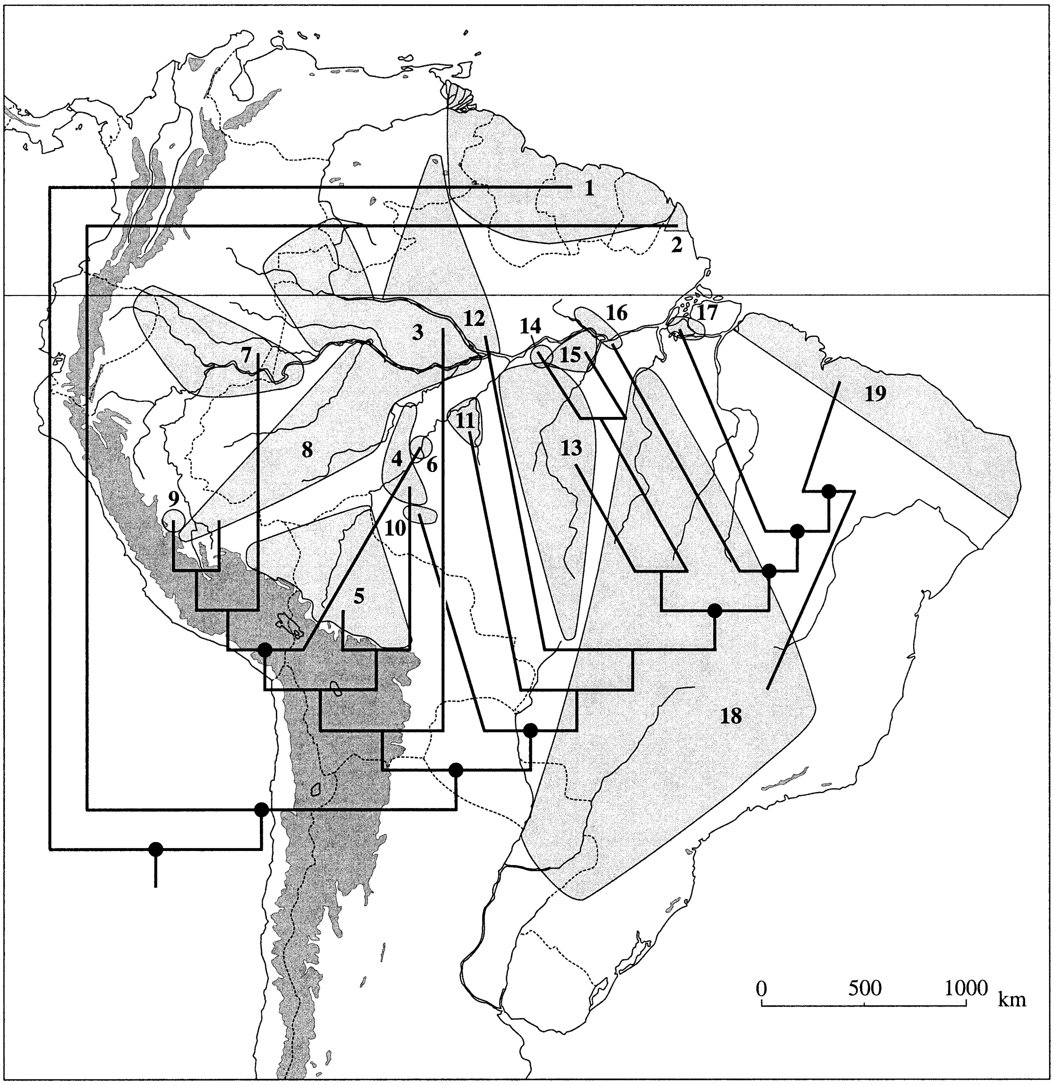
MATERIALS AND METHODS

Material Examined

The geographic distributions of *C. cleonus* group species mapped in Figure 1 are based on specimen label data from the following collections: AME, Allyn Museum of Entomology, Florida Museum of Natural History, Sarasota, Florida; AMNH, American Museum of Natural History, New York; AN, Collection of A. Neild, London; BMNH, The Natural History Museum, London; CJC, Collection of C. Callaghan, Bogotá, Colombia; CMNH, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; FSCA, Florida State Collection of Arthropods, Gainesville, Florida; JBS, Collection of J. Bolling Sullivan, Beaufort, Pennsylvania; MNHN, Museé National d'Histoire Naturelle, Paris; SMF, Senckenberg Museum, Frankfurt, Germany; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; ZMHU, Zoologische Museum für Naturkunde, Humboldt Universität, Berlin, Germany; and ZSM, Zoologische Staatssammlung, Munich, Germany. Approximately 1000 specimens were examined in these collections originating from 119 discrete localities that could be plotted on a map (see Harvey and Hall 2002), although many more localities were recorded that were too close to each other to appear as separate dots on a map. A total of 252 genitalia dissections were made to aid identifications, including representative specimens from each locality (Harvey and Hall 2002).

Cladograms

The cladogram in Figure 1 is the single most parsimonious cladogram generated from a phylogenetic analysis of 36 morphological characters and is adapted from Harvey and Hall (2002; see that paper for details of the analysis). In an effort to compare the Amazonian area cladogram for the *C. cleonus* group of riodinid butterflies with those derived from the study of other organisms, we present eight area cladograms (Fig. 2A–H) for Amazonian amphibians, reptiles, birds, primates, rodents, and marsupials adapted from the literature (Cracraft and Prum 1988; Prum 1988; da Silva and Oren 1996; Bates et al. 1998; Patton et al. 2000; Ron 2000). The area cladogram in Figure 2H for rodents and marsupials (Patton et al. 2000) is a summary of eight originally presented cladograms that was generated using the matrix representation with parsimony method (MRP; Baum 1992; Ragan 1992; Sanderson et al. 1998), which is essentially the same as Brook's parsimony (Wiley 1987, 1988a,b) when an area appears only once on a cladogram. In MRP a new matrix is constructed with each node on a source cladogram yielding a character, with state 1 representing the presence of a taxon in a clade and state 0 its absence. Brook's parsimony analysis was used to convert the cladistic and geographic information in Figure 1 into area cladogram I in Figure 2 for the *C. cleonus* group. The numbered species distributions in Figure 1 were divided into the seven general areas of endemism as follows: 1, 2, Guiana;



