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AFROTROPICAL SKIPPERS (LEPIDOPTERA: HESPERIOIDEA) AND THE EMERGENCE OF THE COMBINED REFUGIUM THEORY

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ABSTRACT. Eighty-nine (89) species of skippers are reported from a collection made in NE Zaïre (esp. the Ituri Forest) during June-July 1991. Eight of these species are reported for the first time from Zaïre (now DR Congo); in five cases these represent sizable eastward range extensions. A discussion of various faunistic, biogeographic, and systematic relationships is provided, particularly with reference to the past fragmentation of Africa's equatorial forest (glacial refugia).

KEY WORDS: Afrotropical biogeography, Hesperidae, Zaïre, Democratic Republic of the Congo, Ituri Forest, refuge theory, forest history, paleoecology, faunistics, vicariance, disjunction, endemism.

INTRODUCTION

The Ituri Forest has intrigued outsiders since H. M. Stanley first made his way through this vast tropical wilderness ('Darkest Africa') in 1887. Inhabited by the world's most diminutive people (Mbuti Pygmies) and an unusual endemic fauna, it has eluded intensive biological study until recently: such striking endemic animals as the okapi or 'rainforest giraffe' (*Okapia johnstoni* (Sclater)) (Figure 1) and Congo peacock (*Afropavo congensis* Chapin) were unknown to Western science until 1900 and 1936, respectively. Despite the compelling interest the Ituri Forest holds in these respects, little intensive work has been undertaken on its lepidopteran fauna (e.g., Talbot 1921, 1922, Barns 1922, Ducarme 1993, 1999).

In 1991, with the support of the Allyn Museum (Florida Museum of Natural History), JFD organized an expedition to Zaïre and spent 40 days collecting Lepidoptera at Epulu, in the heart of the Ituri Forest, aided by Pygmy and Bantu assistants.

METHODS

Butterflies and skippers were collected during the summer of 1991 at three disjunct localities in Haut-Zaïre: Nyankunde (WSW of Bunia) (19 June), Mambasa (20 June), and the general vicinity of Epulu (incl. Lenda and Afarama research camps) (20 June-29 July). The latter two of the three localities lie within the Ituri Forest; Nyankunde represents a different

(i.e., elevated, open) environment (site descriptions below).

In addition to aerial nets, bait traps were used: nylon lines and pulleys placed in trees allowed these to be lowered and checked frequently. *Acraea* skippers (genus *Fresna*) were generally collected while perched on bird droppings on the upper surfaces of mongongo (phrynium) leaves (Marantaceae), 1-2 m above the forest floor (and on moist sand in one case).

Determinations included here are as made by LDM and verified by JFD and others. Nomenclature and the sequence in which taxa are arranged follows Ackery et al. (1995). Specimens are deposited at the Allyn Museum of Entomology (AME), Sarasota, Florida, USA.

Throughout this paper, we use Zaïre as the name of the country under consideration (in lieu of the recently-restored Democratic Republic of the Congo [DR Congo]) because: 1) Zaïre was the country's name when the present study was carried out; 2) the cardinal reference we cite (Ackery et al. 1995) in developing taxonomic and distributional contexts for information in the present paper uses this name.

SITE DESCRIPTIONS

THE ITURI FOREST

Location - The Ituri Forest (0°-3° N, 27°-30° E; Figure 1) is a 65,000-km² expanse of closed evergreen and semi-evergreen forest centered on the upper watershed of the Ituri River; its elevation ranges from 600 to 1200 m. The village of Epulu (1°25' N, 28°35' E, elev. 750 m) in the central Ituri Forest lies on the single E-W-running dirt road traversing the forest (variously called the trans-Ituri road, Kisangani-to-Bunia road, Nia Nia-Mambasa road, and trans-Africa highway).

It is regrettable that the scientific study of Africa's tropical forests lags behind that of the Neotropical realm, both in terms of funding and the number of Western and indigenous researchers who are involved (pers. obs. 1991, Weber and Vedder 2001). The village of Epulu has a rich legacy of traditions in both anthropology and mammalogy (e.g., Turnbull 1965, J. A. Hart and T. B. Hart 1986-2001, Nat. Geogr. Soc. 1992, 1996). The okapi capture station (Station d'Epulu) represents a superb base for research, but as yet it is only rarely used by entomological investigators. Year-round collecting and rearing work carried out there would be well rewarded; lepidopterological studies which suggest themselves include comparative surveys of mixed and mbau forest, vast tracts of which are easily accessible from Epulu. A promising recent development in the area is the establishment in 1992 of a huge sanctuary surrounding Epulu, the 13,726-km² Réserve de Faune à Okapis (RFO) (Okapi Wildlife Reserve) (Hart and Hall 1996, Stephenson and Newby 1997, Curran and Tshombe 2001).

Seasonality - Annual rainfall in the Ituri region is 1700-1800 mm, with a dry season of less than 40 days (Bultot 1971). Mean annual rainfall at Epulu during the period 1987-1993 was 1700 mm (range, 1307-2084 mm) (T. B. Hart 1995).

The central Ituri experiences a single, well-defined dry season ('long dry'), generally extending from mid-December to the end of February (T. B. Hart 1985, Hart and Hart 1989, J. A. Hart 2001). The driest month is January (Bultot 1971). Total rainfall during the three-month period January-March varies widely (76-359 mm) (T. B. Hart 1995). In addition, the Epulu region experiences a variable 'short dry' season from ca. mid-June to mid-August (pers. obs. 1991, S. Shurter pers. comm.).

The rainy season begins in March; the wettest periods are March-May and September-November (Hart and Hart 1989). New leaf-growth in the understory occurs in every month but peaks in February-April at the onset of rains (Hart and Hart 1988).

During the period of collecting work in 1991 (i.e., JFD based at Epulu, 20 June-29 July), excellent conditions for butterfly-collecting prevailed. Most days were sunny. Mornings generally began overcast (misty, gray), clearing to sunshine (often with fair-weather cumulus clouds) by mid- to late morning. Rain (drizzle, thunderstorms) occurred at the site on the average only every three days, and when heavy downpours did occur they tended to happen in the pre-dawn hours of darkness.

HABITATS

Because this is the first in what we hope will be a series of reports (and continuing field work at the sites described), Ituri Forest habitats are described here in some detail. Further useful descriptions of the structure and composition of Central Africa's forests may be found in Chapin (1932), Moreau (1966), White (1983), Sayer et al. (1992), Richards (1996), Morley (2000), and White (2001).

Prior to the immigration of agriculturalists (ca. 1,000-4,000 ybp), the Ituri was comprised of closed primary forest, interrupted only sparingly by small seral communities at treefalls and lightning strikes (Hart and Hart 1986, Wilkie and Finn 1990).

