

Chapter 5

A Regional Analysis of Species Associations and Distributions of Two Caddisfly Families (Trichoptera: Hydropsychidae and Philopotamidae) in Southeastern Madagascar

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Abstract

Specimens of the caddisfly (Trichoptera) families Hydropsychidae and Philopotamidae collected in the Réserve Naturelle Intégrale d'Andohahela and surrounding areas are discussed and identified. An examination of the regional distribution of these caddisflies at the species level using correspondence analysis clearly shows a distinct faunal separation between the humid eastern forests and dry western forest habitats.

Résumé

Des récoltes de Trichoptères Hydropsychidae and Philopotamidae, déterminées au niveau de l'espèce, ont été menées au sein de la Réserve Naturelle Intégrale d'Andohahela et à sa périphérie. Le traitement des données au moyen de l'analyse des correspondances met en évidence une nette séparation entre les faunes de l'habitat humide de l'Est et celle colonisant la zone aride de l'Ouest.

Introduction

For the past 6 years a project entitled "Biotypologie et biodiversité des eaux continentales malgaches," jointly run by ORSTOM (Institut Français de Recherche pour le Développement en Coopération) and CNRE (Centre National de Recherche sur l'Environnement), has been actively studying the freshwater faunas of Madagascar. The aim of this work is to understand certain aspects of freshwater organisms living in the river and stream systems of the island, including taxonomy, ecology, distribution, and biotic and abiotic aspects that are related to their biogeography. Taxa that appear to be good indicators of certain

environmental conditions and are easy to collect were chosen for detailed studies. Among these are Trichoptera (Annulipalpia) belonging to the two families Hydropsychidae and Philopotamidae. We have now obtained sufficient collections and distributional information from southeastern Madagascar, including the Réserve Naturelle Intégrale (RNI) d'Andohahela, to present a synthesis of our results. The geographical area is defined by the hydrological basins of the Mandrare, Efaho, Manampanihy, and all small rivers between the Mandrare to the west and the Manampanihy to the north.

Our analysis emphasizes faunistic associations and linked ecological parameters. One of the main factors that we underline is the role of the eastern primary humid forests of the region, particularly the RNI d'Andohahela and surrounding areas.

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Methods

Sites were chosen in order to include the major climatic zones of the region (western and eastern; see Chapters 1 and 2) and the different stream orders. We also tried to work at different altitudes and in different vegetational zones (or soil occupations). Logistic and climatic conditions have sometimes considerably influenced our choice of sites. To date 56 sites have been sampled at least once in southeastern Madagascar. Although the database is by no means complete, it is sufficient to obtain a broad perspective and detect important ecological parameters associated with the distribution of these trichopterans.

The study of Trichoptera at the species level is only possible with adults (especially males, because most females cannot be specifically identified). Generally these insects are captured using a system of light traps of two types—gas and black light. Nets are also used. General trapping methods are described in more detail by Gibon et al. (1994, 1996). Samples are preserved in alcohol (70%).

We have been working on an almost unknown fauna (Gibon & Elouard, 1996), and much of our ecological work depends first on working out the alpha-taxonomical aspects of these organisms. There are two main collections of Malagasy caddisflies. The first is the Institut de Recherche Scientifique de Madagascar (IRSM) collection deposited at the Muséum National d'Histoire Naturelle (MNHN), Paris. J. Oláh (Czarvas, Hungary) is currently working on this first collection, which contains more than 220 species. He has shared his results, allowing us to coordinate taxonomic studies. The second collection is at the Laboratoire de Recherche sur les Systèmes Aquatiques et leur Environnement (LRSAE), Antananarivo, and contains more than 500 species. The morphology of the male genitalia of all species is studied in detail. This technique, which is basically a morpho-species approach, allows us to complete ecological analyses before Latin binomials are available for many of these organisms and in turn to transfer data to conservation managers without having to wait for long-term taxonomic publications.

Information has been installed into the "Bibisoa" database, written at the LRSAE with NOE software (Hertu & Elouard, 1997). Cartography is realized by CartoNOE software (Hertu, 1995). Data were treated by correspondence analysis (CA) (Gauch, 1992) with ADE software written by Chessel and Dolédec.

Results

The following list contains the sites that have been sampled and used in the analysis presented below. For each station (= St) information is given on (1) the code number of the drainage basin (12 = Mandrare, 41 = Manampanihy, 89 = Efafo, 108 = Tarantsy, and 109 = small coastal basins of Manantenina); (2) the name of the nearest locality (when available); (3) the elevation (meters above sea level [masl]); (4) the longitude; (5) the latitude; and (6) names of captured genera and species or morphospecies (Table 5-1).

Sampled Sites

St12-01—Andratina at Imanombo, 213 m, 45°57'32"E, 24°20'20"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*, *Macrostemum scriptum*; *Chimarra* spp. AH, AI, *Chimarra dybowskina*.

St12-03—Mandrare at Anadabolava, 209 m, 46°18'30"E, 24°13'18"S. *Cheumatopsyche* spp. AH, AI, A, L; *Macrostemum adpictum*, *Macrostemum scriptum*, *Macrostemum* spp. C, K; *Potamyia* sp. F; *Chimarra* spp. E, AH, AI, A, C, Y.

St12-04—Unnamed small tributary at Amboanemba, 223 m, 46°27'45"E, 24°40'33"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*; *Chimarra* spp. AH, AI.

St12-06—Mandrare at Ifotaka, 60 m, 46°08'14"E, 24°47'55"S. *Cheumatopsyche* sp. AH.

St12-07—Unnamed small tributary at Berenty, 20 m, 46°18'14"E, 24°59'37"S. *Chimarra* sp. AH.

St12-08—Sambalaly at Talakifeno, 145 m, 46°40'59"E, 24°49'55"S. *Macrostemum adpictum*, *Macrostemum scriptum*; *Chimarra* sp. AH.

St12-09—Imonty at Imonty, 175 m, 46°41'27"E, 24°48'51"S. *Cheumatopsyche* sp. C; *Macrostemum adpictum*; *Chimarra dybowskina*.

St12-10—Mananara at Betanimena, 118 m, 46°39'20"E, 24°48'17"S. *Macrostemum adpictum*, *Macrostemum scriptum*; *Chimarra* spp. AH, AI, D, O.

St12-12—Imonty at Imonty, 500 m, 46°43'18"E, 24°49'03"S. *Chimarra* spp. AH, I, AF, AU, AG; *Paulianodes* sp. A.

