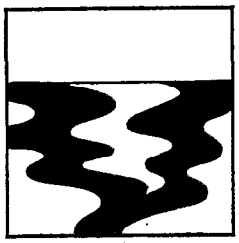

Ecological observations on the caddisflies (Insecta : Trichoptera) from Trinidad and Tobago (W. Indies)

Lazare BOTOSANEANU (1) and Dexter SAKAL (2)

ABSTRACT

The paper presents the ecological results of a campaign of intensive sampling of Trichoptera in a number of localities in Trinidad and Tobago (taxonomic, faunistic, and biogeographic results are published elsewhere [BOTOSANEANU and ALKINS-KOO, in press]). A general review is given of the sampling localities, most of these being in the Northern Range of Trinidad (the "vertebral column" of this study being sampling and observations in the successive stream orders in the catchment of Rio Guanapo), with other sampling localities in Central and South Trinidad, and in Tobago. Autecological notes — but also observations on ethology and trophic guilds — are presented for 42 species (slightly more than 50 species being presently known from the two islands). These results are condensed in a Table in which the succession of species corresponds to a gradient — from species caught only or mainly in springs and in Ist order streams, to those inhabiting Vth order water courses or calm streams of the lowlands. In the final part of the paper are firstly discussed aspects concerning the longitudinal succession (zonation) essentially in the water courses of the Northern Range of Trinidad, the conclusions being that there is a clear-cut limit between Rhithron and Potamon, that diversity and biomasses are highest in III^{d} order and in upper reaches of IVth order streams of densely forested areas, that an association of rather few species inhabits the Crenal and the Epirhithral, and that the fauna is suddenly impoverished starting with the inferior reach of streams of the IVth order; suppositions are advanced concerning the factors responsible for this longitudinal succession; the results are in agreement with the "intermediate — disturbance hypothesis" as applied to lotic ecosystems. Certain regularities have been observed in the distribution of species of Chimarra, Smicridea, *and* Helicopsyche. *Finally, are tackled aspects relative to the distribution of species belonging to the various trophic guilds; our knowledge of trophic peculiarities of caddisfly larvae is often far from perfect, and, in the bibliography, the limits between guilds were too often too rigidly drawn, many species being — or being able to become in certain circumstances — generalists able to exploit several types of resources. All trophic guilds are represented in all stream orders in a Northern Range bassin (there are, nevertheless, also peculiar situations). A conclusion — based on observation of the balance between trophic resources and caddisfly populations development — is that the importance of the trophic factor for the distribution of populations along water courses has probably often been exaggerated. On several points throughout the paper, comparisons are made with the relatively few results already obtained in the West Indies and in Central America.*

KEY WORDS : Trichoptera — Autecology — Zonation — Trophic factor — Trinidad and Tobago — Caribbean — Tropical.

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Résumé

Observations écologiques sur les Trichoptères (Insecta : Trichoptera) de Trinidad et Tobago