At the time of the present study (1991), human disturbance of the forest remained minimal. There are few permanent settlements, and significant stands of mature forest remain intact. Based on satellite imagery, D. S. Wilkie (unpubl. 1989 report cited in J. A. Hart 2001 and Curran and Tshombe 2001) has determined that ca. 90% of the Ituri Forest (RFO area) remains intact, i.e., covered with closed-canopy forest.

Present-day habitats in the central Ituri region consist of the distinct types below. In the present study, skippers were collected in all of these environments.

- | | |
|-----------------------------|--|
| I. Primary forests: | A. Mature upland forests
(1, monodominant mbau; 2, mixed) |
| | B. Riparian/Swamp forests |
| II. Disturbed areas: | A. Open areas |
| | B. Secondary forests |

I. Primary forests

A. Mature upland forests - The Ituri Forest is characterized by two distinct rainforest types, mbau (monodominant) forest ("single-dominant moist evergreen" forest of White 1983) and mixed forest ("mixed moist semi-evergreen" forest of White 1983); the central Ituri region is notable for the close co-occurrence of these (T. B. Hart 1985, 1995, Hart et al. 1989). Both vegetation types are mature upland forest formations dominated by Caesalpiniaceae. The habitat descriptions below are based on the pioneering synecological work of T. B. Hart (1985, 1995, 2001), Hart et al. (1989), and Makana et al. (1998). Further details of habitat description are provided by J. A. Hart (2001; eight habitat types are distinguished in the RFO).

1) Monodominant mbau forest - This evergreen forest type is particularly distinctive. It occurs in large, continuous stands. It is floristically less rich than many other tropical evergreen forests, and than adjoining mixed forests in the Ituri. A single tree species, mbau (*Gilbertiodendron dewevrei* (De Wild.) Léonard (Caesalpiniaceae)), predominates in all size classes (sapling, pole, tree, large tree); in local studies (T. B. Hart 1985, 1995, Hart et al. 1989) it was found to comprise more than 90% of canopy trees and to account for 88% of total basal area.

With the exception of the near-absence of *G. dewevrei* in mixed forest, mbau and mixed forests share the same tree species (Hart et al. 1989). Interestingly, however, the transition from mbau to adjacent mixed forest is floristically abrupt, typically with no zone of intergradation between the communities (Hart et al. 1989).

In both mbau and mixed forests, the canopy attains heights of 30-40 m (Hart et al. 1989). In mbau forest, however, the canopy is more homogeneous (denser, deeper, less broken), the subcanopy is more open, and the understory is more uniformly shady than in mixed forest (T. B. Hart 1985, 1995, Hart et al. 1989). The understory is rather open in both forest types and allows easy foot passage and visibility to 10 m or more (T. B. Hart 1985, pers. obs. 1991).

Mbau forests are steadily encroaching on adjacent mixed forests, and have apparently undergone a marked expansion in the central Ituri region over the last 4,000 yrs. (Hart et al. 1989, Hart et al. 1996). *G. dewevrei* has a low rate of dispersal (White 1983, Hart et al. 1989), and the establishment of monodominant stands (mbau forest) is apparently dependent upon the long-term absence of large-scale disturbances (e.g., fire) or climatic change (Hart et al. 1989).

2) Mixed forest - This semi-evergreen forest type is characteristic of large expanses of the central Ituri region. It is considerably more diverse (more species-rich) than mbau forest (T. B. Hart 1985, Hart et al. 1989), and appears to have undergone large-scale disturbance more recently. The most abundant tree species, *Julbernardia seretii* (De Wild.) Troupin (Caesalpiniaceae), comprises up to 40% of canopy trees and accounts for 32% of total basal area (T. B. Hart 1985, 1995, Hart et al. 1989). Species with the greatest mean basal area after *J. seretii* are *Cynometra alexandri* C. H. Wright (Caesalpiniaceae), *Cleistanthus michelsonii* J. Léonard (Euphorbiaceae), and *Klainedoxa gabonensis* Pierre (Irvingiaceae) (Hart et al. 1989).

The canopy in mixed forest has a more broken aspect than that in mbau forest and is more heterogeneous. Crowns of the dominant and emergent species tend to be broad and shallow and are often not contiguous (T. B. Hart 1985, Hart et al. 1989). Emergent individuals (to

40-50 m) and treefall gaps are more common in mixed than in mbau forest (Hart et al. 1989), and a well-developed subcanopy layer (10-25 m) is dense in irregular patches (T. B. Hart 1985). Lianas are much more abundant in mixed than in mbau forest (Makana et al. 1998). *Scaphopetalum deweyrei* De Wild. and Th. Dur. (Sterculiaceae) treelets dominate in the understory, and dense stands of herbaceous Marantaceae, Commelinaceae, and Zingiberaceae occur in treefall gaps, blowdowns, and swampy areas (Makana et al. 1998, J. A. Hart 2001).

B. Riparian/Swamp forests - These formations (i.e., swamp forest and narrow bands of periodically-inundated forest along streams) comprise a small percentage of the total area in both primary forest types (Hart and Hart 1986, T. B. Hart 1995, Hart et al. 1996, Stephenson and Newby 1997). Swampy sites may include dense stands of herbaceous Marantaceae; swamp forest vegetation in the central Ituri is further described by Hart and Hart (1988, 1989).

II. Disturbed areas

A. Open areas - These consist of roadsides, village settlements, and agricultural clearings (i.e., active gardens, village fields).

B. Secondary forests - The only large areas of secondary forest in the Ituri are of agricultural origin (Hart and Hart 1986). Cultivation of crops in the forest interior apparently began when agriculturalists (i.e., Bantu- and Sudanic-speaking shifting cultivators) advanced into the forest ca. 1,000-4,000 ybp (Hart and Hart 1986, Wilkie and Finn 1990, Hart et al. 1996). Introduction of agriculture (i.e., shifting (swidden) horticulture) into the forest permitted semi-nomadic hunter-gatherers (i.e., Mbuti and Efe Pygmies) to occupy what had been closed forest on a permanent basis (Hart and Hart 1986); long-standing trade relations between Pygmies and forest agriculturalists continue to the present day (Hart and Hart 1986).

More recently, roadside recurrent cultivation has been practiced, and the past 50 years have seen an expansion of slash-and-burn agriculture along roads in the area (Wilkie and Finn 1990, Stephenson and Newby 1997); today, most young secondary forest is concentrated along roads traversing the forest (Hart and Hart 1986).