St12-14—Sahandrojo at Betenina, 325 m, 46°25'25"E, 24°25'12"S. *Cheumatopsyche* sp.

TABLE 5-1. Taxonomic status of Trichoptera (Hydropsychidae and Philopotamidae) known from southeastern Madagascar

Species	Taxonomic status	Bibliography
<i>Cheumatopsyche</i> sp. A	LRSAE (in prep.)	1
<i>Cheumatopsyche</i> sp. AH	Oläh/LRSAE (in prep.)	1
<i>Cheumatopsyche</i> sp. AI	Oläh/LRSAE (in prep.)	1
<i>Cheumatopsyche</i> sp. AK	Oläh/LRSAE (in prep.)	
<i>Cheumatopsyche</i> sp. AF	LRSAE (in prep.)	
<i>Cheumatopsyche</i> sp. C	LRSAE (in prep.)	
<i>Cheumatopsyche</i> sp. L	LRSAE (in prep.)	
<i>Hydropsyche</i> sp. A	LRSAE (in prep.)	
<i>Leptonema conicum</i>	Flint et al. (1987)	4
<i>Leptonema milae</i>	Sykora (1964)	4
<i>Leptonema madagascariense</i>	Ulmer (1905)	4
<i>Leptonema</i> sp. E	LRSAE (in prep.)	
<i>Leptonema</i> sp. G	LRSAE (in prep.)	
<i>Macrostemum adpictum</i>	Navàs (1935)	
<i>Macrostemum placidum</i>	Navàs (1935)	
<i>Macrostemum scriptum</i>	Rambur (1842)	1
<i>Macrostemum</i> sp. C	LRSAE (in prep.)	
<i>Macrostemum</i> sp. D	LRSAE (in prep.)	
<i>Macrostemum</i> sp. K	LRSAE (in prep.)	
<i>Macrostemum</i> sp. O	LRSAE (in prep.)	
<i>Polymorphanisus guttatus</i>	Navàs (1935)	5
<i>Potamyia</i> sp. E	Oläh/LRSAE (in prep.)	
<i>Potamyia</i> sp. F	Oläh/LRSAE (in prep.)	
<i>Chimarra</i> sp. A	LRSAE (in prep.)	1, 3
<i>Chimarra</i> sp. B	LRSAE (in prep.)	1
<i>Chimarra</i> sp. D	LRSAE (in prep.)	2
<i>Chimarra</i> sp. E	Oläh/LRSAE (in prep.)	2
<i>Chimarra</i> sp. F	LRSAE (in prep.)	
<i>Chimarra</i> sp. G	LRSAE (in prep.)	
<i>Chimarra</i> sp. I	Oläh/LRSAE (in prep.)	2, 3
<i>Chimarra</i> sp. O	LRSAE (in prep.)	3
<i>Chimarra</i> sp. Y	LRSAE (in prep.)	
<i>Chimarra</i> sp. AE	Oläh/LRSAE (in prep.)	2
<i>Chimarra</i> sp. AF	Oläh/LRSAE (in prep.)	2
<i>Chimarra</i> sp. AG	Oläh/LRSAE (in prep.)	2
<i>Chimarra</i> sp. AH	Oläh/LRSAE (in prep.)	1, 2, 3
<i>Chimarra</i> sp. AI	Oläh/LRSAE (in prep.)	3
<i>Chimarra</i> sp. AK	Oläh/LRSAE (in prep.)	1, 3
<i>Chimarra</i> sp. AN	LRSAE (in prep.)	
<i>Chimarra</i> sp. AP	LRSAE (in prep.)	
<i>Chimarra</i> sp. AQ	LRSAE (in prep.)	
<i>Chimarra</i> sp. AS	Oläh/LRSAE (in prep.)	
<i>Chimarra</i> sp. AT	LRSAE (in prep.)	
<i>Chimarra</i> sp. AU	Oläh/LRSAE (in prep.)	
<i>Chimarra</i> sp. AV	Oläh/LRSAE (in prep.)	
<i>Chimarra dybowskina</i>	Navàs (1931)	1, 3
<i>Dolophilodes</i> sp. C	LRSAE (in prep.)	
<i>Paulianodes</i> sp. A	LRSAE (in prep.)	
<i>Paulianodes</i> sp. F	LRSAE (in prep.)	
<i>Paulianodes</i> sp. K	LRSAE (in prep.)	
<i>Wormaldia</i> sp. D	LRSAE (in prep.)	

Key to references: 1, Elouard et al. (1994); 2, Gibon et al. (1996); 3, Gibon and Elouard (1996); 4, Flint et al. (1987); and 5, Barnard (1980).