Le travail présente les résultats écologiques d'une campagne de récoltes intensives de trichoptères dans un nombre de localités à Trinidad et Tobago (les résultats taxonomiques, faunistiques et biogéographiques sont publiés ailleurs [Botosaneanu and Alkins-Koo, sous presse*]). Un aperçu général est donné des localités où les récoltes ont été réalisées, surtout dans les bassins du Northern Range de Trinidad (la « colonne vertébrale » de cette étude étant représentée par les récoltes et observations dans les « stream orders » successifs du bassin du rio Guanapo), mais aussi au Trinidad central et méridional, et à Tobago. Des notes autécologiques, mais aussi éthologiques et se rapportant à l'appartenance aux « trophic guilds » sont présentées pour 42 espèces (un peu plus de 50 espèces étant actuellement connues pour les deux îles). Ces résultats sont condensés dans un tableau dans lequel la succession des espèces correspond à un gradient — depuis celles capturées uniquement dans des sources ou dans des ruisselets du I^er^ ordre, jusqu'à celles caractérisant les cours d'eau du V^e^ ordre ou bien les ruisseaux calmes des basses altitudes. Dans le chapitre final sont d'abord discutés des aspects ayant trait à la succession longitudinale (zonation) essentiellement dans les cours d'eau du Northern Range de Trinidad, avec la conclusion de l'existence d'une nette limite entre Rhithron et Potamon, d'une diversité et de biomasses maximales dans les ruisseaux du III^e^ ordre et dans le cours supérieur de ceux du IV^e^ ordre des zones densément boisées, d'une association peu riche en espèces peuplant le Crénal et l'Épirhithral, et d'une faune brusquement appauvrie à partir du cours inférieur des ruisseaux du IV^e^ ordre; des suppositions sont avancées concernant les facteurs impliqués dans cette succession longitudinale; les résultats sont en accord avec la « intermediate — disturbance hypothesis » appliquée aux systèmes lotiques. Une certaine régularité a été observée dans la distribution d'espèces appartenant aux genres* Chimarra, Smicridea, *et* Helicopsyche. *Sont enfin abordés des aspects concernant la distribution des espèces appartenant à divers « guildes trophiques »; on attire l'attention sur le fait que notre connaissance des particularités trophiques des larves de Trichoptères est souvent imparfaite, et que, dans la bibliographie, les limites entre « guildes » ont été trop souvent trop rigidement tracées, de nombreuses espèces étant — ou pouvant devenir — des généralistes capables d'exploiter plusieurs types de ressources. Tous les guildes trophiques sont représentés dans tous les* stream orders *dans un bassin du Northern Range, mais cependant des cas particuliers existent. On aboutit à la conclusion — basée sur l'observation des relations entre ressources trophiques et développement de populations de trichoptères — que l'importance du facteur trophique dans la distribution des populations le long des cours d'eau a probablement souvent été exagérée. Sur plusieurs aspects, des comparaisons sont faites avec les résultats peu nombreux obtenus ailleurs aux Antilles ou en Amérique centrale.*

Mots clés : Trichoptères — Autécologie — Zonation — Facteur trophique — Trinidad et Tobago — Caraïbes — Tropical.

INTRODUCTION

In April 1991 the authors (sometimes with others : see Acknowledgements) have intensively sampled Trichoptera in a number of carefully selected localities in Trinidad and Tobago. The results of this mainly taxonomic, faunistic, and biogeographic study — for which also Trinidad and Tobago material in the USNM (Washington) and in the Department of Zoology, University of the W. Indies at St. Augustine was examined — are published in Botosaneanu and Alkins-Koo *(in press)* and the reader may find there also a complete list of localities.

Adults were sampled mainly during the night with a portable UV-lamp, but in some localities, also during the day. It is clear that sampling adults, especially by light, gives a much more accurate idea on the caddisfly fauna of a locality than bottom sampling, enabling also accurate specific identifications. In every locality also the aquatic instars were searched for, picked by hand or with a forceps, observations were made on the populations in their habitats, and the necessary effort was done for obtaining as many as possible correct associations. About 40 species were named in the above mentioned publication (the fauna of Trinidad and Tobago slightly exceeds 50 species in the present state of our knowledge). Some 5 000 "perfect" adult specimens were examined, as well as large numbers of larvae, pupae, "metamorphotypes" and pharate adults.

The Northern Range of Trinidad is an excellent area for study of running water insects. These low mountains (maximum elevations slightly above 900 m, length of the chain ca 75 km) represent the direct continuation of the Coast Range of eastern Venezuela and thus stand as the extreme outpost of the eastern branch of the Andean mountain system; we have here a deeply dissected mountain range with a marked East-West trend, composed of meta-

morphic rocks (BARR et SAUNDERS, 1965). A rather large number of streams arise — sometimes, maybe, at altitudes as high as ca 700-800 m — from the southern slopes of the Range; the length of their catchments is of the order of 10-20 km. Their water is collected in most cases by River Caroni, the main water course of the island, flowing from E to W at the Range's foot. Shorter or much shorter are the streams arising from the N face of the Range, the mountain sloping here directly down to the Coast.