Patterns of post-cultivation secondary forest succession in the Ituri Forest (incl. clearing/cultivation/forest fallow/reclearing cycles) have been described by T. B. Hart (1985), Hart and Hart (1986), and Wilkie and Finn (1988, 1990). It is characterized by these distinct phases:

- 1) active field (shamba) (2-yr. cultivation cycle);
- 2) years 1-3 post-cultivation, abandoned gardens, "farm-bush" secondary communities: open sere colonized by herbaceous and shrub species (incl. feral cultigens and pioneer plant species);
- 3) years 4-20, young regrowth forest: *Musanga cecropioides* (Moraceae) and other emergent tree species become dominant, canopy height 10-20 m, dense understory and middle layers (large, contiguous zones of *M. cecropioides*-dominated secondary forest now border roads in the region);
- 4) years 21-50, old seral forest: replacement of senescing trees by slow-growing, late-seral species which persist in canopy until sere is no longer distinguishable from climax forest (T. B. Hart 1985);
- 5) years 50-100, regenerated climax forest.

Introduction of agriculture into the Ituri has essentially extended the forest-savanna ecotone into the forest interior (Hart and Hart 1986). Relative to Epulu (at the center of the Ituri Forest), the closest forest/savanna border is more than 150 km distant to the NE (Makana et al. 1998, T. B. Hart 2001). In this connection it is interesting to note the capture in the present study of several open-country and transition-zone skipper species (Kielland 1990, Larsen 1991) in the vicinity of Epulu: *Eretis lugens* (Rogenhofer), *Sarangesa maculata* (Mabille), *Fresna netopha* (Hewitson), *Fresna nyassae* (Hewitson), and *Borbo holtzi* (Plötz). Also, Carcasson (1964) indicated that the presence within the forest of such open-country forms as *Coeliades forestan* (Stoll), *Tagiades fesus* (Fabricius), *Borbo borbonica* (Boisduval), and *Gegenes niso* (Linnaeus) tends to reflect these adaptable species' ability to colonize man-made clearings.

COLLECTING LOCALITIES

Collecting was carried out at seven localities in Haut-Zaïre: each of these has been assigned a three-letter code name, indicated below. Lenda (LDA) and Afarama (AFM) are research reserves administered by WCS-IZCN (Wildlife Conservation Society [formerly the New York Zoological Society] and the Institut Zaïrois pour la Conservation de la Nature [now the Institut Congolais pour la Conservation de la Nature (ICCN)]). Skippers were collected at all

of these localities except sites MMB and LDA; the great majority of the specimens are from the general vicinity of Epulu (EVC).

1) **NYK**: village of Nyankunde, 45 km WSW of Bunia, esp. grounds of the Centre Medical Evangelique (CME).

2) **MMB**: village of Mambasa (disturbed ground).

3) **EVC**: vicinity of Epulu, elev. ca. 750 m; mosaic of habitats (mbau forest, mixed forest, secondary forest, active gardens/cleared agricultural fields) (specimens were generally collected within a one-hour walk of Epulu; few or none were collected in the village itself).

4) **TLD**: trail (footpath) to Lenda, commencing 6 km E of Epulu on the E-W Bunia-to-Kisangani road, running 8 km S to site LDA; northerly 2.5-3 km of trail traverses second-growth forest with small settlements and plantations, remainder of trail traverses mosaic of mbau and mixed forest.

5) **LDA**: Lenda Study Area (LSA), 15-km² research camp established by Drs. J. A. Hart and T. B. Hart at S terminus of TLD; 12 km SE of Epulu, elev. ca. 700 m; mosaic of monodominant mbau forest, including stands of up to 10 km² in which mbau comprises more than 70% of the large trees (Hart et al. 1996).

6) **TAF**: trail (footpath) to Afarama (AFM), commencing 10 km W of Epulu on the E-W Bunia-to-Kisangani road, running 19 km N to site AFM; mixed forest.

7) **AFM**: Egoro Study Area (ESA) ("Afarama"), 45-km² research camp established by Drs. J. A. Hart and T. B. Hart at N terminus of TAF, at confluence of Egoro and Afarama rivers; 22 km NNW of Epulu, elev. ca. 850 m; broken-canopy mixed forest (habitats at ESA are further described by Hart and Hart 1988, 1989).

RESULTS AND DISCUSSION

FAUNISTIC AND BIOGEOGRAPHIC RELATIONSHIPS

I. Composition of fauna

A. Numbers of individuals collected - Lindsey and Miller (1965) commented on the paucity of HesperIIDae (i.e., 1-3% of all lepidopteran specimens) in various collections made in the forests of West and Central Africa, and suggested that collections in which skippers comprise 7-10% probably provide a truer picture of the fauna in these areas. Skipper specimens ($n = 501$) comprise 13% of the total collection of Rhopalocera ($n = \text{ca. } 3,933$) resulting from the collecting work in 1991. (It should be noted that a concerted effort was made by JFD and assistants to collect Hesperioidea, along with other relatively neglected groups (e.g., Satyridae, Lycaenidae).) Within the HesperIIDae, specimens collected in 1991 were distributed as follow: Coeliadinae, $n = 25$ (5% of total); Pyrginae, 96 (19%); Hesperinae, 380 (76%).

B. Species diversity - Skipper species ($n = 89$) comprise 21% of the ca. 431 species of Rhopalocera collected in 1991. An analysis of species diversity by subfamily within the HesperIIDae appears in Table 1. Eighteen percent (18%) of the known Afrotropical skipper fauna is represented in the 1991 collection; the proportions in which species in each of the three hesperiid subfamilies were collected closely matches the proportions these groups comprise in the Afrotropical fauna overall. Further collecting in the Epulu area, especially during other parts of the year, will no doubt augment the list of species now known from the site (cf. Ducarme 1999).

Table 1. HesperIIDae resulting from the collecting work in Haut-Zaïre ("1991" column) compared to total numbers of species listed for the Afrotropical Region by Ackery et al. (1995) ("Afrotrop." column). In each case, the number of species is followed in parentheses by the same expressed as a percent of total.

	1991	Afrotrop.	1991 as % of Afrotrop.
Coeliadinae:	5 (6)	18 (3)	28
Pyrginae:	21 (23)	145 (29)	14
Hesperinae:	63 (71)	340 (68)	19
TOTAL:	89 (100)	503 (100)	18

C. Sex ratios - Most species of skippers collected in this study show a strong apparent bias toward ♂♂ in terms of numbers of individuals captured. Interestingly, however, in two species, the observed sex ratio did not differ significantly from 50:50 (i.e.: *Tagiades fiesus*, $\chi^2 = 0.04$, $P >> 0.05$; *Semalea pulvina*, $\chi^2 = 0.64$, $P >> 0.05$).

II. Endemics

Two taxa known to be endemic to the Ituri region are represented among the species collected: *Celaenorrhinus b. beni* Bethune-Baker and *C. boadicea howarthi* Berger (*howarthi* is also known from Uganda).