- AH; *Macrostemum adpictum*; *Chimarra* spp. AH, AI.
- St12-15—Bezavo at Iloty, 525 m, 46°36'32"E, 24°38'10"S. *Cheumatopsyche* spp. AH, A, C; *Macrostemum adpictum*; *Chimarra* spp. AS, AH, AI.
- St12-16—Marotoko upstream of Hazofotsy, 98 m, 46°35'46"E, 24°48'47"S. *Cheumatopsyche* sp. AH, C; *Macrostemum adpictum*; *Chimarra* sp. AH.
- St12-17—Mananara at Hazofotsy, 98 m, 46°35'46"E, 24°48'57"S. *Cheumatopsyche* sp. C; *Macrostemum adpictum*; *Chimarra* sp. AH.
- St12-19—Mananara-Sud near Amboasary, 46 m, 46°26'34"E, 24°51'03"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*.
- St12-20—Marotoko, 2 km north of Mananara, 275 m, 46°38'50"E, 24°44'02"S. *Cheumatopsyche* spp. AH, C; *Macrostemum adpictum*, *Macrostemum scriptum*; *Chimarra* spp. AH, AI.
- St12-21—Tributary of Mananara at Amboanemba, 223 m, 46°27'45"E, 24°40'40"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*; *Chimarra* spp. AH, AI.
- St12-22—Manambolo at 7 km north of Berohanga, 440 m, 46°35'11"E, 24°35'07"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*, *Macrostemum scriptum*; *Chimarra* spp. AS, AH, AI.
- St12-23—Bezavo at Berohanga near Lotibe, 550 m, 46°36'07"E, 24°38'57"S. *Cheumatopsyche* spp. AH, A; *Macrostemum adpictum*, *Macrostemum scriptum*; *Chimarra* spp. AS, AH, AI, AK.
- St12-25—Small tributary of Mandrare between Tranomaro and Tsivory, 280 m, 46°24'25"E, 24°24'27"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*; *Chimarra* spp. AH, AI.
- St12-26—Small unnamed tributary at Tsivory, 324 m, 46°00'21"E, 24°06'43"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*, *Macrostemum scriptum*; *Chimarra* sp. AH.
- St12-27—Sakamamba at Imanombo, 340 m, 45°45'59"E, 24°28'32"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*, *Macrostemum scriptum*; *Chimarra* spp. AH, AI, *Chimarra dybowskina*.
- St12-29—Antalimanga at Besomosoy, 272 m, 46°27'59"E, 24°05'45"S. *Cheumatopsyche* spp. AH, AI, A; *Macrostemum adpictum*; *Chimarra* spp. AH, AI.
- St12-30—Small unnamed tributary near Andaza, 315 m, 46°34'05"E, 24°03'16"S. *Cheumatopsyche* spp. AH, AI, A; *Macrostemum adpictum*, *Macrostemum scriptum*; *Potamyia* sp. F; *Chimarra* spp. AH, AI.
- St12-31—Tributary of Sohitay at Ankazomanga, 430 m, 46°37'23"E, 24°02'37"S. *Cheumatopsyche* spp. AH, A, C; *Macrostemum adpictum*, *Macrostemum scriptum*; *Potamyia* sp. F; *Chimarra* spp. AH, B, O.
- St12-33—Manambolo tributary of Mandrare at Maromby, 345 m, 46°34'39"E, 24°23'36"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*; *Potamyia* sp. F; *Chimarra* spp. AH, AI.
- St12-34—Abetolo tributary at Esira, 400 m, 46°41'07"E, 24°18'00"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*; *Chimarra* spp. AH, AI.
- St12-35—Anatranatra between Esira and Maroasara, 325 m, 46°39'04"E, 24°17'37"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*; *Potamyia* spp. F, *Chimarra* spp. AH, AI, O.
- St12-36—Betroky at Tranomaro, 260 m, 46°28'30"E, 24°35'47"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*; *Chimarra* sp. AH.
- St12-37—Esomony at Esomony, 475 m, 46°37'28"E, 24°30'53"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*; *Chimarra* sp. AH, *Chimarra dybowskina*.
- St12-38—Sakamalio in the RNI d'Andohahela, 750 m, 46°40'56"E, 24°32'07"S. *Cheumatopsyche* spp. AH, A, AF, C; *Leptonema conicum*, *Leptonema* sp. G; *Macrostemum scriptum*; *Potamyia* sp. E; *Chimarra* spp. AS, I, AV, *Chimarra dybowskina*, *Chimarra* sp. AU.
- St12-39—Sakamalio in the RNI d'Andohahela, 725 m, 46°40'49"E, 24°32'13"S. *Cheumatopsyche* sp. A; *Macrostemum adpictum*, *Macrostemum scriptum*; *Potamyia* sp. E; *Chimarra* sp. I, *Chimarra dybowskina*, *Chimarra* sp. AU.
- St41-01—Tributary of Manampanihy at Fenoevo, 72 m, 46°53'39"E, 24°41'00"S. *Macrostemum scriptum*; *Chimarra* spp. AS, AV, AK, *Chimarra dybowskina*, *Chimarra* spp. AF, A, F, G; *Paulianodes* sp. A.
- St41-05—Manampanihy at Manantenina (ferry crossing), 2 m, 47°18'57"E, 24°16'08"S. *Macrostemum scriptum*; *Chimarra* spp. AK, A.
- St41-06—Manampanihy at Enosiary, 98 m, 46°49'19"E, 24°40'37"S. *Cheumatopsyche* sp. A; *Macrostemum placidum*, *Macrostemum*

- scriptum*, *Macrostemum* sp. D; *Potamyia* sp. E; *Chimarra* spp. AH, AN, AQ.
- St41-07—Andranohela at Bevoay, 98 m, 46°49'25"E, 24°40'00"S. *Cheumatopsyche* sp. A; *Macrostemum placidum*, *Macrostemum scriptum*; *Potamyia* sp. E; *Chimarra dybowskina*, *Chimarra* spp. AN, AQ.
- St41-09—Andranohela at camp 1 in the RNI d'Andohahela, 440 m, 46°45'34"E, 24°36'43"S. *Cheumatopsyche* sp. L; *Hydropsyche* sp. A; *Leptonema milae*; *Macrostemum* sp. O; *Polymorphanisus guttatus*; *Chimarra* spp. AH, AP, AG; *Paulianodes* sp. F.
- St41-12—Andranohela at camp 2 in the RNI d'Andohahela, 810 m, 46°44'25"E, 24°35'47"S. *Leptonema milae*; *Macrostemum* sp. O; *Paulianodes* sp. A.
- St41-13—Tributary of Andranohela at camp 2 in the RNI d'Andohahela, ~810 m, 46°44'09"E, 24°35'40"S. *Leptonema* sp. E; *Macrostemum* sp. O.
- St41-15—Andranohela at camp 2 in the RNI d'Andohahela ~810 m, 46°44'19"E, 24°35'33"S. *Leptonema milae*; *Macrostemum* sp. O; *Chimarra* sp. F.
- St89-01—Efaho at Ifarantsa, 20 m, 46°52'12"E, 24°55'37"S. *Cheumatopsyche* spp. A, C; *Macrostemum adpictum*, *Macrostemum placidum*, *Macrostemum scriptum*; *Chimarra* spp. AH, AT.
- St89-02—Efaho at Soanierana, 20 m, 46°52'07"E, 24°48'20"S. *Cheumatopsyche* sp. A; *Macrostemum adpictum*, *Macrostemum scriptum*.
- St89-03—Small unnamed tributary at Ranopiso I Ambany, 45 m, 46°40'23"E, 25°02'13"S. *Cheumatopsyche* sp. AH; *Macrostemum scriptum*; *Chimarra* sp. AH, *Chimarra dybowskina*, *Chimarra* spp. B, O.
- St89-04—Ambahibe at Isaka-Ivondro, 50 m, 46°51'46"E, 24°47'03"S. *Macrostemum scriptum*; *Chimarra* sp. AV, *Chimarra dybowskina*, *Chimarra* sp. A.
- St89-05—Ambahibe at Isaka-Ivondro, 70 m, 46°51'53"E, 24°46'47"S. *Cheumatopsyche* sp. AF; *Leptonema conicum*; *Macrostemum placidum*, *Macrostemum scriptum*; *Potamyia* sp. E; *Chimarra* spp. AH, A, *Chimarra dybowskina*, *Chimarra* sp. O.
- St89-06—Ambahibe in the RNI d'Andohahela, 330 m, 46°51'09"E, 24°45'07"S. *Cheumatopsyche* sp. AK; *Dolophilodes* sp. C; *Paulianodes* spp. A, F; *Wormaldia* sp. D.
- St89-07—Ambahibe in the RNI d'Andohahela, 100 m, 46°51'39"E, 24°46'23"S. *Paulianodes* sp. F.
- St89-08—Ambahibe at Ezoambo, 25 m, 46°51'59"E, 24°49'10"S. *Cheumatopsyche* sp. A; *Macrostemum adpictum*, *Macrostemum placidum*, *Macrostemum scriptum*.
- St89-09—Small unnamed tributary at Manambaro, 20 m, 46°49'35"E, 25°01'27"S. *Macrostemum adpictum*, *Macrostemum scriptum*; *Chimarra* sp. AH.
- St89-10—Antsanira at Ranopiso II Ambony, 100 m, 46°39'30"E, 25°01'27"S. *Macrostemum scriptum*; *Chimarra dybowskina*.
- St89-11—Ambahibe in the RNI d'Andohahela, 200 m, 46°51'07"E, 24°46'17"S. *Paulianodes* spp. F, K.
- St89-12—Small unnamed tributary at Soanierana, 20 m, 46°52'28"E, 25°00'10"S. *Chimarra* sp. AH.
- St89-13—Small unnamed tributary, 120 m, 46°52'11"E, 24°46'38"S. *Macrostemum adpictum*, *Macrostemum placidum*, *Macrostemum scriptum*; *Potamyia* sp. E; *Chimarra* sp. AH, AV, AK, *Chimarra dybowskina*, *Chimarra* sp. O.
- St108-01—Tarantsy at Bevilany, 75 m, 46°35'28"E, 25°00'13"S. *Chimarra* spp. AH, A.
- St108-04—Tarantsy at Antsovela, 20 m, 46°28'12"E, 25°04'47"S. *Chimarra* sp. AH.
- St109-02—Antorendrika at Belavenoka, 20 m, 47°05'02"E, 24°50'18"S. *Chimarra* sp. C.
- St109-04—Anandrano, 12 m, 46°58'53"E, 24°56'43"S. *Chimarra* sp. A.