1. *Charis cleonus*
2. *Charis rocana*
3. *Charis negro*
4. *Charis ariquemes*
5. *Charis manu*
6. *Charis humaita*
7. *Charis iquitos*
8. *Charis tefe*
9. *Charis palcazu*
10. *Charis cacaulandia*
11. *Charis manicore*
12. *Charis ipiranga*
13. *Charis cuiaba*
14. *Charis maues*
15. *Charis tapajos*
16. *Charis santarem*
17. *Charis breves*
18. *Charis brasilia*
19. *Charis caryatis*

FIG. 1. A phylogenetic hypothesis for the *Charis cleonus* group of riodinid butterflies (adapted from Harvey and Hall 2002) overlaid on a South American map of their distributions, creating an area cladogram for the region. The best supported cladogram nodes (those with bootstrap values of > 70 and/or decay indices of > 3) are marked with a black circle.

3, Imeri; 4–6, Inambari; 7–9, Napo; 10, 11, Rondônia; 12–18, Pará; 19, Belém. *Charis ipiranga* (12 in Fig. 1) is tentatively placed within the Pará center of endemism, although the area between the eastern Amazon River and the mountains bordering the Guianas is variably treated as being part of the Guiana or Pará areas of endemism, in part due to a dearth of sampling there. The majority of localities for *C. ipiranga* are in the vicinity of Manaus with a single outlier in southeastern Venezuela, and its wing pattern and certain genital elements are intermediate between those of species from the Rondônia and Pará areas of endemism, leading us to believe that perhaps a change in river course has enabled its expansion northward.

The summary area cladogram in Figure 2J was generated using MRP to combine the topologies of all source cladograms in Figure 2. This method was used because a consensus cladogram is generated for which branch support values can be ascertained. The strength of branch support was estimated by means of 1000 bootstrap replicates (Felsenstein 1985) in PAUP version 4.0b4a (Swofford 2000) and by calculating decay indices (Bremer 1988, 1994) using the program AUTODECAY version 4.0 (Eriksson

1998) in combination with PAUP. The Pará-Belém branch in Figure 2E was treated as a sister pair of areas and of the two Inambari branches in Figure 2G only that clustering with Imeri and Napo was retained because these relationships are supported in the majority of the remaining area cladograms.