III. Geographic range extensions

Some of the Ituri specimens appear to represent considerable range extensions of the species involved. In some cases, indicated with asterisks (*), these appear to be the first known records of particular species from Zaïre.

A. Eastward extensions (disjuncts?) - The most striking biogeographic patterns evident within the Ituri Forest collection are sizable eastward extensions of the known ranges of some species, hitherto known only from western Africa. Whether these represent truly disjunct populations in the Ituri region or are an artifact (i.e., poor sampling in intervening areas, Louette 1984, Mayr and O'Hara 1986, Hamilton 1992) is not clear. The Ituri species involved are:

**Coeliades bixana* Evans (also collected in E Zaïre by Ducarme 1999);

**Xanthodisca rega* (Mabille);

**Meza mabillei* (Holland);

**Caenides maracanda* (Hewitson);

**Melphina tarace* (Mabille) (also collected in E Zaïre by Ducarme 1999).

Taxa previously known or suspected to show this disjunct (E-W) distribution pattern are also represented in the Ituri collection, i.e.: *Celaenorrhinus beni* Bethune-Baker, *Celaenorrhinus bitjena* Evans, *Eagris subalbida aurivillii* (Neustetter), *Sarangesa thecla* (Plötz), *Acleros sparsum* Druce, *Semalea atrio* (Mabille), **Fresna carlo* Evans, and **Fresna cojo* (Karsch).

This distributional pattern is of interest in that it may reflect the locations of prehistoric refugia in Africa's central and western forest blocks (PALEOECOLOGY, below).

B. Other range extensions - The Haut-Zaïre records of each of three species reported herein may represent eastward extensions of their respective known ranges within Zaïre: *Pardaleodes edipus* (Stoll), *Andronymus helles* Evans, and *Borbo f. fanta* (Evans). In addition, specimens in the Ituri collection appear to extend the known ranges of **Sarangesa thecla mabira* Evans (west- & southwestward) and *Meza larea* (Neave) (northward).

PALEOECOLOGY OF THE ITURI REGION ('OKAPILAND')

Forest dynamics - Contrary to first impressions, perhaps, the Congo Basin's vast forest belt has not always been continuous and green. Large areas of it are underlain by wind-blown Kalahari sands, giving evidence that at arid times in the past desert conditions have stretched north to join with the southern Sahara (Moreau 1966, Kingdon 1971, 1989, Maley 1996, Larsen 1997, Livingstone 2001, White 2001).

Tropical rainforest areas themselves have not all been the havens of long-term stability they were once thought to represent. It is now clear that the Pleistocene was a time of great climatic instability in tropical Africa: throughout the Quaternary, wide fluctuations in climate have periodically altered environments across the continent.

Periods of global climatic cooling were apparently associated with tropical aridity and forest retreat, alternating with warmer, wetter periods which allowed the forest to advance. During glacial intervals (cool, dry) in tropical Africa, lowland rainforests were apparently drastically reduced in area, contracting to relatively stable refuge sites (ecological islands) (Figure 1) around the periphery of the present forest belt where relatively high rainfall persisted. These purported sanctuaries are variously called refugia, core areas, centers of endemism, and (more recently) biodiversity "hotspots". With the subsequent return of favorable conditions during interglacial intervals (warm, wet), the forest apparently expanded from these refuge sites to colonize intervening areas from which it had disappeared. Rainforest organisms were then able to emanate into the reforested areas, and did so at varying rates.

Repeated fragmentation and coalescence of the forest in this manner during glacial/interglacial cycles is thought to have functioned as one mechanism of, or as one 'engine' driving, speciation ('species pump' of Morley 2001, part of 'evolutionary whirlpool' of Kingdon 1989). Recognition of the idea that much of the tropical rainforest is not very old geologically and that its periodic fragmentation has influenced speciation was pioneered by work on

Amazonia by Haffer (1969) and on African environments by Chapin (1932), Carcasson (1964), Moreau (1966, but see Diamond and Hamilton 1980 and Hamilton 1982), Kingdon (1971), and others.

It appears that at least 21 glacial/interglacial cycles have occurred in the past 2.3 million yrs. (Hamilton 1988, 1992, Livingstone 2001, White 2001), each of them presumably with some degree of concomitant retreat and subsequent advance of organisms from forest refugia. The last of these (the most recent world glacial maximum, ca. 18,000 ybp) appears to have been of extreme severity (Hamilton 1988, Larsen 1997); it appears that rainforest has spread out fairly recently from particular refugia, beginning ca. 12,000 ybp *fide* Hamilton (1976, 1988).

Support for the validity of the 'Pleistocene Refuge Theory' in tropical Africa as outlined above has come from the work of many authors, e.g., Hamilton (1976, 1982, 1988, 1992), Kingdon (1980, 1989), Prance (1982a), Maley (1987, 1996, 2001), Richards (1996), van der Maesen et al. (1996), Morley (2000), and Hamilton et al. (2001).

In addition, studies of particular groups of African forest organisms have provided support for the theory and rather wide agreement about the locations of postulated refugia: **plants** (van der Maesen et al. 1996, Hamilton et al. 2001); **butterflies** (Carcasson 1964, Larsen 1997, Hamilton et al. 2001); **reptiles and amphibians** (Laurent 1973, Lawson and Klemens 2001); **birds** (Diamond and Hamilton 1980, Crowe and Crowe 1982, Mayr and O'Hara 1986, Prigogine 1988, Dowsett-Lemaire and Dowsett 2001, Hamilton et al. 2001); **mammals** (Booth 1958, Bigalke 1968, Kingdon 1971, 1980, 1989, Grubb 1978, 1982, Rodgers et al. 1982, Hamilton 1976, 1988, Hamilton et al. 2001, Ray 2001, Tutin and Vedder 2001); **other organisms** (Prance 1982a; summaries by Hamilton 1976, 1982, and by Rodgers et al. 1982).

The Ituri Forest - Africa's two most species-rich forest blocks, Cameroon/Gabon and E Zaire, lie on either side of the great, forested, Congo Basin (Carcasson 1964, Diamond and Hamilton 1980, Hamilton 1982, 1992, Hamilton et al. 2001). The Ituri Forest adjoins closely and overlaps the postulated location of the E Zaire refugium (Figure 1). The Ituri region illustrates well the three characteristics typical of forest refugia outlined by Hamilton (1976, 1982, 1988, 1992), Diamond and Hamilton (1980), Mayr and O'Hara (1986), Kingdon (1989), and others: 1) high species richness; 2) high levels of endemism; 3) the presence of isolated populations of disjunctly-distributed taxa. The spatially coincident occurrence of these sorts of centers gives support to the view that the Ituri region has served as a refugium in which lowland forest has persisted during climatic vicissitudes of the Quaternary.