Information on the stream ecology of each site is presented in Table 5-2. As usual in studies associated with the distribution of organisms on Madagascar, the first major separation of Trichoptera groups falls out according to eastern (humid) and western (dry) habitats. For this reason subsequent analyses have been conducted separately for each habitat type, and also the two trichopteran families have been separated. Four factorial diagrams are presented corresponding to: (1) Hydropsychidae species of the Mandrare and Tarantsy basins plotted according to the 1st and 2nd axes (Fig. 5-1); (2) Philopotamidae species of the Mandrare and Tarantsy basins plotted according to the 1st and 2nd axes (Fig. 5-2); (3) Hydropsychidae species of the eastern basins plotted according to the 3rd and 4th axes (the 1st and 2nd axes isolate, respectively, *Leptonema madagascariense* and *Cheumatopsyche* sp. AK, both of

TABLE 5-2. Various parameters associated with each station sampled.

Station	Altitude (m)	Distance* (km)	Width (m)	Water temperature (°C)	Gallery forest†	Habitat around station
St108-01	75	17	60	20	—	spiny forest
St108-04	20	36	6	25	—	spiny forest
St12-01	213	48	20	21	—	wooded savannah
St12-03	209	110	50	30	—	wooded savannah
St12-04	223	4	0.2	22	—	spiny forest
St12-06	60	210	200	22	—	spiny forest
St12-07	20	235	250	23	—	spiny forest
St12-08	145	8	3	19	—	xerophilous forest
St12-09	175	8.5	10	19	—	steppe
St12-10	118	16	12	19	+	spiny forest
St12-12	500	1	5	17	+	xerophilous forest
St12-14	325	1	1.8	20	—	steppe
St12-15	525	7.5	1.5	20	—	spiny forest
St12-16	98	23	4	19	—	spiny forest
St12-17	98	24.5	6	18	—	spiny forest
St12-19	46	41.5	8	22	—	spiny forest
St12-20	275	11	5	16	—	xerophilous forest
St12-21	223	32	4	16	—	spiny forest
St12-22	440	19	3	16	+	grassland
St12-23	550	6	2	18	+	grassland
St12-25	280	13	0.5	19	—	steppe
St12-26	324	9.5	1	21	—	grassland
St12-27	340	18.5	3	24	—	wooded savannah
St12-29	272	11	0.3	27	—	steppe
St12-30	315	13	12	25	—	steppe
St12-31	430	2	0.1	25	+	steppe
St12-33	345	50	7	25	—	wooded savannah
St12-34	400	9	0.1	27	+	steppe
St12-35	325	21.5	0.4	25	+	steppe
St12-36	260	19	15	24	—	grassland
St12-37	475	3	1	24	+	spiny forest
St12-38	750	3	1	22	+	grassland
St12-39	725	8	12	21	+	grassland
St41-01	72	10.5	5	21	—	grassland
St41-05	2	90	400	25	—	grassland
St41-06	98	18	35	19.5	—	grassland
St41-07	98	17	15	23	—	grassland
St41-09	525	5	15	21	+	primary humid forest
St41-12	850	4.5	10	17	+	primary humid forest
St41-13	925	3.5	4	18	+	primary humid forest
St41-15	900	4	5	18	+	primary humid forest
St89-01	20	27	20	26	—	steppe
St89-02	20	38	200	20	+	spiny bush
St89-03	45	4	2.5	20	+	steppe
St89-04	50	6.5	7	20	+	secondary humid forest
St89-05	70	3.5	5	26	+	secondary humid forest
St89-06	330	3	6.5	16	+	secondary humid forest
St89-07	100	5	4.5	19	+	secondary humid forest
St89-08	25	11	10	20	—	spiny bush
St89-09	20	16	50	17	—	spiny bush
St89-10	100	2	2	20	—	grassland
St89-11	200	1	11.5	16.5	+	secondary humid forest
St89-12	20	33.5	110	17	—	spiny bush
St89-13	120	3	4	24	+	secondary humid forest
St109-02	20	12.5	40	23	—	wooded savannah
St109-04	12	3	10	23.5	—	grassland

See text for explanation of station acronyms.

