Chapter 9

Spatial Distribution of Some Aquatic Insects in the Réserve Naturelle Intégrale d'Andringitra, Madagascar

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Abstract

The study of some groups of lotic insects (Trichoptera: Philopotamidae; Diptera: Simuliidae; Ephemeroptera: Leptophlebiidae and Euthyplociidae) of the Réserve Naturelle Intégrale d'Andringitra highlights an important faunistic difference between the eastern forested slopes and the western "open" slopes within the reserve. Altitudinal zonation appears in the forest area, which separates localized "high-altitude species" and broadly distributed "low-altitude species." The species found on the western slopes generally have wider distributions on the island than those on the eastern slopes.

Résumé

L'étude de quelques groupes d'insectes lotiques de la Réserve Naturelle Intégrale d'Andringitra met en évidence une profonde différence faunistique entre le versant oriental forestier et le versant occidental ouvert. Sur le versant forestier apparaît une zonation altitudinale qui oppose des formes d'altitude très localisées et des formes de basse altitude un peu plus répandues. Les espèces du versant occidental offrent généralement une vaste aire de répartition.

Introduction

Among Malagasy freshwater organisms, the fish fauna is relatively well known (Kiener, 1963), and some information has been published for the macrocrustaceans, but there is little information on aquatic insects. Furthermore, for this latter group the information available is not evenly distributed. For example, about 144 species of Odonata have been described from Madagascar (Schmidt, 1951; Fraser, 1956), compared to only 24 Ephemeroptera, 22 Trichoptera, and 12 Diptera: Simuliidae. This is in contrast to the more than 1,600 species recorded for these latter three groups in continental Africa. On Madagascar, the low number of species probably reflects our current knowledge rather than the actual diversity.

This lack of information has two important consequences concerning the present inventory of the Réserve Naturelle Intégrale (RNI) d'Andringitra. A large proportion of the aquatic insects collected are unknown to science, and with our current level of knowledge it is impossible to interpret the level of endemicity of these groups within the reserve. In this paper we focus roughly on the ecology of these organisms with reference to their elevational distribution, stream ecology, and general habitat specificity (see Malicky & Chantaramongkol, 1993, for a review of these points).

TABLE 9-1. Altitudes, stream orders, and water temperatures of the sampling stations.

Sampling station no.	Altitude (m)	Stream orders	Water temperature (°C)	Biome
Eastern slope				
1	717	5	16	Degraded forest
2	720	4	15	Degraded forest
3	720	5	16	Degraded forest
4	735	4	18	Degraded forest
5	750	3	17	Primary forest
6	750	2	...	Primary forest
7	900	4	16	Primary forest
8	1180	3	14	Primary forest
9	1210	3	14	Primary forest
10	1625	1	11	Primary forest
11	1630	1	11	Primary forest
Western slope				
12	600	5	22	Savannah
13	1400	4	21	Savannah
14	1900	2	19	Savannah
15	1950	2	19.5	Savannah

Study Sites

This study was carried out in November 1993 within the four elevational transect zones (720, 810, 1210, and 1625 m) on the eastern slope of the massif (see Chapter 1 for a description of the sites) and in November 1994 at three additional sites in the summit zone and on the western side of the massif. The sampling of high-altitude rivers of the western slope was undertaken to distinguish the influences of different biomes (forest, degraded forest, and savannah, etc.) from those of altitude and stream order. The major parameters for each collection site are listed in Table 9-1.

Eastern Slope Stations

720 m ELEVATIONAL ZONE—Hydrobiological collections were made at three sites within this zone. The Iantara River passes adjacent to the 720 m camp and within a zone of partially degraded forest at the edge of swidden agriculture sites. The river is generally 10–15 m wide; in several places it is as wide as 30 m. For most of this length, the forest canopy does not overlap the river and the gallery forest is partially broken. The Iantara River is of stream order 5 (see Table 9-1). The main features of the river are strong flowing waters, alternating with basins and slow water flow. The Iantara River was sampled in two places: station 3 (17 November 1993), located in the rockbound stretch upstream from the 720 m camp, and station 1 (16 November 1993), located 200 m downstream from station 1, just after the confluence of the Intara and Lalangina rivers. The vegetation along the Lalangina River, station 2 (17 November 1993), a tributary of stream order 4, consisted largely of gallery forest. At the station 2 sampling site, about 40 m above the confluence, the river banks were overgrown with brush.

810 m ELEVATIONAL ZONE—Three stations were sampled within this zone. Station 5 (21 November 1993) was situated just below the 810 m camp, along the Sahanivoraky River, a tributary of the Sahavatoy. This watercourse (stream order 3) ran under a gallery forest with overlapping canopy. The river was torrent-like, running along a relatively steep route, broken by waterfalls. Rocky elements within the river were medium-sized to large boulders. Station 6 (21 November 1993) was in a small watercourse (stream order 2) inside the forest. The flow of water was very slow, with a discharge of a few liters per second. The substrate was gravel and sand. Station 4 (20 November 1993) was along the Sahanivoraky River (stream order 4) and in an area of nonoverlapping gallery forest. The river course is chaotic, hindered by masses of rocks that act as numerous natural dams.

1210 m ELEVATIONAL ZONE—Station 9 (22 November 1993) was along a tributary of the Sahavatoy River, known locally as the Volotsangana River, and situated close to the 1210 m camp. This waterway, of stream order 3, was bordered with a partly overlapping gallery forest. The watercourse was characterized by large boulders, alternating with numerous waterfalls. The overall waterway was steep (> 45°). Station 8 (23 November 1993) was along another river of the same order and parallel to the Volontsangana River, but at a slightly lower elevation; it was sampled only for Simuliidae. This river had a strong water flow and ran under an overlapping gallery forest. Its steepness was less than that of station 9, and the substrate was predominantly pebbles.