1) Species richness - The E Zaire refugium was the largest, most ecologically varied, and most centrally located of the three great African forest core areas (Upper Guinea, Cameroon/Gabon, E Zaire), and it is presently faunally the most species-rich of the three (Kingdon 1971, Hamilton 1976, Wilkie and Finn 1988; forest mammals, Bigalke 1968, Rodgers et al. 1982; forest passerine birds, Diamond and Hamilton 1980). The Albertine Rift region of Central Africa (where Zaire, Uganda, Rwanda, and Burundi meet), in fact, leads the continent in overall biodiversity (Pomeroy 1993).

The Ituri region is wonderfully rich in species, representing a wide range of taxonomic groups. Gradients of biotic diversity can be seen to fall away in every direction from the Ituri core area (Figure 1). About 1,000 species of forest butterflies (Hesperioidea and Papilionoidea) are estimated to occur in the E Zaire (Ituri) region; within Africa this number is exceeded only by that in the Cameroon/Gabon core area, where more than 1,400 species occur (Carcasson 1964, Larsen 1997).

2) Endemism - Among the species endemic to the Ituri Forest are some of the continent's most unusual and intriguing forms (e.g., Kingdon 1971, 1989). About 15% of forest mammal species in the Ituri region are endemic to NE Zaire/DR Congo (Bigalke 1968, Hart and Hart 1992). The okapi (Figure 1), the 'flagship species' of the Ituri ecosystem, has become an icon in Zaire and a symbol of Zairian national identity (pers. obs. 1991). The importance of E Zaire as a refugium and center of endemism has been discussed as it concerns forest mammals by Bigalke (1968), Rodgers et al. (1982), and Grubb (2001), and concerning forest birds by Diamond and Hamilton (1980) and Prigogine (1988, Albertine Rift Refugium). Maley (2001) and others have argued that the numerous endemic taxa typical of particular precincts within the forest could have resulted from repeated forest fragmentation in times past, each time with refuges in approximately the same locations.

3) Disjunct populations - Some of the most compelling evidence for the existence and locations of former refugia in the African forest belt comes from the present-day distributions of particular organisms: core areas tend to be foci of isolated populations of species showing disjunct (apparently relictual) distributions (e.g., Hamilton 1988). Numerous taxa in Africa are represented by widely-separated, isolated populations at the western and eastern

periphery of the Congo Basin; the most common pattern of disjunction involves populations centered on Cameroon/Gabon and on E Zaïre (e.g.: butterflies and skippers, Carcasson 1964, present study; forest birds, Diamond and Hamilton 1980, Prigogine 1988). The distribution of populations of the gorilla (*G. gorilla* (Savage and Wyman)) is a well-known example of this pattern: western and eastern subspecies are separated by a gap of ca. 750 km of unoccupied rainforest (Hamilton 1982, 1992, Tutin and Vedder 2001). The most likely explanation for these disjunct distributions in many cases is that a once continuous range was split during a previous interval or intervals of forest contraction, and with subsequent forest expansion the respective isolated populations have been slow to colonize the relatively recently-established intervening areas of suitable habitat (i.e., they have not yet come into secondary contact) (Diamond and Hamilton 1980, Mayr and O'Hara 1986, Hamilton 1992).

Although additional field work in the central Congo Basin (between the sites of postulated refugia) might fill in some of the distributional gaps (Louette 1984, Dowsett-Lemaire and Dowsett 2001), there is little doubt that the patterns of disjunction are real, and that the area of intervening Congolese forest is faunally depauperate (Moreau 1966, Kingdon 1971, Crowe and Crowe 1982, Hamilton 1982, 1992, Louette 1984, Mayr and O'Hara 1986, Grubb 2001).

The validity of the refuge theory as outlined above has been challenged (e.g., Connor 1986, Endler 1982 [though refuted by Mayr and O'Hara 1986], White 1993), and alternative explanations for the observed patterns of biodiversity have been put forth (e.g., Endler 1982 (incl. butterflies, birds), Colyn et al. 1991 and Grubb 2001 (mammals)). However, a preponderance of scientific evidence supports the view that isolation in glacial refugia has been a prime factor in the speciation of rainforest organisms, and the theory has gained wide acceptance (e.g., Diamond and Hamilton 1980, van der Maesen et al. 1996, Larsen 1997, Weber and Vedder 2001).

The refuge model outlined here does not exclude the validity of other models (Prance 1982b, Maley 2001), and factors other than vicariance (isolation in refugia) have no doubt been important in speciation in many taxa; an excellent summary of the possible role of other factors contributing to speciation is provided by Carcasson (1964). A more robust, composite theory ('combined model') is now emerging, one in which the idea of isolation in larger refugia is retained but which recognizes: 1) that peripheral regions of gallery forests and small patches of lowland forest probably remained within the Congo Basin during arid intervals (Grubb 2001, White 2001); 2) that additional 'forcing mechanisms' were at work (e.g., orogeny, rivercourses, various ecological barriers) inhibiting gene flow and dispersion (e.g., Morley 2000, Maley 2001); 3) that multiple immigrations into colonizing forest (rather than persistence in ancient forest) may have occurred (Colyn et al. 1991 (primates)); and 4) that a major lowland or fluvial refuge existed in the S/SW portion of the Congo Basin (shown as site B, Figure 1).

It also seems that speciation of rainforest organisms (including butterflies) began and has taken place over much longer time periods than was previously thought, apparently antedating events of the late Pleistocene (e.g., Hamilton 1976, Larsen 1997, Morley 2000). The suggestion made by Larsen (1997), that disjunct populations have been slow to differentiate, is borne out by our own observations, e.g., that the genitalia of ♂ specimens (*Coeliades bixana* Evans, *Meza mabiliei* (Holland)) from disjunct populations in West Africa (Ghana) and the Ituri Forest show no important differences.

SPECIES ACCOUNTS: HESPERIIDAE

Five hundred and one (501) skippers representing 89 species were collected, as follow.

COELIADINAE

Coeliades bixana Evans. 1♂; site EVC; 28.vi.1991.

The range of this lowland forest species is described in Ackery et al. (1995) as "west Africa from Guinea to Angola". Although the ♂ collected may represent a stray, the possibility of disjunct populations exists, in NE Zaïre and possibly in Shaba (5 specimens in the AME collection are labeled "Katanga: Kafakumba"). Ducarme (1999) reports having collected this species at Beni and Mangina (Nord-Kivu) and at Teturi (Haut-Zaïre). The Zaïrian records reported here represent large eastward extensions of this species' known range.

Comparisons of the genitalia of the Ituri ♂ with AME specimens from Ghana (Likpe [TL is "Gold Coast"]) and Katanga ("Kafakumba") show no important differences.