Most of our sampling localities are in the Northern Range, the "vertebral column" of this study being sampling and observations in the watershed of River Guanapo, located in the central part of the Range. Here sampling sites were chosen on Ist and IInd order streams (ca 420-480 m a.s.l.), on R. Guanapo where it is a IIIrd order and an upper reach of a IVth order stream (these two being practically identical from all points of view; at ca 200 m a.s.l.), on R. Guanapo where it becomes a lower reach of a IVth order water course (less than 100 m a.s.l.), and finally in its lowest reach, after confluence with the fundamentally similar River Arima and just before joining R. Caroni (order V; elevation ca 20 m a.s.l.). Streams from order I to upper reach of order IV are practically always under the forest cap, often magnificent rain forest, sometimes secondary forest, including abandoned cocoa estates; their width varies from a few dm for order I to about 3-4 m for order III-upper reach of IV; they are perfectly pristine and clear water courses; in the smallest streamlets the bottom is rocky with some loose stones; in order III — upper reach of order IV streams larger or smaller stones are forming the substrate, and there is alternation of longer riffles with some pools; the current is swift, although the slope cannot be considered as really steep; the water temperature is everywhere ca. 21-22 °C, probably only with slight diurnal and seasonal variation; protection from the forest cover ensures a relatively low degree of exposure to direct sunlight, and an eustatic flow regime — supposedly, even when spates occur they have no devastating effects; despite the low insolation degree, the bioderm on rock and stones is well developped, the most conspicuous element being the colonies of the red alga *Hildenbrandtia rivularis*; there are everywhere large amounts of vegetable material in the stream beds. The lower reach of an order IV water course, like Guanapo, is completely different: the river flows moderately fast through open landscape, although there are riparian trees and bushes; its width is ca. 10 m; the water is still rather clear, and pollution not significant; the river bed is filled with gravel, with some larger stones; on gravel and stones not only a well developed periphyton (high degree of exposition to direct sunlight) but also abundant growth of filamentous algae; the flow regime is very astatic, frequent spates having visible effects on the fauna which may be flushed away in large proportions: our observations in April and July 1991; the temperature varied between 23 and 25 °C during an April day. In an order V river the change is, again, important: about 12 m wide, fairly deep, the very turbid (brownish) water flowing smoothly on a substrate represented mainly by silt, without apparent aquatic vegetation, and between banks covered by grass with sparse trees; the river has here certainly highly astatic thermic and flow regimes; during an April day the water temperature varied between 24 and 27.5 °C. Finally, River Caroni, the main water course of Trinidad, is unfortunately so strongly polluted from the main urban agglomeration of the island, that it is almost certainly a desert for caddisflies.

We have used for this study also material from other water courses of the Northern Range: Blue Bassin, Maracas, Arima, Paria, Cumaca (Oropuche), trying — not always successfully — to determine the respective stream orders. Two sampling stations are just below two waterfalls. Another locality sampled was a rheocrenous spring with madicolous habitats, on the northern coast of Trinidad. Waterfalls and spring enabled us to obtain a broader view on the habitat and faunal spectrum.

It is not easy to find in Central and South Trinidad (which are considered in this paper as "lowlands of Trinidad" despite the fact that here are located the forested hills known as "Central Range" and "Southern Range", with maximum elevations of about 270-300 m) good sampling localities for caddisflies, because — although the map shows many streams — most of them are uninteresting, intermittent, often strongly modified by man and/or polluted (by oil in S. Trinidad). Nevertheless, two "good" streams, slowly running on sandy bottom through secondary forest, were sampled.