1625 m ELEVATIONAL ZONE—Two steep watercourses were sampled. These were small streams cascading onto flagstone. Station 10 (25 November 1993) was in a relatively open area, and water discharge was less than 1 liter per second. Station 11 (24 November 1993) was in forest largely composed of bamboo and had a discharge of a few liters per second.

Western Slope Stations

Four stations were sampled on the western slope, all of them along the Zomandao River, a confluent of the Mangoky Basin. Three sites were sampled during the November 1993 mission (stations 13, 14, and 15; 28–30 November 1993), whereas station 12 was sampled during the November 1992 field trip. It was retained because it lay on the Zomandao River at an altitude close to that of stations 1, 2, and 3 on the eastern slope. Station 12 was located near Ankaramena, along a sandy stretch of the Zomandao River (stream order 4), at 600 m. Here the watercourse was regularly broken by rocks and was situated in a savannah area. Station 13 was at the level of Antanifotsy (1400 m); a rocky shelf and large boulders impeded the medium water flow (stream order 3). This river ran through a zone of savannah. Station 14 was on the western part of the high plateau of the reserve, at an altitude of 1900 m. The site was near a small lake formed by the widening of the river (stream order 2), where it passed through a zone of grassy savannah interlaced with Ericaceae bush. The river course was relatively level and was made up of flagstone, forming shelves, that alternated with deeper water zones that had stony-gravel bottoms. Station 15 was located at the edge of the high plateau, at an altitude of 1950 m and a short distance from the source zone. At this site, the river ran through a zone of grassy savannah. Its steepness was slight (stream order 2), and the river bottom was made up of either flagstone or pebbles.

Methods

Sampling Techniques

Three different methods of sampling were used:

EVENING LIGHT TRAPS—This method was used to collect adults of aquatic insects with nocturnal flight activity. A large shallow pan was filled with water that was mixed with a tension-active agent (soap). The light sources were a white light generated by a natural gas lamp (camping stove type), and an ultraviolet (UV) light produced by a battery lamp with a UV tube. The trap was placed along the river bank, illuminated 10 minutes before sunset, and switched off 1 hour later. Ephemeroptera and other fragile insects were collected and preserved individually as they were caught in the trap. The other insects were filtered and preserved in 70% ethanol. This method was highly efficient for the sampling of Trichoptera, less so for Ephemeroptera, and generally useless for Simuliidae.

BUTTERFLY NET—This method was used primarily to capture adult Ephemeroptera, which swarm during the day and at dusk, and adult Odonata.

COLLECTION OF AQUATIC STAGES—The different river substrates (pebbles, vegetation, fallen leaves) were sampled using a submerged net laid downstream. Aquatic stages were also collected directly on the substrates. All substrate types were sampled thoroughly. In many cases the larval stages of various aquatic insects are known, and this technique complements and augments species collection by light traps. It was the only effective method for capturing Simuliidae.

Results

The collections made during the survey of the RNI d'Andringitra were sorted and sent to numerous specialists. Definitive results for numerous groups are not yet available, and the following results are far from complete for all aquatic insects. Descriptions of numerous new genera and species will be published elsewhere.

In general our current knowledge of the species limits and geographical distribution of all aquatic insects is too imprecise for us to present a general review of the endemicity and ecological requirements of this group. Herein we concentrate on three groups that we studied: Diptera (Simuliidae), Ephemeroptera, and Trichoptera.

Diptera: Simuliidae

Simuliidae females in the imaginal stage are hematophagous, whereas males are floricolous. Larvae live in well-oxygenated water. The identification of the *Simulium* species was relatively easy with pupae, particularly using characters associated with the form and the number of gill filaments. The identification of larvae and adults to species level is more difficult; these life stages are seldom captured.

Nine *Simulium* species were identified from the 15 stations. Among these nine species, four were previously described (*Simulium gyas, S. pentacer-*

os, S. iphias, and *S. imerinae*), although the *S. iphias* is problematical and may comprise four distinct species (see below). Two species are new to science and are known only from the Andringitra Massif (*S. metecontae* n. sp. and *S. brunhesi* n. sp.) (see Chapter 11).

Within our material of *Simulium iphias* from the Andringitra Massif there are several morphological species, each of which is distinguishable from the others by its number of pupal gill filaments (herein filaments are designated "f"), and each of which apparently lives in unique ecological conditions. Four *Simulium iphias* s.s.l. morphospecies are recognized from the reserve: *S. iphias* 8f, *S. iphias* 10f, *S. iphias* 15f, and *S. iphias* 19f.

Distribution of *Simulium* in the Andringitra Area

Species found on the eastern slopes of the reserve included *S. metecontae* n. sp., *S. iphias* 10f, *S. pentaceros,* and *S. gyas*; those on the western slopes included *S. brunhesi* n. sp., *S. imerinae, S. iphias* 8f, *S. iphias* 15f, and *S. iphias* 19f. No *Simulium* species occurring in the forested areas along the eastern slopes was found on the western side of the reserve; species within this genus thus appear to have relatively strict ecological requirements (Fig. 9-1).