Correlation between Range Sizes and Elevation

Observing that large species ranges in the *C. cleonus* group appear to be confined to higher ground around the periphery of the Amazon basin and smaller ranges to the lower ground on the middle and lower Amazon, we looked for a possible correlation between the total distribution area and the percentage of that area above 100 m for the 19 *C. cleonus* group species. The figure of 100 m was chosen because this is generally regarded as a reasonable estimate of sea-level rises in the late Tertiary and Quaternary (e.g., Haq et al. 1987; Nores 1999 and references therein). This value thus allows the hypothesis of whether past sea-level rises have affected current distribution patterns in the *C. cleonus* group to be assessed. It does, of course, assume that the topography of the relatively recent past agrees reasonably well with the topography of today. Total distribution areas were estimated by dividing South America into 150 × 150 km grid squares and treating species as present in a square if their ranges included at least half of it. Species ranges were delimited by straight lines around the outermost locality points. The area above 100 m for each species was determined in the same way using American Geography Society of New York 1: 1,000,000 scale maps on which the 100-m contour is marked.

RESULTS

The cladogram for the *cleonus* group is overlaid on a map of South America in Figure 1 to form an area cladogram for the region (Nelson and Platnick 1981; Humphries and Parenti 1986). The *cleonus* group is divided into two basal Guianan species and sister clades of upper and lower Amazonian species, which can be further subdivided into six widely recognized Amazonian regions of endemism, namely Imeri, Inambari, Napo, Rondônia, Pará, and Belém (Haffer 1974, 1985; Cracraft 1985; Cracraft and Prum 1988; Prum 1988; Bates et al. 1998). The pattern of historical interrelationships described in Figure 1 is Guiana + ((Rondônia + (Pará + Belém)) + (Imeri + (Napo + Inambari))). The entire *cleonus* group and the basal nodes within it, and the lower Amazon clade as well as its terminal nodes have strong branch support whereas the upper Amazon clade is only weakly supported.

The general area cladogram for *Charis* butterflies in Figure 2I, in which the 19 areas of endemism have been condensed