The highest hills of Tobago — roughly along the transect Roxborough-Parlatuvier —, covered by a lush primary forest getting down almost to sea level, are feeding rather numerous pristine, larger or smaller streams. Three of them (stream orders probably II-III, one below a waterfall) have enabled excellent sampling, but it is certain that much more effort is necessary to get a correct idea of the caddisfly fauna of this island.

In the present paper we shall present autecological notes on most of the species caught, summarizing these data in Table I. Under "Discussion" will be tackled mainly aspects related to longitudinal (altitudinal) change along the water courses (zonation, trophological aspects). In a few papers on Central America or the Caribbean the question *"what hap-*

TABLE I

Distribution of caddisfly species in the various types of running water in Trinidad and Tobago
Distribution des espèces de Trichoptères dans les différents types d'eaux courantes de Trinidad et Tobago

Column I : left half, springs; right half, smallest streams, orders I and II; mostly in forested areas of mainly higher elevations; roughly : Crenal + Epirhithral. Column II : eustatic, swiftly flowing water courses of IIIrd order, or upper reaches of IVth order, in primary or secondary forest (assimilated are medium-size streams below rather large waterfalls, even if of lower stream order); roughly : Meta + Hyporhithral. Column III : astatic water courses, outside forest cover (left half, lower reaches of IVth order; right half : order V, and — assimilated — smaller, slow streams of lower elevations in Central and S. Trinidad); roughly : (Epi) potamal. The species are arranged according to a gradient, taking into account all available information on their combined frequency and abundance — represented by single, double, or triple stripes. Species not found by us, or underrepresented in our material, are omitted.

Colonne I : partie gauche, sources; partie droite, petits ruisseaux d'ordre I et II; surtout dans les régions forestières et d'altitude élevée; essentiellement Crenal + Epirhithral. Colonne II : cours d'eau eustatiques, rapides, d'ordre III, ou cours supérieurs d'ordre IV en forêt primaire ou secondaire (on inclut ici les cours d'eau de dimension moyenne en aval de chutes importantes, même s'ils sont d'ordre inférieur); domaine Meta- à Hyporhithral. Colonne III : cours d'eau astatiques, hors couverture forestière (à gauche partie aval des cours d'eau d'ordre IV; à droite, ordre V et petits ruisseaux calmes de faible altitude du sud et du centre de Trinidad) : (Epi)potamal. Les espèces sont classées en fonction de leur fréquence et abondance, en ordre croissant de 1 à 3 traits. Les espèces que nous n'avons pas collectées, ou sous-représentées dans nos échantillons, n'ont pas été prises en compte.

pens along water courses?" was asked by the authors : BOON, JUPP and LEE, 1986 ; BUENO SORIA, PADILLA and RIVERA, 1981 ; FLOWERS, 1991 ; HARRISON and RANKIN, 1975, 1976 ; HYNES, 1971 ; MCKILLOP and HARRISON, 1980 ; STARMÜHLNER and THEREZIEN, 1982, 1983 a, 1983 b. These papers strongly differ concerning methodology, group(s) taken into consideration, accuracy and completeness of identifications, philosophy — or absence of philosophy — behind the study.

AUTECOLOGICAL NOTES ON THE SPECIES

Protoptilinae

Protoptila ignera Flint, 1974
Mexitrichia simla Flint, 1974

Despite differences in their distribution (*ignera* in the Northern Range of Trinidad but also in the Tobago hills ; *simla* found only in the Northern Range) they have generally the same distribution pattern and are often found together. Are not inhabited (or, maybe, inhabited only exceptionally and in very small populations) the smallest water courses : springs, order I and II streamlets ; not inhabited, too, rivers (stream order V) ; but from the upper reach of stream order III to the lower reach of stream order IV they are generally very abundant, the typically "scrapper" larvae carrying their tortoise-shaped cases forming sometimes enormous populations (on stones, in clear, swiftly running water).