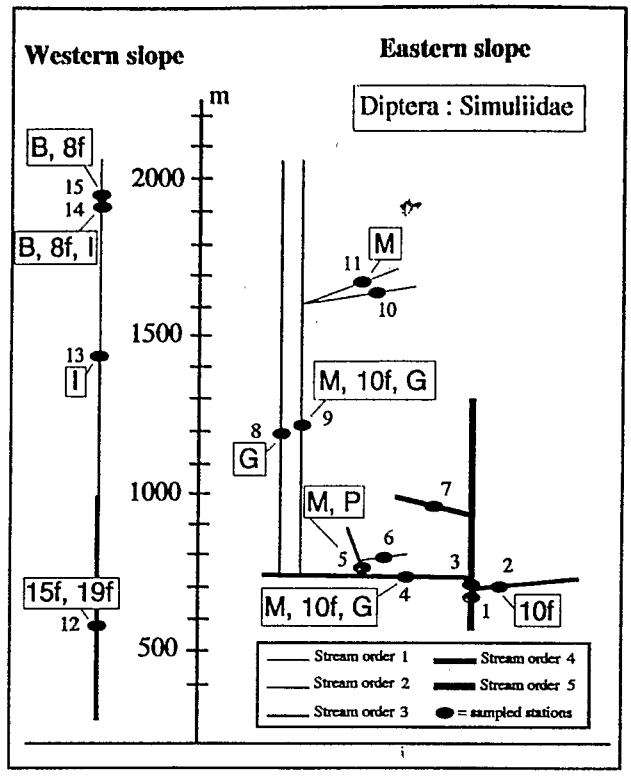

FIG. 9-1. Altitudinal distribution of *Simulium* in the RNI d'Andringitra on the basis of 11 sites on the eastern slopes and four sites on the western slopes. Key to species: I = *Simulium imerinae,* B = *S. brunhesi,* G = *S. gyas,* M = *S. metecontae,* P = *S. pentaceros,* 8f = *S. iphias* with eight filaments, 10f = *S. iphias* with 10 filaments, 15f = *S. iphias* with 15 filaments, and 19f = *S. iphias* with 19 filaments.

Eastern Slope *Simulium*

Simulium iphias 10f—This form was collected at stations 2, 4, and 9, of stream order 3, 4, and 5 (not respective). It was not found at stations 3 and 8. Stations 2, 4, and 9 had mean water flow ranging between 0.7 and 1.5 m/s. In contrast, water flow was slower at sampling stations 3 and 8.

This species occurs all along the eastern coast of Madagascar, in small rivers running through zones of primary or degraded forest. It is absent from rivers and streams in completely degraded zones.

Simulium metecontae n.sp.—This species is currently only known from the Andringitra Massif (see Chapter 11). It was first encountered in the 820 m zone at the four stations (4, 5, 9, and 11) on rivers of stream order 1, 3, and 4. Altitude and stream order may be critical parameters for the distribution of this species. Indeed, water flow is relatively slow for stations 6, 8, and 10, where this species was not collected.

Simulium pentaceros—This species was found only at station 5. It is an infrequently collected species of *Simulium,* although it is also known from two forested rivers near Ranomafana, Ifanadiana. It is difficult to make any general statements on its ecology. However, the two rivers near Ranomafana are of the same stream order as station 5 and at about 850 m.

Simulium gyas—This species was found at three stations (4, 8, and 9) of stream order 4 and 3, but not at station 5. *S. gyas* is broadly distributed along the eastern coast from Antsiranana to Tolagnaro in small to medium-sized rivers running through primary or degraded forest. It has a broad elevational distribution.

Western Slope *Simulium*

Simulium iphias 8f—This species was collected at stations 14 and 15, located on the high plateau

of the Andringitra Massif. The only other known record of this form is from the Ankaratra Massif, at the level of the source of the Sisaony River (1800 m). It is a *Simulium* of high altitude and open zones.

Simulium brunhesi n.sp.—This species is currently known only from the ericaceous savannah of the RNI d'Andringitra (see Chapter 11). It presumably will be found at other high mountain sites on the island with similar habitats (e.g., Tsaratanana and Ankaratra).

Simulium imerinae—This species was collected at stations 13 and 14, along the Zomandao River and above 1300 m. It has been previously recorded in numerous highland and foothill areas in the southern and eastern portions of the island. This species prefers small brooks running across flagstone, with water flow of 1.2–2 m/s.

Simulium iphias 15f—This species was found only at station 12, on the western slope. It has previously been collected in foothill areas in the southern and western parts of Madagascar from the Mandrare River to the Betsiboka River.

Simulium iphias 19f—As with *S. iphias* 15f, *S. iphias* 19f was collected only at station 12. It inhabits areas with rapids on large highland rivers. Ankaramena is the lowest altitude at which it has been recorded. The cold waters of the RNI d'Andringitra may account for its low altitudinal distribution.

Conclusions—Simuliidae

The eastern and western slopes of the RNI d'Andringitra are inhabited by different species of *Simulium*. Water temperature and aquatic vegetation (nutrients) are known to be important variables accounting for these differences. Adult female *Simulium* are hematophagous, and their feeding regimens may be strict and dependent on specific hosts (e.g., batrachians, reptiles, and mammals), perhaps at the family, genus, or species levels. Thus, local extirpation of vertebrates associated with deforestation may have a profound effect on the distribution of *Simulium*. The aquatic habitat of larvae and pupae may be only one of the distribution parameters for *Simulium* species.

Species diversity is greatest in medium to large rivers on both the eastern and western slopes of the massif, particularly in waters of stream orders 2, 3, and 4. The extreme stream orders 1 and 5 are inhabited by only one *Simulium* species. In our sampling of *Simulium* in the RNI d'Andringitra, five species were found on the western slopes and four species on the eastern slopes. A single species new to science was found on each slope.