* Distance refers to estimated or measured distance of sampling site from sources.

† Gallery forest refers to the presence (+) or absence (—) of forest along the banks of the river or stream in the vicinity of the sampling station.

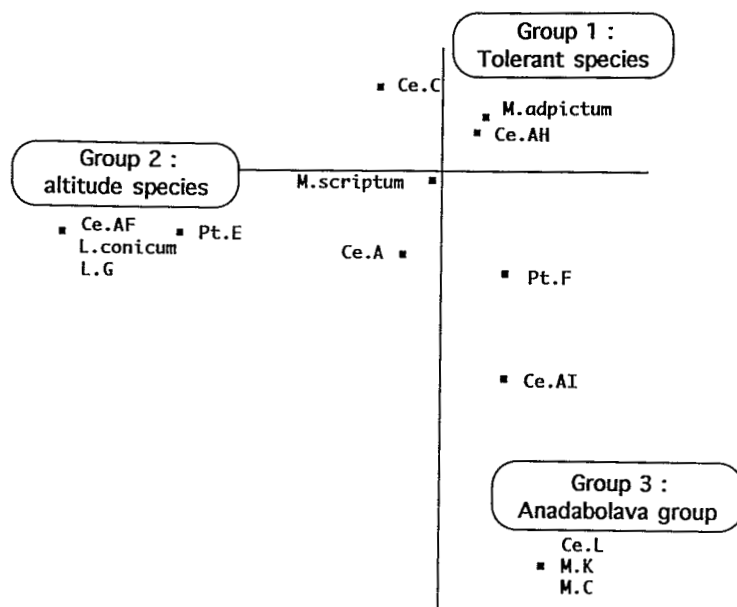


FIG. 5-1. Hydropsychidae species of the Mandrare and Tarantsy basins plotted according to the first and second axes of correspondence analysis. Generic codes: *Ce.* = *Cheumatopsyche*, *H.* = *Hydropsyche*, *Pt.* = *Potamyia*, *M.* = *Macrostemum*, *L.* = *Leptonema*, *Po.* = *Polymorphanius*, *Ci.* = *Chimarra*, *W.* = *Wormaldia*, *D.* = *Dolophilodes*, and *Pl.* = *Paulianodes*.

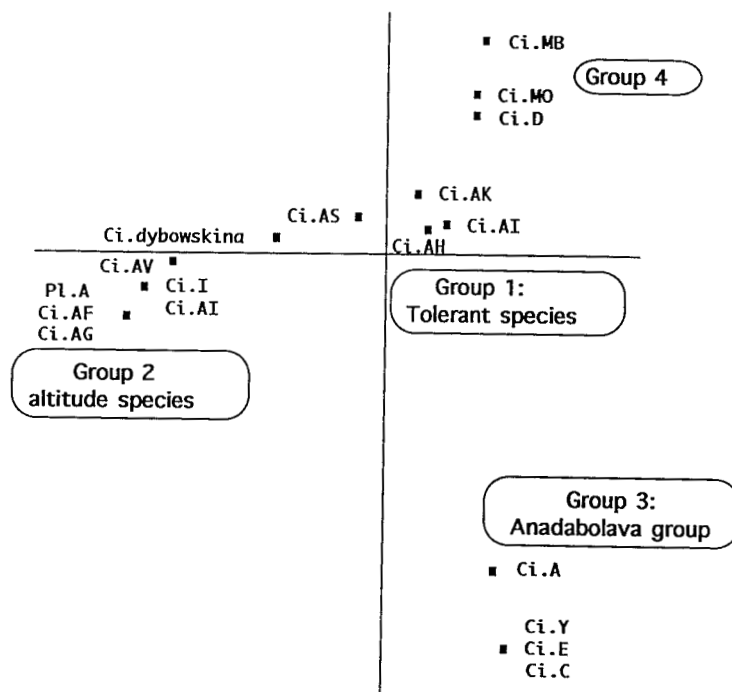


FIG. 5-2. Philopotamidae species of the Mandrare and Tarantsy basins plotted according to the first and second axes of correspondence analysis. For a key to the generic codes, see the legend to Figure 5-1. For species abbreviations see Table 5-1.

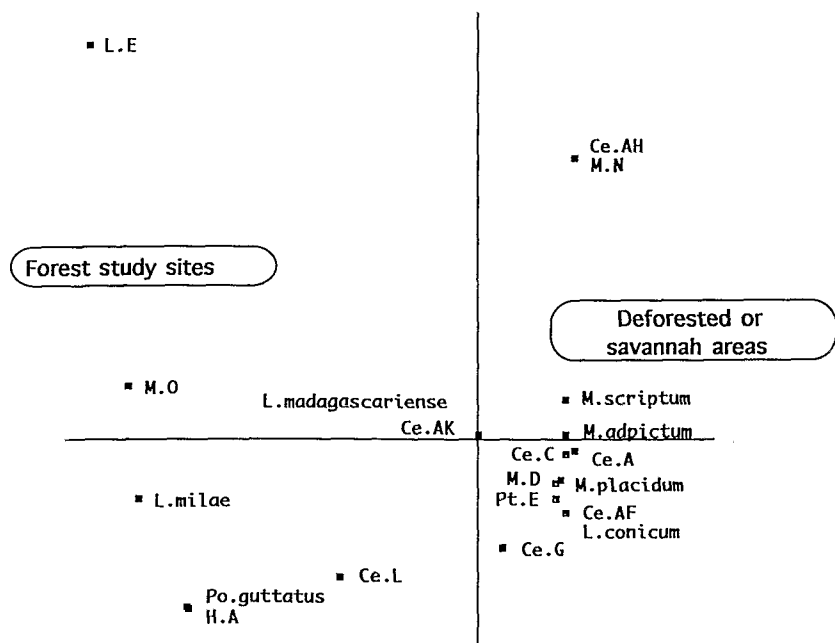


FIG. 5-3. Hydropsychidae species of the eastern basins plotted according to the third and fourth axes of correspondence analysis. For a key to the generic codes see the legend to Figure 5-1. For species abbreviations see Table 5-1.

which were only captured once at stations where no other species occurred) (Fig. 5-3); and (4) Philopotamidae species of eastern basins (from Efaho to Manampanihy) plotted according to the 2nd and 3rd axes (Fig. 5-4) (the 1st axis isolates *Chimarra* sp. C, which was captured only once on a small coastal tributary where no other species occurred).