Leucotrichiini

Larvae in the last instar of all species live in cases fixed to the stony substrate in swiftly running water (also, for instance, on rocks splashed by water from a waterfall), and can feed only by extending their slender head + thorax from the anterior opening of the case, and grazing on periphyton or gathering FPOM in the immediate vicinity of their location (apparently an intermediate category between scrappers and gatherers). The largest pristine water courses (lower reach of order IV ; order V), as well as the relatively sluggish streams in Central and South Trinidad, do not offer habitats for Leucotrichiini, which are concentrated in smaller water courses (in some localities — IInd and IIIrd order streams — several species may coexist : *Z. anomaloptera* with *L. fairchildi* and *L. inflaticornis* ; *L. limpia* with *L. inflaticornis, L. termitiformis*, and one more *Leucotrichia*).

Zumatrichia anomaloptera Flint, 1968

Distribution in Trinidad and Tobago rather strange : only few localities seem to be inhabited (on some Lesser Antilles this is an extremely common species ! Maybe some competitive exclusion is responsible for this situation ?) but the populations may be very large.

Leucotrichia fairchildi Flint, 1970

Not present either in the smallest, or in the largest (pristine) water courses. Probably prefering rather large streams (order III, upper reach of order IV).

L. limpia Ross, 1944

We have here a clear case of a species inhabiting — in Trinidad — the smallest water courses : springs, streamlets of orders I and II.

L. inflaticornis Botosaneanu, 1993

Found, in Trinidad, in one order II and one order III stream ; possibly intermediate in its requirements between *fairchildi* and *limpia* ?

L. termitiformis Botosaneanu, 1993

Habitats (Trinidad) roughly similar to those of *inflaticornis* (in one case : on rocks splashed by water from a high waterfall).

Two new species belonging to a new hydroptilid genus

Unfortunately, no larva or pupa could be associated with any of these two species.

Sp. 1.

Rather frequent in Trinidad, at least in some cases forming very large populations. Frequents from the smallest water courses (springs, order I streams) to order III streams (never larger ones), maybe with some preference for swiftly running water below waterfalls.

Sp. 2

Found only in Tobago in one locality ; habitat spectrum possibly similar to that of sp. 1.

Hydroptilidae other than Leucotrichiini

The larvae of several of these builders of transportable "purse-like" cases are traditionally reputed as feeding on living filamentous algae ("piercers-suckers") : but is this really *always* so ? Probably *not*. If this is probably true for *Oxyethyra*, and for *some Hydroptila* or *Ochrotrichia*, several others are certainly feeding (also) on diatoms and other microscopic algae scrapped from the substrate (*Neotrichia* is probably in this situation).

Ochrotrichia (O.)

Inhabited are exclusively the smallest and medium-size streams (orders I-III) of the Northern Range, as well as springs.

O. (M.) platigona Botosaneanu, 1993

Has roughly the same distributional pattern as the preceeding species, but was found in the Tobago hills too.

O. (M.) favus Botosaneanu, 1993

Was found only in a Ist order stream. Possibly restricted, in the Trinidad Northern Range, to the smallest water courses.

Neotrichia pequenita Botosaneanu, 1977

This species is, clearly, an inhabitant — in northern Trinidad — of the largest, turbid but more or less pristine water courses (order V), or of the streams southward from the Northern Range, but never of swiftly flowing water courses in the higher mountains. This is in agreement with its presence in the sluggish streams of Barbados.

N. armata Botosaneanu, 1993

Found only (certainly large population) in one swiftly flowing, rocky, relatively large stream below a waterfall, in Tobago.

N. intortigona Botosaneanu, 1993

Found only in one calm streamlet in South Trinidad.

N. lauricornis Malicky, 1980

In Trinidad and Tobago a rather large habitat spectrum characterizes this species (spectrum neither including the smallest water courses, nor the largest pristine ones). Apparently not forming large populations on these islands (the contrary may be true for some Lesser Antilles).

N. unamas Botosaneanu, 1993

From the sampled material a preference results for medium-size, swiftly flowing pristine streams in the Northern Range of Trinidad, as well as in the Tobago hills.