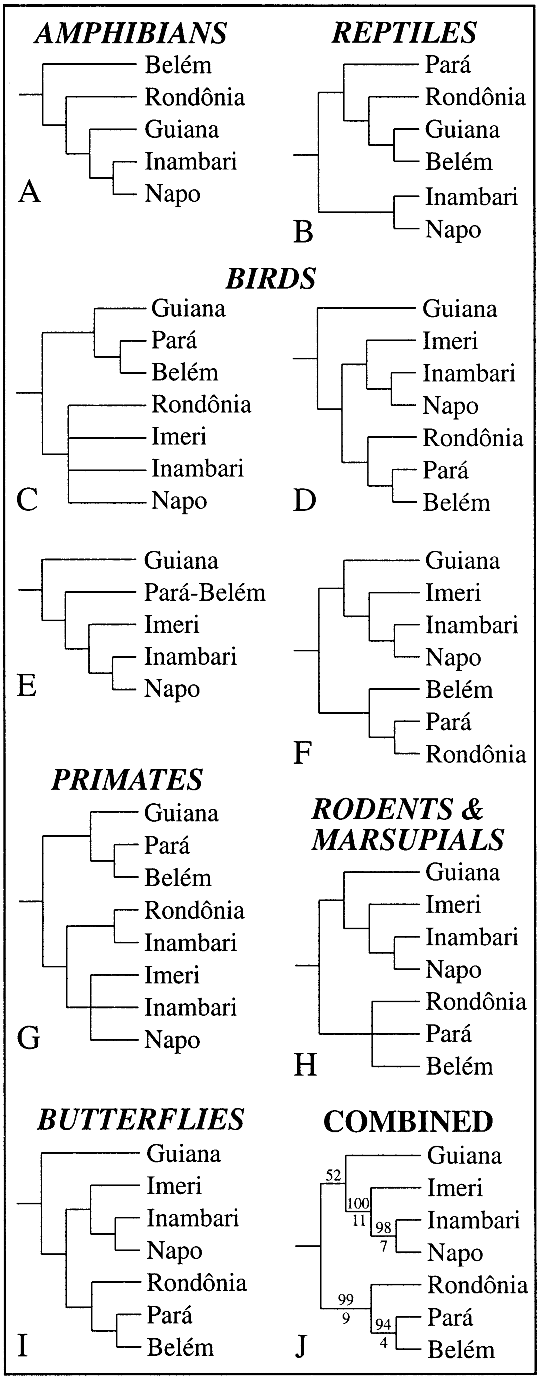


FIG. 2. General area cladograms that have been proposed for areas of endemism in the Amazon basin based on: (A) parsimony analysis of endemicity (PAE) for 342 species of anurans (Ron 2000); (B) PAE for 107 species and subspecies of lizards (Ron 2000); (C) maximum-parsimony (MP) analysis using morphological characters for three clades (10 species) of toucans (Prum 1988); (D) MP using morphological characters for eight clades (37 species) of toucans, woodpeckers, manakins, and cotingas (Prum 1988); (E) MP using morphological characters for four clades (25 species) of parrots and toucans (Cracraft and Prum 1988); (F) PAE for all Neotropical passerine birds (1717 species and subspecies; Bates et al. 1998); (G) PAE for all Amazonian primates (51 species; da Silva and Oren 1996); (H) MP using mtDNA characters for 17 species (including multiple geographic haplotypes for most species) of sciurid, murid, and echimyid rodents and marsupials (Patton et al. 2000); the presented cladogram is a summary of eight original cladograms, generated using MRP (see below and methods section); (I) MP using morphological characters for the *Charis cleonus* group of riodinid butterflies (this study); and (J) a summary area cladogram for Amazonia generated by using the matrix representation with parsimony method to combine the topologies of cladograms A–I (Baum 1992; Ragan 1992; Sanderson et al. 1998); branch support estimates are bootstrap values above nodes and decay indices below nodes.

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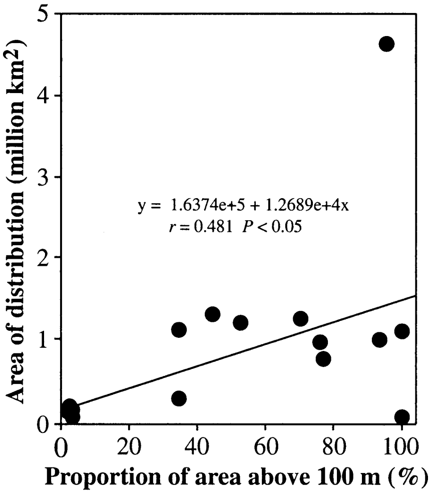

FIG. 3. A graph illustrating the significant positive correlation between total distribution area and percentage of distribution area above 100 m for 19 *Charis cleonus* group species. The outlier with the large area is *C. brasilia* and the outliers with the small areas are *C. palcazu* and *C. cacaulandia* (represented by the same point).

into the seven most widely recognized endemic centers, is very similar to those for rodents and marsupials and several of the bird cladograms. It is identical to that in Figure 2D proposed for several clades of relatively sedentary toucans, woodpeckers, manakins, and cotingas (Prum 1988). The area clades Pará + Belém, and Imeri + (Inambari + Napo) occur repeatedly in the source cladograms and thus have very high branch support in Figure 2J. Although the clade Rondônia + (Pará + Belém) does occur commonly in the source cladograms, its very high branch support in Figure 2J is due to the fact that this clade was undifferentiated in all the rodent and marsupial cladograms of Patton et al. (2000). The most inconsistently placed area is Guiana, which most commonly appears either at the base of all the remaining areas or as sister to the upper Amazon clade (as very weakly supported in Fig. 2J).

Figure 3 illustrates that there is a significant positive correlation between total distribution area and the percentage of that distribution area above 100 m for *C. cleonus* group species (regression: $N = 19$, $r = 0.481$, $P < 0.05$). If the single large area outlier (*C. brasilia*) is removed, r increases to 0.493 ($P < 0.05$), and if the two small area outliers (*C. palcazu* and *C. cacaulandia*; represented by the same point in Fig. 3), whose ranges are undoubtedly currently underestimated, are additionally removed, r increases to 0.812 ($P < 0.01$).