The geographic distribution of some representative species of Philopotamidae (Fig. 5-5—*Chimarra* spp. and *Paulianodes* spp.) and Hydropsychidae (Fig. 5-6—*Cheumatopsyche* spp., *Macrostemum* spp., *Leptonema*, *Polymorphanisus*, *Hydropsyche*, and *Potamyia*) are presented.

Analysis and Discussion

Hydropsychidae, Western Region

Three groups of species related to three different ecological conditions can be distinguished from the analysis (Fig. 5-1).

The first group (*Macrostemum scriptum*, *M. adpictum*, *Cheumatopsyche* spp. AH and C) is composed of widespread species that are broadly distributed in Madagascar, especially in the western

and central regions of the island; they are able to endure significant variation in water level change between the dry and wet seasons and heavy loads of suspended material. One, two, or more constituting species of this group can be found over the complete scale of stream orders, and nearly across the whole basin (Fig. 5-6). Within the western region there are two localized exceptions that are presented as the second and third groups.

The second group (*Cheumatopsyche* sp. AF, *Leptonema conicum*, and *Leptonema* sp. G) is composed of species captured on the western slopes of Pic Trafonaomby (Fig. 5-6), where several variables, including lower temperatures, higher water velocities, heavier and more regular precipitation, and vegetation along the watercourse, create better ecological conditions for the benthic fauna.

The third group (*Cheumatopsyche* sp. L, *Macrostemum* spp. K and C) was characterized by only one station along a medium-sized stream (Fig. 5-6). This atypical element, called the Anadabolava group (from the name of the nearest locality), occupies a quite peculiar intermediate situation. Upstream, the rivers and their smaller tributaries undergo brutal level variations due to irregularity of rains and associated heavy loads of

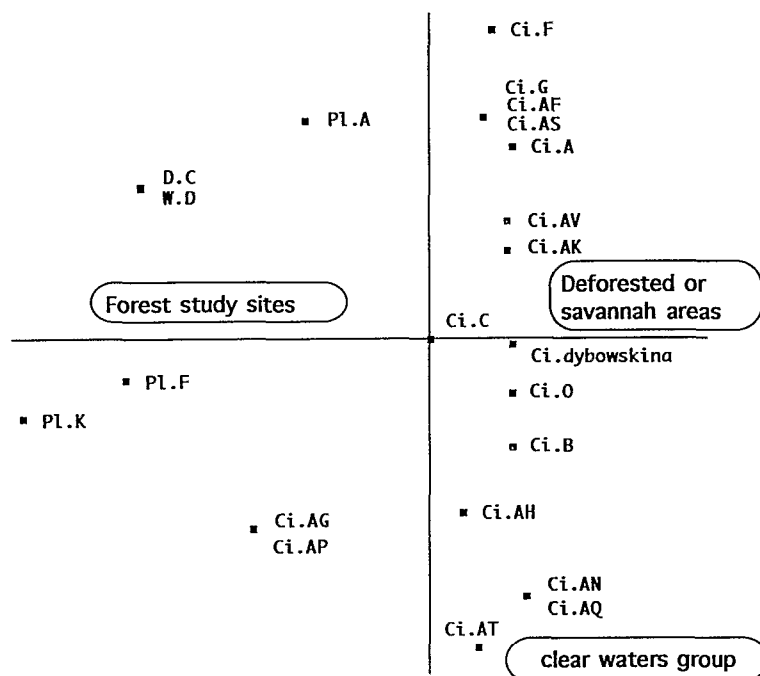


FIG. 5-4. Philopotamidae species of the eastern basins (from Efaho to Manampanihy) plotted according to the second and third axes of correspondence analysis. For a key to the generic codes see the legend to Figure 5-1. For species abbreviations see Table 5-1.

transported sediments. The fauna consists of a group 1 species (*Cheumatopsyche* sp. AH) that appears to be less particular in its habitat requirements. Downstream the river broadens, deepens, and rapids become rare; thus the conditions are less favorable for rheophile species. In the area of Anadabolava a large portion of the coarse suspended matter has already settled, and the river's output is more regular than on smaller tributaries although conditions are not yet really potamic. It is in this habitat that a narrow ecological niche probably exists. The zone described is poorly represented in this study but is suggested by the presence of three species found nowhere else on the Mandrare River.

Philopotamidae, Western Region

This analysis is a little more complicated than the previous one, but the general structure is similar (Fig. 5-2).

The first group is composed of two cosmopolitan and ubiquitous species (*Chimarra* spp. AH and AI). These two species are very tolerant of turbidity and water level variation, and they have

broad distributions, with the exception of the highest altitudes (Fig. 5-5).

The second group is constituted of species found on the higher slopes. These organisms were found on the western slope of Trafonaomby (as for Hydropsychidae) and on the high tributaries of the Mananara River. *Chimarra* sp. AS and *C. dybowskina* constitute a transition group between the two situations.

The third group (*Chimarra* spp. A, Y, C, and E) characterizes the Anadabolava study site (Fig. 5-5); there is a direct parallel to the Hydropsychidae and strong support for the preceding analysis. Three of the Philopotamidae species were found nowhere else during this study on the Mandrare River, and two of them (*Chimarra* spp. V and E) were scarce and probably characteristic of these clear, warm rivers.

The fourth group forms a distinct cluster and is composed of *Chimarra* spp. B, O, and D. On the basis of current information, this group does not have an equivalent among the Hydropsychidae. This atypical association, which is clearly distinguished from *Chimarra* sp. AS and *C. dybowskina*, can nevertheless occur in the same geographical and morphological conditions. Our hy-