Coeliades c. chalybe (Westwood). 3♂♂, 1♀; site EVC; 3-11.vii.1991.

Coeliades f. forestan (Stoll). 2♀♀; site EVC; 27.vi.-23.vii.1991.

Coeliades hanno (Plötz). 1♀; site EVC; 18.vii.1991.

Coeliades libeon (Druce). 12♂♂, 5♀♀; sites EVC, AFM; 2-28.vii.1991.

PYRGINAE

Celaenorrhinus b. beni Bethune-Baker. 1♂; site AFM; 20.vii.1991.

Subsp. *beni* is an Ituri District endemic; Miller (1971) observed that it appears to be rather rare and local.

Celaenorrhinus bitjena Evans. 1♂; site EVC; 23.vii.1991.

Ducarme (1999), too, reports having collected *bitjena* at Epulu. This species (figured in Evans 1937) is known only from Cameroon, Gabon, and the Ituri Forest (Ackery et al. 1995).

Celaenorrhinus boadicea howarthi Berger. 1♂; site EVC; 25.vi.1991.

Subsp. *howarthi* is restricted to the Ituri region and Uganda (Ackery et al. 1995).

Celaenorrhinus galenus (Fabricius). 4♂♂, 2♀♀; sites EVC, TAF; 26.vi.-22.vii.1991.

Celaenorrhinus homeyeri (Plötz). 2♂♂; site EVC; 28.vi.-10.vii.1991.

Celaenorrhinus n. nigropunctata Bethune-Baker. 1♂, 1♀; site EVC; 28.vi.-25.vii.1991.

Celaenorrhinus ovalis Evans. 2♂♂, 2♀♀; site EVC; 24.vi.-17.vii.1991.

Celaenorrhinus proxima (Mabille). 4♂♂, 2♀♀; site EVC; 28.vi.-26.vii.1991.

Tagiades flesus (Fabricius). 12♂♂, 13♀♀; site EVC; 23.vi.-28.vii.1991.

Eagris lucetia (Hewitson). 2♂♂; site EVC; 26-30.vi.1991.

Eagris subalbida aurivillii (Neustetter). 9♂♂, 4♀♀; site EVC; 26.vi.-28.vii.1991.

An apparently disjunct population of subsp. *aurivillii* is known in E Cameroon (Ackery et al. 1995).

Eagris t. tigris Evans. 1♂; site EVC; 16.vii.1991.

Callegris lacteus (Mabille). 4♂♂; site EVC; 29.vi.-23.vii.1991.

Lindsey and Miller (1965) questioned whether it is appropriate to recognize any subspecies within this species.

Eretis lugens (Rogenhofer). 5♂♂; site EVC; 29.vi.-28.vii.1991.

Sarangesa bouvieri (Mabille). 1♂; site EVC; 1.vii.1991.

Sarangesa b. brigida (Plötz). 6♂♂, 1♀; site EVC; 13-28.vii.1991.

Sarangesa maculata (Mabille). 1♂; site EVC; 23.vii.1991.

Sarangesa tertullianus (Fabricius). 1♂; site EVC; 24.vi.1991.

Sarangesa thecla mabira Evans. 6♂♂; site EVC; 25.vi.-28.vii.1991.

Ducarme (1999) reports having collected *mabira* at Beni (Nord-Kivu) and at Mt. Hoyo (Haut-Zaïre). His records, the Ituri specimens reported here, and 2♂♂ from Katanga ("Kafakumba" and "Kapanga") in the collection at AME are apparently the first records of *thecla* for Zaïre and represent west- and southwestward extensions of the known range of subsp. *mabira* (Ackery et al. 1995).

Abantis contigua Evans. 1♂; site EVC; 11.vii.1991.

Spialia p. ploetzi (Aurivillius). 4♂♂, 2♀♀; site EVC; 26.vi.-18.vii.1991.

This is the only species of *Spialia* confined to evergreen forest (Kielland 1990, Larsen 1991); de Jong and Congdon (1993) cite it as an example of a species which has successfully made the adaptive shift from open grassland to forest.

HESPERINAE

Gorgyra bina Evans. 1♂; site EVC; 16.vii.1991.

Teniorhinus ignita (Mabille). 21♂♂, 1♀; sites EVC, AFM; 23.vi.-28.vii.1991.

Teniorhinus watsoni Holland. 6♂♂; sites EVC, AFM; 3-25.vii.1991.

Records of *T. watsoni* exist from as far east as Uganda (Lindsey and Miller 1965).

Teniorhinus niger (Druce). 1♂; site AFM; 20.vii.1991.

T. watsoni and *T. niger* are sympatric in Cameroon, where they behave as distinct species (Lindsey and Miller 1965; T. B. Larsen *in litt.*, 5 Dec. 1996). The capture of *T. watsoni* and *T. niger* in flight at the same Ituri microlocality on the same day (AFM, 20.vii.) lends support to the view that they are distinct entities.

Ceratrachia aurea Druce. 5♂♂, 2♀♀; sites EVC, AFM; 28.vi.-21.vii.1991.

Ceratrachia h. hollandi Bethune-Baker. 8♂♂, 3♀♀; sites EVC, AFM; 30.vi.-28.vii.1991.

Ceratrachia semilutea Mabille. 1♂; site AFM; 21.vii.1991.

Ceratrachia wollastoni Heron. 3♂♂; sites EVC, AFM; 25.vi.-21.vii.1991.

Pardaleodes bule Holland. 7♂♂, 3♀♀; site EVC; 29.vi.-22.vii.1991.

One pair was captured while *in copula*, 29.vi.

Pardaleodes edippus (Stoll). 4♂♂, 6♀♀; site EVC; 27.vi.-28.vii.1991.

Pardaleodes incerta (Snellen). 25♂♂, 7♀♀; site EVC; 24.vi.-27.vii.1991.

Pardaleodes sator (Westwood). 2♀♀; site EVC; 4-8.vii.1991.

Pardaleodes t. tibulkus (Fabricius). 2♂♂, 1♀; site EVC; 25.vi.-18.vii.1991.