On the basis of variables associated with sampling stations (Table 9-1), it is difficult to state precisely what effects altitude and stream order have on *Simulium* distribution, because small and cold water bodies are located at the highest altitudes, and there is no large high-mountain river on the Andringitra Massif.

Ephemeroptera

Little is known about this order of insects in Madagascar (Demoulin, 1970). We are in the process of conducting inventories around the island. Many species were collected in the RNI d'Andringitra, the majority of which are new to science and are currently being studied by several specialists. Two familiés are considered here, Euthyplociidae and Leptophlebiidae. It is important to remember that the standard emergence period for most mayflies is usually at the end of the rainy season (April and May), and that the Andringitra field trip was during the month of November.

Euthyplociidae

Only one genus of this family has been recorded from Madagascar (*Proboscidoplocia* Demoulin, 1966). Until recently, this genus was thought to be monospecific, represented by *Proboscidoplocia sikorai* (Vayssière, 1895).

Extensive studies are being jointly carried out by the Laboratoire de Recherche sur les Systèmes Aquatiques et leur Environnement (LRSAE), Antananarivo, and the Musée Cantonnal de Zoologie de Lausanne. This research has shown that at least 10 *Proboscidoplocia* species occur on Madagascar (Elouard et al., unpublished data). Among these 10 species, three are known from the Andringitra Massif: *Proboscidoplocia sikorai* sensu stricto (s.s.) (stations 1, 4, 5, and 6); *Proboscidoplocia vayssieri* n. sp. (Elouard & Sartori, in press) (station 9); and a third species, recorded only at station 4, known only from females, and identified by eggs. The *P. sikorai* s.s. and *P. vayssieri* n. sp. are easily distinguished by the shape of male genitalia. *Proboscidoplocia* pupae live under rocks in permanent water and were captured with deep nets placed under rocks. Imagos

were caught by evening light traps. Most Ephemeroidea appear in masses a few days per year. The November Andringitra mission coincided with one of these synchronous emergences. Specimens of males and females were captured at several stations.

Distribution of Euthyplociidae in the RNI d'Andringitra

Proboscidoplocia were collected only on eastern rivers (Fig. 9-2). The distribution of *P. sikorai* s.s. appears to be independent of stream order and forest cover. This species occurs in rivers of stream orders 5 and 2, passing through degraded and primary forest. Altitude appears to be a major factor for the separation of these two species, which are not elevationally sympatric on the massif. Differences in elevation are related to water temperatures. No *Proboscidoplocia* adults or pupae were found in the 1625 m zone (stations 10 and 11), although these sites were thoroughly inspected. At this time it is impossible to affirm that their absence from the upper forest zone of the mountain is related to stream order or altitude. *Proboscidoplocia sikorai* s.s.d. has been recorded in the RNI de Marojejy (Fontaine, 1968), although no information is available on stream order.

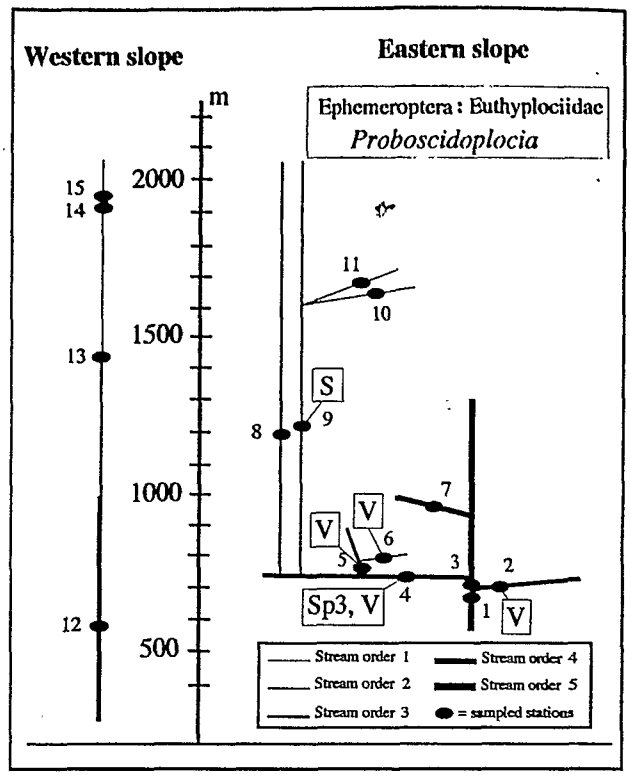

FIG. 9-2. Altitudinal distribution of *Proboscidoplocia* in the RNI d'Andringitra on the basis of 11 sites on the eastern slopes and four sites on the western slopes. Key to species: V = *Proboscidoplocia vayssieri*, S = *P. sikorai*, and Sp3 = *P.* sp. 3.

Leptophlebiidae

Only five species of Leptophlebiidae are described from Madagascar. Two are known from the nymphal stage and three as imagos. On the basis of our recent collections from numerous sites and systematic studies at LRSAE, there are more than 50 species occurring on the island. This family is essentially forest-dwelling. One specialist, W. L. Peters, is carrying out an extensive systematic revision of this family in Madagascar.

Twelve species of Leptophlebiidae were collected on the Andringitra Massif, 11 of which are new to science. We have classified these 12 taxa as subimaginal and imaginal morphospecies. The only named species is *Nesophlebia adusta* Peters and Edmunds, 1964, which is referred to here as Lepto-Q.