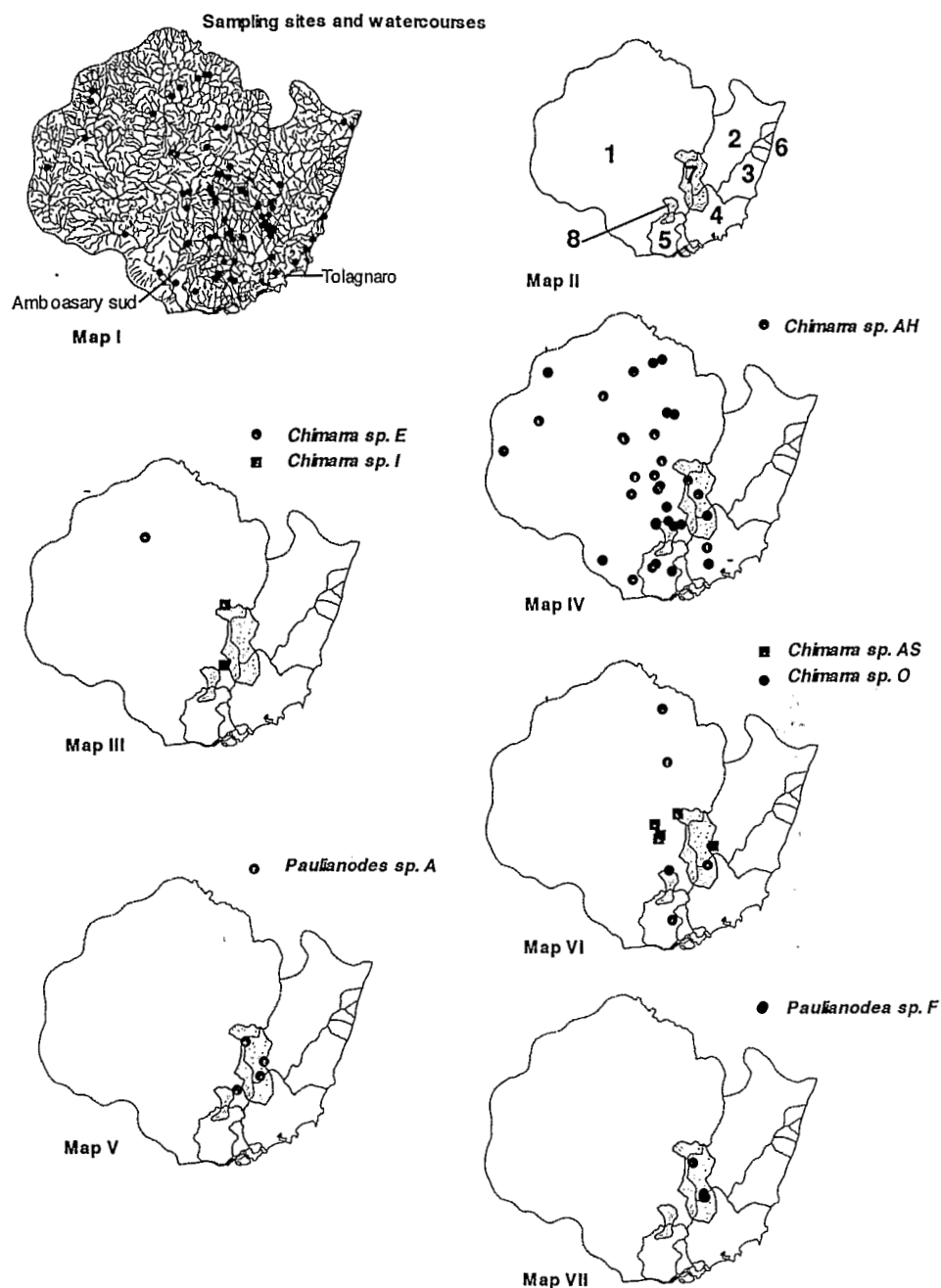


FIG. 5-5. Distributions of some representative species of Philopotamidae. Map I shows the watersheds of the region. Key to localities figured on Map II: 1—Mandrare Basin; 2—Manampanihy Basin; 3—Ebakika Basin; 4—Efaho Basin; 5—Tarantsy Basin; 6—small coastal basins; 7—RNI d'Andohahela (parcel 2); and 8—RNI d'Andohahela (parcel 1). Maps III–VI show the distributions of some representative species of Philopotamidae.

pothesis is that these species occupy sites whose vegetation (not the riparian vegetation, but that of the drainage area) is preserved. This hypothesis is supported by the few available data from other

basins. For example, before this work *Chimarra* sp. B was recorded only from small watercourses in the Zombitse Forest near Sakaraha (Elouard et al., 1994).