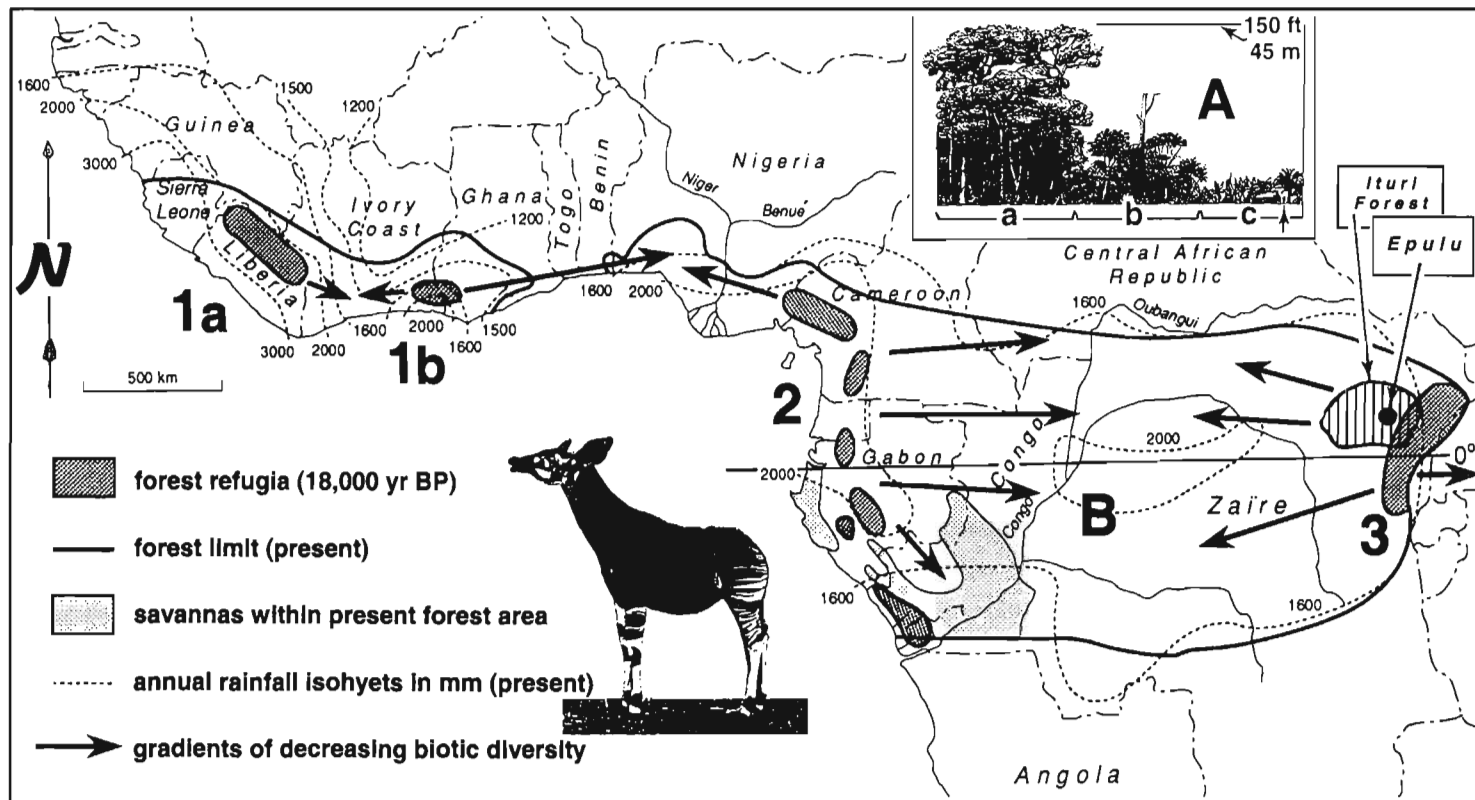


Figure 1. The Ituri Forest of NE Zaïre in relation to postulated lowland forest refugia of West and Central Africa during the last world glacial maximum (ca. 18,000 ybp), at which time cool, dry conditions prevailed across equatorial Africa. The indicated refugia appear to have been important as moist-forest sanctuaries during dry periods in past millennia; from them, newly-differentiated species have apparently emanated during favorable periods when wetter conditions prevailed across the region. The Ituri region is an important component of the E Zaïre center of endemism. (Map modified after Maley (1987, 1996, 2001) and Richards (1996); diversity-gradient arrows within the forest belt follow Carcasson (1964) and Hamilton (1982, 1988, 1992).)

(1), Upper Guinea core area (1a, Sierra Leone/Liberia; 1b, E Ivory Coast/W Ghana);

(2), Cameroon/Gabon core area;

(3), E Zaïre core area (Central Refuge of Kingdon 1971, 1980, 1989; Albertine Rift Refugium (in part) of Prigogine 1988).

(A) (inset), forest profile (Ituri region), adapted from Chapin (1932): a, primary forest; b, secondary forest; c, agricultural clearing (village garden). (For a further sense of scale, arrowhead to right of "c" points to a relatively minuscule 6-ft-tall villager standing to the right of a dwelling-place.)

(B), location of S/SW Zaïre Basin lowland refuge postulated by Laurent (1973), Kingdon (1980, 1989), Prigogine (1988, Congo Basin Refugium), and Maley (1996, 2001) (also cf. Major Fluvial Refuge of Colyn et al. 1991, Salongo and Kasai centers within Fluvial Super-Refuge of Grubb 2001). Not shown: Montane forest refugia to E and W of Zaïre Basin (e.g., Kingdon 1989, Maley 1996).

Other inset features are adapted as follow: Mbuti arrow indicating north is from Turnbull (1965); okapi image (center) is from Kenneth W. Fink-Root Resources.

Although Lindsey and Miller (1965) concluded that *torensis* Bethune-Baker is indistinguishable from subsp. *tibullus*, *torensis* is now recognized as a distinct subspecies (LDM). Ducarme (1999) reports having collected *torensis* at Beni and Mt. Atonza (Nord-Kivu), and at Katanga [sic] and Mt. Hoyo (Haut-Zaïre).

Ankola fan (Holland). 22♂♂, 4♀♀; site EVC; 24.vi.-27.vii.1991.

Xanthodisca rega (Mabille). 1♂; site EVC; 10.vii.1991.

The range of this species as described in Ackery et al. (1995) is Senegal to Cameroon and Gabon; the Ituri record is apparently the first for Zaïre and extends the known range of this species far to the east.

Rhabdomantis galatia (Hewitson). 1♂; site EVC; 11.vii.1991.

Osmodes adonia Evans. 2♂♂; sites EVC, AFM; 1-21.vii.1991.

Osmodes adosus (Mabille). 3♂♂, 2♀♀; sites EVC, AFM; 26.vi.-21.vii.1991.

Osmodes distincta Holland. 1♂, 4♀♀; sites EVC, TAF, AFM; 9-22.vii.1991.

Osmodes laronia (Hewitson). 2♂♂; site EVC; 4-14.vii.1991.

Osmodes thora (Plötz). 4♂♂, 2♀♀; site EVC; 28.vi.-26.vii.1991.

Paracleros biguttulus (Mabille). 7♂♂, 4♀♀; sites EVC, TLD, TAF, AFM; 27.vi.-28.vii.1991.