Eastern Slope Leptophlebiidae

Eleven species were collected along the eastern slopes of the RNI d'Andringitra. It is difficult to give precise details of habitat preferences of the various morphospecies on the basis of variables associated with collection stations. In general, only the following statements can be made: (1) At stations 1 and 5, five species were obtained at each station, and the species assemblages were totally different from one another. (2) No imago Leptophlebiidae was collected in the 1625 m zone (stations 10 and 11), although indeterminate larvae belonging to this family were found on these two small tributaries. The low nymphal densities unquestionably account for the absence of adults. (3) Lepto-P, Lepto-N, Lepto-S, and Lepto-AA were found only in the Iantara River. Stream order may be a critical parameter in the distribution of these species. (4) *Nesophlebia adusta* (Lepto-Q) occurs in both the Iantara River (station 1) and one of its small tributaries (1210 m, station 9). For this species, stream order is of least importance in the stock range established in the RNI d'Andringitra. Although this species was not collected at stations 2, 3, 4, and 5, its absence at these stations is not proven. Once again, density and emergence periods may account for their local absence at these sites. (5) Lepto-Y, Lepto-W, and Lepto-Z were found at three stations of sim-

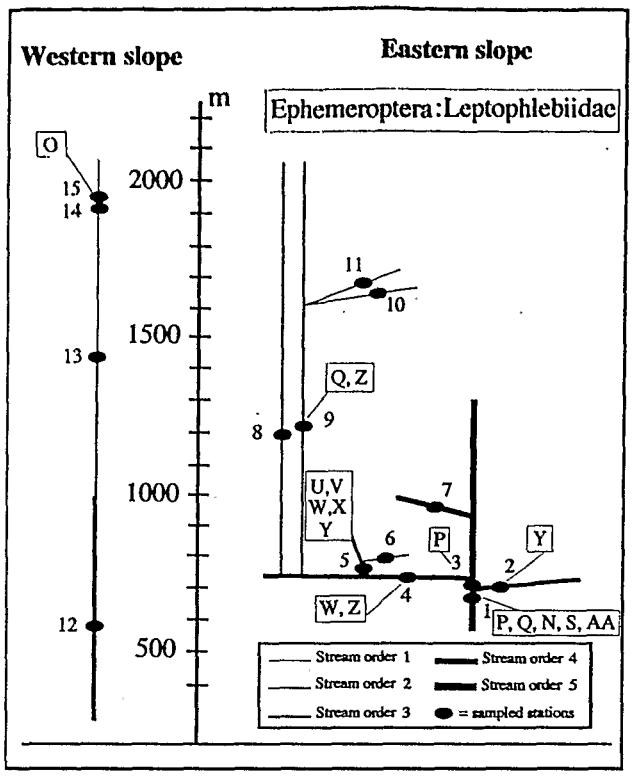

FIG. 9-3. Altitudinal distribution of Ephemeroptera: Leptophlebiidae in the RNI d'Andringitra on the basis of 11 sites on the eastern slopes and four sites on the western slopes. Key to species: AA = Lepto-AA, N = Lepto-N, O = Lepto-O, etc.

ilar stream order. (6) Lepto-U and Lepto-V occurred only at station 5.

Western Slope Leptophlebiidae

Only one species, Lepto-O, was collected along the western slopes of the RNI d'Andringitra, thus supporting the idea that this family is largely forest-dwelling. At station 12, three Leptophlebiidae subimagos were collected. At this development stage there are no clear characters for morphospecies determination. These three subimagos appear to be different from subimagos obtained on the eastern slopes and from station 15. On the basis of current information, Lepto-O is known only from the high plateau ericaceous savannah of the RNI d'Andringitra, where it is presumably endemic.

Other Ephemeroptera Species

Among the other Ephemeroptera species collected during the 1993 mission to the RNI d'Andringitra and currently under study by specialists are: (1) Several Baetidae (> 25 species). (2) One Ephemerellidae species. This family lives in cold waters with aquatic vegetation, and it is practically unknown in Africa. Only three species are recorded from South Africa (Demoulin, 1970). In Madagascar, only one specimen was previously known, a larva identified as belonging to the genus *Ephemerella* (*Eurylophella*); this identification may be incorrect. The shape of the nymph and the genitalia of the imago belong to Ephemerellidae and not Telagodinae. In the RNI d'Andringitra we were able to collect all developmental stages of a mayfly that does not correspond to *Ephemerella.* The RNI d'Andringitra material unquestionably belongs to an undescribed genus. (3) Larvae of Trichorthidae, but no imago. (4) Larvae and adults of Prosopistomatidae that are probably referable to *Prosopistoma variegatum.* In view of the poor original description of this species, however, examination of the holotype is needed to confirm this identification. Unfortunately, it appears that the holotype is lost. (5) Heptageniidae (see Chapter 10).

Conclusions—Mayflies

More than 40 species of mayflies were collected during the Andringitra mission. The great bulk of these species are new to science and have been distributed to specialists for study. These descriptions will be published in due course. The RNI d'Andringitra material will be used in the broad context of an island-wide survey of the aquatic insects of Malagasy rivers, with specific reference to speciation and ecological preferences.

The order Ephemeroptera is a good indicator of environmental conditions. However, the imaginal sampling of this group is seasonal, and imagos have a short existence, in general less than 1 day. Furthermore, emergence of most mayfly families on Madagascar is synchronous. Nevertheless, the presence of pupae in rivers is constant, and their collection can provide species identifications in most cases. Few associations between larvae and adults, however, are known. Rearing of larvae is critical in determining the life history stages of each species, and this fieldwork is time-consuming.