DISCUSSION

Distribution Patterns

Perhaps the most important question to ask about the distribution patterns of *C. cleonus* group species is how congruent they are with those of other organisms. Although such a highly fragmented set of parapatric species distributions is very rare among the Amazonian biota, the fine-grained patterns of endemic centers for ithomiine, heliconiine (Brown 1982, 1987), and papilionid subspecies (Tyler et al. 1994) do match reasonably well with those for the *C. cleonus* group. Broad similarities can also be found with the proposed endemic centers of other organisms such as plants (Prance 1982a). However, because the parapatric distributions for *Charis* species are expected to cover the entire Amazon basin, this translates into endemic centers for *Charis* in Figure 1 that are generally larger, especially around the periphery of the Amazon basin. Several small endemic areas are recognized here along the Madeira and lower Amazon Rivers that have not previously been hypothesized for butterflies. This latter pattern is not unique, however, and it very closely matches that for species in the marmoset genus *Callithrix*, which also contains species confined to the vicinities of Humaitá on the Madeira and Maués on the lower Amazon (areas 6 and 14, respectively, in Fig. 1; Ferrari and Lopes 1992a,b; Mittermeier et al. 1992).

We propose two interrelated hypotheses to explain the clustering of large ranges in the *C. cleonus* group around the upland periphery of the Amazon basin, with most small ranges confined to the low-lying central and lower Amazon, based on the significant positive correlation between the proportion of range area above 100 m and total range size for each species presented in Figure 3. Nores (1999) has suggested that the high levels of Amazonian bird diversity might be explained by Quaternary and upper Tertiary sea-level rises of up to 100 m that would have fragmented the lower Amazonian environment into numerous islands. Although such sea-level rises may also in part explain the high diversity of the *C. cleonus* group in the lower Amazon, perhaps the repeated confinement of lower Amazon species to very small areas of higher ground during sea-level rises, and the resulting habitat instability, led to their small current range sizes. It is puzzling that the Maués region and the Ilha de Marajó (areas 14 and 17, respectively, in Fig. 1) currently harbor endemic species of *Charis* and other butterfly taxa, such as subspecies of Ithomiinae (Brown 1979), despite essentially lying at sea level with no higher ground in the immediate vicinity. This suggests either significant migration into the area or recent in situ differentiation. However, the fact that those species with the smallest range sizes are not necessarily the most derived argues against the latter hypothesis.

Secondly, if large rivers are assumed to be important barriers to dispersal for these shade-loving sedentary butterflies, as they are in even some highly vagile organisms such as birds (Capparella 1988, 1991; although not rodents, Patton et al. 1994, 2000), it seems possible that those species with a large proportion of their geographic range on higher ground may have the largest ranges because they can easily cross the narrow headwaters of rivers and disperse down the land corridors between them. Perhaps the range of *C. brasilia* is so large because its center of distribution now, and perhaps its sole area of distribution in the past, lies at the headwaters of seven major rivers, three running to the Atlantic and four to the Amazon. While raised sea levels were receding, species such as *C. brasilia* would also be able to expand their ranges quickly, whereas species confined to tiny islands along the course of the lower Amazon would not.

Unfortunately, it is not clear exactly how important rivers have been or continue to be in the current distribution of *C. cleonus* group species because some of the central and lower

Amazonian material is historical and the label data probably generalized; in such cases, uncertainty remains as to which bank specimens were really collected from, especially with the possibility of subsequent shifts in river course. Having said this, several lines of evidence do suggest that rivers have been influential in shaping the current distributions of *C. cleonus* group species. First, there is no evidence from modern label data that the same species exists on both sides of the Amazon River at its broadest between the Peru/Brazil border and Santarém, where *C. santarem* is known with certainty to live on both banks. In primates, whose ranges have long been known to be heavily influenced by river courses (Wallace 1852; Hershkovitz 1977; Ferrari and Lopes 1992a; Peres et al. 1996), Ayres and Clutton-Brock (1992) found a similar pattern and attributed the secondary increase in the similarity of primate faunas toward the mouth of the river as a probable consequence of the historical instability of its course and the existence of island bridges. Second, the distribution pattern in Figure 1 is noticeably spokelike, with many ranges (particularly 3, 7, 8, 12, 13) extending from the Amazon River outward, suggesting that they may be confined to the land corridors between one or, if the species extends as far as the headwaters, more rivers. Finally, at least two of the smallest *Charis* distributions, those of *C. humaita* and *C. maues*, match those of species in the marmoset genus *Callithrix*, whose small ranges are attributed primarily to close confinement by several river tributaries (Ferrari and Lopes 1992a,b; Mittermeier et al. 1992).