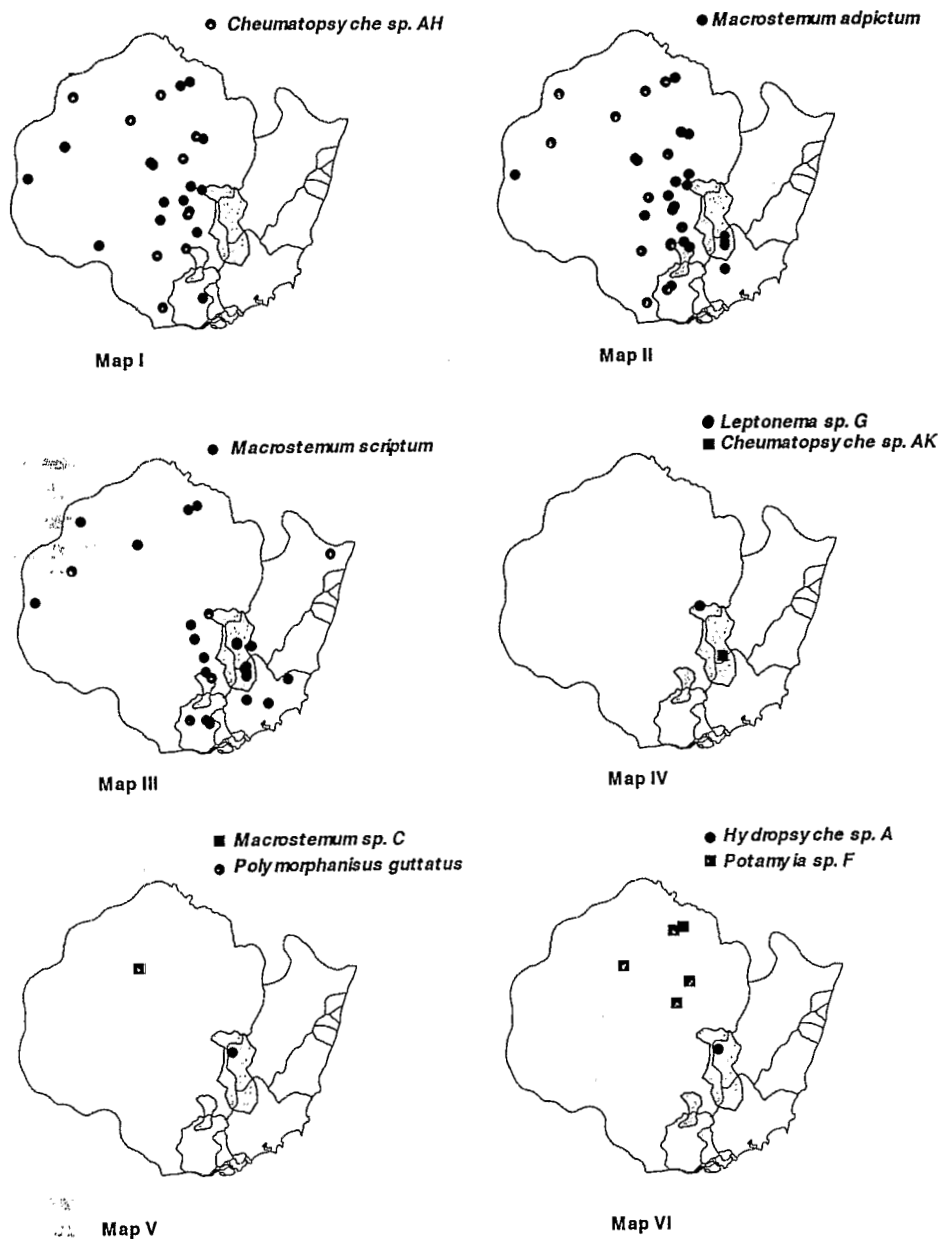


FIG. 5-6. Distributions of some representative species of Hydropsychidae (Maps I-VI).

Hydropsychidae, Eastern Region

The first axis of Figure 5-3 distinguishes two groups:

The first group corresponds to species living in the primary forest zones and the upper tributaries of the Manampanihy River. These species are roughly stratified according to elevation; the sec-

ond axis reflects an altitudinal gradient starting at about 500 m, where the genera *Polymorphanisus* and *Hydropsyche* were captured, and ending at 900 m, where *Leptonema* sp. E was obtained. The data are not extensive, and species richness along these slopes is probably underestimated. Nonetheless there is an altitudinal effect similar to that found on the Andringitra Massif (Gibon et al.,

1996). The significance of this result is fundamental for conservation—the eastern primary forests have an aquatic fauna that is unique and intolerant to changes in vegetational structure.

The second group corresponds to species associated with secondary forest, savannah, or agricultural areas. This fauna includes western species belonging to the first group, some of which penetrate slightly into the eastern area (e.g., *Cheumatopsyche* sp. AH), whereas others are common and broadly distributed (*Macrostemum* spp.). The species separation is based on the same gradient observed in the western region (from *Cheumatopsyche* sp. AH to *Leptonema conicum* and *Cheumatopsyche* sp. AF). The interpretation of this gradient, which is clearly linked with the altitude in the west region, is more ambiguous in the east; most of these sites are located between 50 and 120 m. Apparently, species restricted to high altitudes in the Mandrare Basin can also be found at much lower elevations in the east, where precipitation is more abundant and regular throughout the year. Once again, vegetation seems to play a major role. *Cheumatopsyche* sp. AH occurs in the agricultural coastal plain and *Leptonema conicum* and *Cheumatopsyche* sp. AF occur in grassland and secondary forests.

Philopotamidae, Eastern Region

The results from this group confirm those from the Hydropsychidae, although new aspects of groupings appear that are more difficult to explain.

The first group is fauna of the primary forest. It is in the strict sense a world apart. Within this group each station has a unique fauna. As for the Hydropsychidae, this indicates that the data are probably incomplete and that speciosity is underestimated.

The second group is the fauna of secondary forest, savannah, or agricultural areas. Several of the sites have elements of the western fauna, but data are incomplete because some of the species were collected only once or twice. Furthermore, the environments are very diverse: they include a mosaic of secondary forests, cultivations, meadows, rice fields, etc. Thus, to properly analyze these different habitats, more samples are needed.

Even given these limitations in the data, several points are worth mentioning. Three eastern species (*Chimarra* spp. AN, AQ, and T) in this sample do not occur in the western region. Their oc-

currence is correlated with the presence of forest or with high elevations, but they are apparently associated with relatively clear waters. Our hypothesis is that they are found in savannah with low water turbidity either because they have descended from the upstream forest zone or because the vegetation, although for the greater part grass, is sufficiently dense to bind the soil and avoid erosion. These species are clearly distinguished from *Chimarra* sp. AS or *Chimarra dybowskiana*, both of which are generally associated with waters of high turbidity (e.g., in agricultural areas).

Conclusion

The longitudinal species distribution within hydrographical systems constitutes a fundamental ecological problem, but there are few studies of such situations from tropical zones (see Botosaneanu, 1979, and Malicky & Chantaramunkol, 1993). This near void in information is due to limited systematic studies of invertebrates and a lack of synthetic analyses for the little data that is available. In temperate regions, according to the theory of longitudinal zonation (Illies & Botosaneanu, 1963) or the river continuum concept (Minshall et al., 1985), faunistic transitions exist from the headwaters of rivers to their estuaries.

On the basis of the analysis presented here, the same pattern holds for the hydrological systems of southeastern Madagascar. However, at least two other factors affect the distribution of species or groups of species. The first, which we call the "Anadabolava effect," is a good example of the effect of intermediate human perturbation of the environment. The existence on the Mandrare River of a rich fauna wedged between irregular muddy upstream tributaries and a large homogeneous downstream river is one interesting result of this study. The second is the importance of intact vegetation and intact soil cover in the drainage area. The primary forests of RNI d'Andohahela have a rheophile fauna of Hydropsychidae and Philopotamidae. Local endemism for forest species of these families is very high (Gibon et al., 1996). Deforestation is followed by extreme faunistic changes, with the appearance of species resistant to high levels of suspended matter in the water. Beyond the question of the forest that was the aim of this paper and for which results are well defined, we suspect the existence of a species community inhabiting open ecosystems at low eleva-

tions, but requiring clear waters associated with weakly perturbed areas. This is an interesting topic for future hydrobiological research in the region.

Acknowledgments

The lack of a firm taxonomical basis for the organisms discussed herein is a major obstacle in quickly advancing this line of research. The sampling process is also tedious and often difficult. We are very grateful to those who have contributed and helped in many ways, in particular Fabienne Ranaivoharindriaka, Jean-Marc Elouard, Désiré Randriamasimanana, and Théogène Pilaka. We thank Fred Bastian and Steve Goodman for correcting the manuscript. This is contribution 10 of the "Biotypologie et biodiversité des eaux continentales malgaches" project, run jointly by CNRE and ORSTOM.

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