Trichoptera

The families and genera collected during this study were Hydropsychidae: *Macrostemum, Cheu-*

TABLE 9-2. Distribution of Leptophlebiidae in the RNI d'Andringitra (see Fig. 9-3).

	Eastern stations									Western stations			
Species	1	2	3	4	5	7	9	10	11	12	13	14	15
Lepto-P	+		+			Rain							
Lepto-Q	+					Rain	+						
Lepto-N	+					Rain							
Lepto-S	+					Rain							
Lepto-AA	+					Rain							
Lepto-Y		+			+	Rain							
Lepto-U					+	Rain							
Lepto-V					+	Rain							
Lepto-W				+	+	Rain							
Lepto-X					+	Rain							
Lepto-Z				+		Rain	+						
Lepto-O						Rain							+

matopsyche, and *Leptonema*; Hydroptilidae: *Hydroptila, Orthotrichia,* and *Oxyethira*; Philopotamidae: *Chimarra, Dolophilodes,* and *Paulianodes*; Ecnomidae: *Psychomyiellodes*; Pisuliidae: *Pisulia*; Lepidostomatidae: *Goerodes*; Polycentropodidae: *Paranyctionphylax* and *Pseudoneureclipsis*; and Leptoceridae: *Adicella, Oecetis, Trianodes, Setodes, Leptocerus,* and *Athripsodini.*

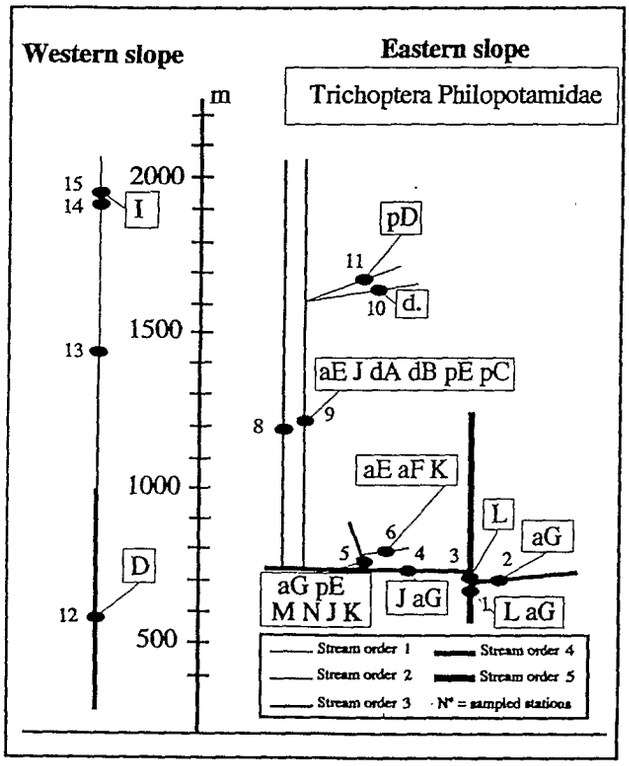

FIG. 9-4. Altitudinal distribution of Trichoptera: Philopotamidae in the RNI d'Andringitra on the basis of 11 sites on the eastern slopes and four sites on the western slopes. Key to species: I = *Chimarra* sp. I; D = *Chimarra* sp. AH, sp. D, and sp. E; pD = *Paulianodes* sp. D; pC = *Paulianodes* sp. C; pE = *Paulianodes* sp. E; aG = *Chimarra* sp. AG; L = *Chimarra* sp. L; aE = *Chimarra* sp. AE; M = *Chimarra* sp. M; N = *Chimarra* sp. N; J = *Chimarra* sp. J; aF = *Chimarra* sp. AF; dA = *Dolophilodes* sp. A; dB = *Dolophilodes* sp. B; d. = *Dolophilodes* sp.; and K = *Chimarra* sp. K.

On the large rivers, the caddisfly populations are dominated by the genus *Macrostemum* and the *Athripsodini* group, the latter remarkable for its high species diversity. We present an analysis of the family Philopotamidae, because this group was captured commonly and its alpha taxonomy is relatively straightforward.

Philopotamidae

Philopotamidae were caught at almost all stations (Fig. 9-4 and Table 9-3). Three genera were identified: *Paulianodes* (three species), *Dolophilodes* (two species), and *Chimarra* (eight species from the forest of the eastern slope and one species on the high plateau at the foot of Pic Boby). Three *Chimarra* species collected on an earlier mission to the region and outside the reserve along the Zomandao River (Mangoky Basin) were taken into consideration in order to compare the eastern and western slopes of the massif.

All of the *Paulianodes, Dolophilodes,* and *Chimarra* species collected are undescribed (Table 9-4). Most species are being studied at the LRSAE, Antananarivo. Some of these taxa are represented in the collections of the Museum National d'Histoire Naturelle (MNHN), Paris; these species will be described by J. Oläh, who kindly communicated his results. This taxonomic information allowed us to identify the species collected during this study and to summarize the available information on their geographical distributions.

TABLE 9-3. Distribution of the Philopotamidae in the RNI d'Andringitra.