Area Relationships

Substantial congruence exists between the general area cladograms for amphibians, reptiles, birds, primates, rodents, marsupials, and butterflies (Fig. 2), with virtually all at least highlighting the existence of Guianan and upper and lower Amazon clades. Such corroborative pieces of independent evidence strongly suggest a common history of vicariant isolation events (Platnick and Nelson 1978) and argue against parapatric speciation models (Cracraft and Prum 1988) and those invoking ecological conditions of taxonomically narrow relevance (Tuomisto et al. 1995; Tuomisto and Ruokolainen 1997). It is to be expected that there will be minor differences in the topologies of each of these cladograms because palaeoclimatic and palaeogeographic events as well as differing ecologies are sure to have influenced the distribution of each set of organisms in different ways. For example, it is noteworthy that those area cladograms based on relatively sedentary organisms (e.g., the birds in Fig. 2D and the butterflies in Fig. 2I) include Guiana as the most basal area, whereas those based on higher-vagility organisms tend to include Guiana as sister to the upper Amazon areas (as in the summary area cladogram in Fig. 2J). The different methodologies used to generate the cladograms in Figure 2 may also be partly responsible for the observed differences. It has yet to be convincingly shown that cladograms generated by the increasingly used parsimony analysis of endemicity (e.g., da Silva and Oren 1996; Bates et al. 1998; Ron 2000), a method proposed by Rosen (1988) in which geographic areas are treated as taxa and the presence or absence of natural taxa is treated as a character in a phylogenetic analysis, accurately and consistently match those generated by maximum-parsimony analysis (e.g., Cracraft and Prum 1988; Prum 1988; Patton et al. 2000; this study).

Although riverine barriers may have been important in shaping the current distribution patterns of the *C. cleonus* group, it is unclear what other barriers may have been responsible for the vicariant patterns evident in the group's area cladogram. Speciation within Amazonia has undoubtedly been highly complex, and probably a mixture of many of those mechanisms outlined in the first paragraph have influenced the organismal distribution patterns of today (Bush 1994; Bates et al. 1998). Any hypothesis must take into account that, contrary to the temporal framework within which at least the refugial debate has typically been discussed, molecular clock data indicate many Amazonian taxa, including subspecies and even taxonomically unrecognized populations, differentiated from one another before the Quaternary (birds: Capparella 1988; rodents: Patton et al. 2000), or if during the Pleistocene, at least not during the most recent glacial events (butterflies: Brower 1994a,b).

Future Research

Much fieldwork remains to be done to clarify the distributions of *C. cleonus* group species, particularly those known from only one or two localities. It is possible that additional species, and therefore potentially unrecognized areas of endemism, remain to be discovered in remote parts of the Amazon basin, perhaps in the central and lower regions, where species range sizes are so small. The areas most in need of more collecting include southern Venezuela, southeastern Colombia, central Peru, and the Brazilian states of Acre, Rondônia, Mato Grosso, Amazonas (southeast and northeast), Pará (north and southeast) and Amapá, areas that have consistently been highlighted as undersampled for many other groups of organisms (Oren and Albuqueque 1991; Heyer et al. 1999). A more detailed knowledge of species distributions based on modern locality data would enable firmer conclusions to be drawn concerning the role of rivers as barriers to dispersal and a more accurate delineation of the proposed centers of endemism. The better defined areas of endemism are in a study, the more powerful a tool that study can become in helping to shape national conservation priorities throughout Amazonia (Brown 1987; Rylands 1990).

If sufficient alcohol-preserved material for DNA analysis could be collected, it would be interesting to compare phylogenetic hypotheses for the *C. cleonus* group derived from molecular and morphological data and a combination of both. The latter would be a robust hypothesis to which molecular clock data could be applied to tentatively determine the age of each node on the cladogram (Brower 1994b) and thus the age of differentiation of the Amazonian areas of endemism. This information combined with available geoscientific data could then be used to assess what was the most likely cause of the prolific speciation in this group and, by extrapolation, perhaps in others.

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