The genitalic pattern of the Ituri ♂♂ closely matches that of AME specimens of *P. biguttulus* from Kenya we examined, and contrasts with *P. placidus* (Plötz) from Ghana.

Acleros bibundica Strand. 2♂♂, 1♀; site EVC; 26.vi.-11.vii.1991.

Acleros nigrapex Strand. 2♂♂, 2♀♀; site EVC; 8-26.vii.1991.

Acleros ploetzi Mabille. 10♂♂, 3♀♀; site EVC; 26.vi.-28.vii.1991.

Acleros sparsum Druce. 4♂♂; site EVC; 24.vi.-26.vii.1991.

This species appears to consist of two disjunct populations, one in the Ituri Forest and one in Cameroon (Ackery et al. 1995).

Semalea arela (Mabille). 26♂♂, 12♀♀; sites EVC, AFM; 25.vi.-27.vii.1991.

Semalea atrio (Mabille). 1♂; site AFM; 21.vii.1991.

This species apparently consists of separate West African and E Zaïrian populations (Ackery et al. 1995).

Semalea pulvina (Plötz). 22♂♂, 17♀♀; sites EVC, NYK (1♀); 19.vi.-28.vii.1991.

Semalea sextilis (Plötz). 3♂♂; site EVC; 18-26.vii.1991.

This species is apparently rare throughout its range (Larsen 1991).

Hypoleucis ophiura ophir Evans. 1♂; site EVC; 14.vii.1991.

Meza cybeutes pallida (Evans). 1♀; site AFM; 21.vii.1991.

Meza indusiata (Mabille). 1♀; site EVC; 17.vii.1991.

Meza larea (Neave). 1♀; site EVC; 28.vii.1991.

It is interesting that Lindsey and Miller (1965) placed 1♀ *Meza* sp. from Liberia doubtfully as *larea*.

Meza mabillei (Holland). 4♂♂, 1♀; sites EVC, AFM; 30.vi.-23.vii.1991.

This species' range as described in Ackery et al. (1995) is Sierra Leone to Nigeria and Gabon; the Ituri records are apparently the first for Zaïre and extend the known range of *mabillei* far to the east.

Comparison of ♂ genitalia shows no important differences between the Ituri specimens and AME specimens of *mabillei* from Ghana.

Meza meza (Hewitson). 8♂♂, 6♀♀; site EVC; 27.vi.-18.vii.1991.

Andronymus caesar philander (Hopffer). 2♂♂, 1♀; site EVC; 25.vi.-28.vii.1991.

Andronymus fenestrella Bethune-Baker. 3♂♂; sites EVC, AFM; 8-20.vii.1991.

Andronymus helles Evans. 4♂♂; site EVC; 28.vi.-4.vii.1991.

Ducarme (1999) reports having collected *helles* at Mt. Hoyo (Haut-Zaïre).

Andronymus n. neander (Plötz). 22♂♂, 5♀♀; sites EVC, NYK (1♂); 19.vi.-27.vii.1991.

Chondrolepis cynthia Evans. 1♂; site EVC; 14.vii.1991.

Although the range of this species is described in Ackery et al. (1995) as highland forest in E Zaïre and SW Uganda, the specimen reported here is from lowlands, as are two Ugandan specimens in the AME collection (Entebbe).

Chondrolepis n. niveicornis (Plötz). 1♂, 1♀; site EVC; 27-30.vi.1991.

Gamia shelleyi (Sharpe). 1♀; site EVC; 24.vi.1991.

Gretna cylinda (Hewitson). 2♂♂; site EVC; 30.vi.-23.vii.1991.

Caenides dacela (Hewitson). 3♂♂; site EVC; 23.vi.-17.vii.1991.

Caenides dacena (Hewitson). 3♂♂, 2♀♀; sites EVC, AFM; 20-26.vii.1991.

Caenides kanguensis Holland. 1♀; site EVC; 29.vi.1991.

Caenides maracanda (Hewitson). 1♀; site TLD; 9.vii.1991.

The range of this species, extremely rare in collections, is described in Ackery et al. (1995) as Nigeria, Cameroon, and Angola. The Ituri specimen, and 1♀ in the AME collection labeled

"Katanga: Kapanga", are apparently the first records of *maracanda* from Zaïre and extend the known range of this large skipper far to the east.

Monza alberti (Holland). 1♂; site EVC; 15.vii.1991.

Monza cretacea (Snellen). 2♂♂, 1♀; sites EVC, NYK (1♂); 19.vi.-26.vii.1991.

Melphina flavina Lindsey and Miller. 1♂; site EVC; 8.vii.1991.

Melphina tarace (Mabille). 1♂; site EVC; 23.vii.1991.

The range of this species as described in Ackery et al. (1995) is Sierra Leone, Ivory Coast, Nigeria, Cameroon, and the Congo Republic; the Ituri ♂, and the collection record from Beni (Nord-Kivu) reported by Ducarme (1999), are apparently the first records of *tarace* from Zaïre and extend this species' known range far to the east. In addition, the collection at AME includes a long series of *tarace* from Ghana (coll. Fr. Theo. Maessen) and one specimen from the Central African Republic (coll. S. C. Collins).

Melphina unistriga (Holland). 1♂, 1♀; site EVC; 28.vi.-26.vii.1991.

Fresna carlo Evans. 1♂; site EVC; 4.vii.1991.

This rare species (figured in Evans 1937) has been known heretofore only from Ivory Coast, Nigeria, Cameroon, and W Uganda (Ackery et al. 1995).

Fresna cojo (Karsch). 1♀; site EVC; 23.vii.1991.

The Ituri specimen, and 1♀ in the AME collection labeled "BELG. CONGO: Kafakumba", appear to be the first Zaïrian records of this rare species (Ackery et al. 1995). Its range may be comprised of two disjunct populations (Senegal to Nigeria; Uganda to W Kenya, and W Tanzania *vide* Kielland 1990).

Fresna netopha (Hewitson). 1♂; site EVC; 23.vii.1991.

Fresna nyassae (Hewitson). 2♂♂, 1♀; site EVC; 23-27.vii.1991.

Platylesches galesa (Hewitson). 1♂; site EVC; 27.vi.1991.

Borbo b. borbonica (Boisduval). 1♀; site EVC; 17.vii.1991.

Borbo f. fanta (Evans). 5♂♂, 2♀♀; site EVC; 29.vi.-18.vii.1991.

Borbo f. fatuellus (Hopffer). 1♂; site EVC; 12.vii.1991.

Borbo holtzi (Plötz) [epithet is often misspelled *holtzii*]. 1♀; site EVC; 14.vii.1991.

Gegenes niso brevicornis (Plötz). 4♂♂, 2♀♀; sites EVC, NYK (1♂, 1♀); 19.vi.-27.vii.1991.

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