Sampling station:	15 (west)	12 (west)	11 (east)	10 (east)	9 (east)	6 (east)	5 (east)	4 (east)	2 (east)	3 (east)	1 (east)
Altitudinal zone (m):	2000	580	1625	1625	1210	810	810	810	720	720	720
Chimarra sp. E	▲	+	+	+	+	+	+	+	+	+	+
Chimarra sp. AH	+	▲	+	+	+	+	+	+	+	+	+
Paulianodes sp. D	+	+	▲	+	+	+	+	+	+	+	+
Dolophilodes sp.	+	+	+	▲	+	+	+	+	+	+	+
Dolophilodes sp. A	+	+	+	+	▲	+	+	+	+	+	+
Dolophilodes sp. B	+	+	+	+	▲	+	+	+	+	+	+
Paulianodes sp. C	+	+	+	+	▲	+	+	+	+	+	+
Chimarra sp. AE	+	+	+	+	▲	▲	+	+	+	+	+
Paulianodes sp. E	+	+	+	+	▲	+	▲	+	+	+	+
Chimarra sp. J	+	+	+	+	▲	+	▲	▲	+	+	+
Chimarra sp. AF	+	+	+	+	+	▲	+	+	+	+	+
Chimarra sp. K	+	+	+	+	+	▲	▲	+	+	+	+
Chimarra sp. M	+	+	+	+	+	+	▲	+	+	+	+
Chimarra sp. N	+	+	+	+	+	+	▲	+	+	+	+
Chimarra sp. AG	+	+	+	+	+	+	▲	▲	▲	+	▲
Chimarra sp. L	+	+	+	+	+	+	+	+	+	▲	▲

Table 9-3 lists the species found within the reserve and the collecting stations.

Conclusions—Caddisflies

The caddisflies show a considerable faunal dissimilarity between the western and eastern slopes of the Andringitra Massif, specifically between the Zomandao River (Mangoky Basin) and the Sahavatoy and Iantara rivers (Manampatrana Basin), respectively. There are some exceptions: at least one *Athripsodini* species, one *Hydroptila* species, and three *Orthotrichia* species occur upstream in both basins. For the Philopotamidae the faunal dissimilarity is complete.

It is interesting to examine this dissimilarity, because there are few available data on the geographical distribution of aquatic insect species in Madagascar. (1) "Open area" species of the western slope—*Chimarra* sp. I, *C.* sp. D, and *C.* sp. E—also occur upstream of the Mandrare Basin (especially on the Mananara River). *Chimarra* sp. AH is one of the most common Trichoptera species known in Madagascar, especially in the southern and western regions. (2) Forest species on the eastern slope—*Chimarra* sp. N, *C.* sp. K, *Paulianodes* sp. D, *P.* sp. C, *P.* sp. E,

TABLE 9-4. List of Philopotamidae species.

Species	Taxonomic status	Proposed name	Material
Paulianodes sp. C	Gibon (in prep.)	*fabienneae*	LRSAE
Paulianodes sp. D	Gibon (in prep.)	*langrandi*	LRSAE
Paulianodes sp. E	Gibon (in prep.)	*goodmani*	LRSAE
Dolophilodes sp. A	Gibon (in prep.)	*andringitra*	LRSAE
Dolophilodes sp. B	Gibon (in prep.)	*sahavatoyae*	LRSAE
Chimarra sp. K	Gibon (in prep.)	*vorombola*	LRSAE
Chimarra sp. N	Gibon (in prep.)	*sahanivorakyae*	LRSAE
Chimarra sp. J	Gibon (in prep.)	*michaeli*	LRSAE
Chimarra sp. L	Gibon (in prep.)	*erici*	LRSAE
Chimarra sp. AE	Olàh (in prep.)	*chatugana*	LRSAE and MNHN
Chimarra sp. AF	Olàh (in prep.)	*nadia*	LRSAE and MNHN
Chimarra sp. AG	Olàh (in prep.)	*watayana*	LRSAE and MNHN
Chimarra sp. M	Olàh (in prep.)	*wigota*	LRSAE and MNHN
Chimarra sp. I	Olàh (in prep.)	*atana*	LRSAE and MNHN
Chimarra sp. D	Gibon (in prep.)	*elatrasoa*	LRSAE
Chimarra sp. E	Gibon (in prep.)	*anadabolava*	LRSAE
Chimarra sp. AH	Olàh (in prep.)	*anka*	LRSAE and MNHN

Dolophilodes sp. A, and *D.* sp. B—are known only from the primary forests of the RNI d'Andringitra. *Chimarra* sp. AF, *C.* sp. AE, *C.* sp. J, and *C.* sp. L are also known from the Namorona Basin in the primary forests of the Parc National de Ranomafana. *Chimarra* sp. AG occurs from the Mandraka River (Mangoro Basin) and the upper Mananara River. *Chimarra* sp. I has been collected from the latter locality. Finally, *Chimarra* sp. M occurs on one tributary of the Mangoro River in the forested area south of Moramanga (Anosibe an'ala).

The "open area" or savannah species are known from other open areas (western and southern Madagascar), whereas "forest species" are known from other forests (eastern Madagascar) or known only from the RNI d'Andringitra. From an ecological point of view, two distinct faunal assemblages are present on the island: a humid forest group and a savannah group. There is probably no endemicity with regard to streams. However, because parameters accounting for the distribution of Philopotamidae (physicochemistry of water, substrates, and nutrition resources) are dependent on the vegetation prevailing around the stream, the effects of the biome are determinant factors. These biogeographical results parallel results from studies conducted on west African *Cheumatopsyche* (Statzner, 1984) and *Chimarra* (Gibon, 1985), and they confirm that the geographical distributions of these lotic insects depend more on vegetation zones or biomes than on stream orders.

A second point associated with the distribution of species on the eastern slopes (see Table 9-4) is that each of the four elevational zones (710, 820, 1210, and 1625 m) appears to have a relatively distinct fauna. The highest sampled zone on the eastern slopes (1625 m) consists only of small streams, where *Paulianodes* sp. D was collected, together with a species belonging to *Dolophilodes.* The torrent at 1210 m is where *Paulianodes* sp. C, *Dolophilodes* sp. A, and *D.* sp. B were found. The zone around 820 m had the highest species diversity, including *Chimarra* sp. AF, *C.* sp. K, *C.* sp. M, and *C.* sp. N. *Chimarra* sp. L was limited to rivers in the 710 m zone. The remaining species were distributed in two zones: between 820 m and 1210 m (*Chimarra* sp. AE, *C.* sp. J, and *Paulianodes* sp. E), and between 710 m and 820 m (*C.* sp. AG).

It is premature to provide precise details on habitat specificity of these Philopotamid species given the period of study and the number of specimens collected. However, our current information shows a clear pattern of altitudinal distribution of the various species that can be divided into "faunal zones" (Table 9-3).

If no endemicity is demonstrated at the level of the lower rivers, then the faunistic changes related to elevational variables would support the idea of local endemicity in the mountainous streams. This hypothesis is supported by the fact that the species collected in the 1210 and 1625 m zones are known only from the Andringitra Massif, whereas the majority of the species collected at lower elevations (710 and 820 m zones) are also known from other forests (Ranomafana, Andohahela, or Moramanga).

The three genera of Philopotamidae occurring on the Andringitra Massif are distinct clades (Ross, 1956). *Paulianodes* is endemic to Madagascar and is a primitive element of the fauna; it has probably been isolated since the beginning of the Cretaceous. On the other hand, the genus *Chimarra,* which is distributed worldwide, has colonized Madagascar in more recent geological time (Miocene). *Dolophilodes* may occupy an intermediary position; its status is still poorly known. It is interesting to note that elements that represent the highest level of endemicity (the subfamily Paulianodinae) and that are among the oldest representatives of the Malagasy fauna are restricted to small, high-altitude tributaries in primary forests. Before this study, the genus *Paulianodes* was only known from one specimen (*P. tsaratananae* Ross, 1956), reported from identical environments on the Tsaratanana Massif. Other species belonging to *Paulianodes* and *Dolophilodes* are being studied at the LRSAE. All of these specimens were caught in intact primary forests (Ranomafana, Andohahela, and Montagne d'Ambre), and each locality has its own species assemblage. This confirms the hypothesis of endemism localized in high mountain areas.

The highest species richness of Philopotamidae (six species) occurs in the intermediary forest streams (station 5 and 9). Small tributaries were probably undersampled because of the method used (light traps). In contrast, the faunas of the larger rivers (Sahavatoy and Iantara) are relatively depauperate. This is due to the combination of steep slopes, frequent torrents, and dramatic increases in water level that disrupt the benthic environment and suppress the diversification of the bank ecosystems.

Other Aquatic Insects

Among the other aquatic insects of relative importance collected during the Andringitra mission are Megaloptera and Plecoptera.

MEGALOPTERA—Several pupae belonging to two species were collected; one was found in the 710, 820, and 1210 m zones and the second at 1625 m. Three Megaloptera species are currently known from Madagascar—*Protosialis afra* Navás 1936, *P. madegasca* Navás 1927, and *Madachaulioda torrentialis* (Paulian, 1951). *Protosialis* spp. are known from the high mountain regions of Tsaratanana and Ankaratra (Paulian, 1951). The two species recorded in Andringitra seem to belong to the genus *Madachaulioda.* At least one of the species is known to science. Because the pupae of other Malagasy species have not yet been described, we could not identify our specimens.

PLECOPTERA—All known Malagasy Plecoptera belong to the genera *Madanemura* and *Tsaranemura* (Paulian, 1951). Three species had been previously described by Paulian (1959): *Madanemura andringitrinsis, M. perrieri,* and *M. descarpentriesi.*

During the sampling of the RNI d'Andringitra, we collected only pupae of Plecoptera between 750 and 1210 m (stations 5 and 9). The specimens collected in 1993 are probably not representative of species described from the massif by Paulian (1959), because all of those taxa were taken either at the base of Pic Boby (within the Sohanihindrano Plateau) or at the peak. In these areas, ranging from 2000 to 2600 m, the vegetation is sclerophyllous forest. Malagasy Plecoptera are known from all the main massifs—Andringitra, Ankaratra, Tsaratanana, and Montagne d'Ambre. In all known cases the species are endemic and represent geographical isolates.

General Conclusions

The results presented in this chapter illustrate the main problem associated with research on tropical invertebrates. The vast majority of species collected during the mission are new to science. The proper study of these undescribed forms takes a considerable amount of time and needs to be integrated in a broad systematic review of the specific group. Moreover, the importance of these data in regard to species conservation can only be determined after extensive fieldwork and collecting in order to gather data on geographical and ecological distribution. This type of information is generally lacking for most new species.

On the basis of the few groups of aquatic insects that we have studied on Madagascar, the following conclusions can be presented: (1) There are clear differences between the faunas found on the eastern slopes, in humid forest, and those on the western slopes, in open savannah. (2) For several groups there is elevational variation in the distribution of various taxa, although the precise parameters giving rise to this pattern (e.g., river substrates, water temperatures, and the importance of the overlapping canopy) are unclear. (3) Open area species from the western slopes generally have a broader geographical distribution than humid forest species. Upstream species have more restricted ranges than downstream species. (4) In the case of Madagascar, elements presenting the greatest level of endemicity (*Paulianodes,* representing a subfamily endemic to the island; Megaloptera; and Plecoptera) are restricted to rivers associated with primary and high-altitude forests.

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