Hydroptila veracruzensis Flint, 1967

This is, everywhere in Trinidad, one of the species abundantly inhabiting the most varied kinds of water courses : from springs and the smallest streamlets, to IVth order streams — but no larger rivers. In some (probably rare) cases it may coexist with the clearly less frequent and abundant *H. grenadensis* Flint, 1968

H. acutissima Botosaneanu, 1993

This species has, roughly, the same ecological spectrum as *veracruzensis*, with which it often coexists. Less often found than *veracruzensis* in Trinidad, it is relatively frequent in streamlets and streams in Tobago.

H. tobaga Botosaneanu, 1993

A typical rhithrobiont in Tobago

Oxyethira (L.) azteca (Mosely, 1937)

O. (L.) tica Holzenthal and Harris, 1992

The first of these two species is considerably more frequent and abundant than the second one. In most localities where is was caught, *tica* is accompanied by *azteca*. Both species are clearly absent from the smallest water courses (springs and madicolous habitats, Ist order streams) and apparently also from Vth order rivers. But a slight tendency is discernable in *tica* towards avoidance of swiftly running water (like streams just below waterfalls, IInd order streamlets) and preference for calm streams of the Trinidad lowlands (where *azteca* was not found, being, instead, extremely abundant in swift streamlets and streams of the Tobago hills).

Philopotamidae, Polycentropodidae, Hydropsychidae

All these belong — with the various types of "fishing nets" of their larvae, turned towards the water current and fastened on rocks, stones, and logs — to the trophic guild of filter feeders adapted for filtering seston.

Wormaldia planae Ross and King, 1956

Typically rhithro-and crenobiont on both islands, this species does not occur downstream from order III-upper reach of order IV streams, being absent also even from small water courses of Central and South Trinidad.

Chimarrhodella tobagoensis Blahnik and Holzenthal, 1992

Apparently an inhabitant of mainly small streams (Tobago).

Chimarra (C.) flinti Bueno Soria, 1985

C. (C.) spangleri Bueno Soria, 1985

C. (C.) caribea Flint, 1968

By far the most frequent and abundant representative of the genus in the Northern Range of Trinidad and in the Tobago hills, *C. flinti* is found

— often in very large populations — in streams especially of the orders III-IV, being absent from springs and Ist order streamlets, as well as from larger, turbid, Vth order rivers. The situation of the two remaining species is probably fundamentally similar, but they are much less frequent and abundant, and not (yet) found in Tobago. Coexistence of two (maybe even three ?) *Chimarra* species in one locality is not infrequent.

Polyplectropus pugiunculatus Botosaneanu, 1993

All known localities are small or medium size, swift, clear streams (orders II-III), either in the Northern Range of Trinidad, or in the Tobago hills.

Leptonema albovirens (Walker, 1852)

Extremely frequent and abundant species in Trinidad and Tobago ; being also one of the two largest caddisflies on the two islands, its contribution to the biomass must be considerable in many localities. Frequents, in the Northern Range of Trinidad and in the hills of Tobago, most not strongly polluted water courses, including Ist order streamlets at one end of the spectrum, and Vth order rivers at the other end (but, of course, no springs or madicolous habitats). Its absence from Central and South Trinidad is either only apparent, or maybe (?) due to exclusion by the following species.

Macrostemum ulmeri (Banks, 1913)

The only known locality is a streamlet in South Trinidad ; it is probably well distributed in the, mostly calm, water courses of the lowlands, South from the Northern Range.

Centromacronema pygmaeum Botosaneanu, 1993

The only specimen of this 3rd species of Macronematine Hydropsychids known from Trinidad, was caught by a spring with madicolous habitats, far from any other water course. This seems to be not simply by chance, and it is possible that we have here the unusual case of an at least crenophile Macronematine.

Smicridea (S.) bivittata (Hagen, 1861)

S. (S.) tobada Flint and Denning, 1989

S. (S.) anomala Flint and Denning, 1989

This case is in some respects similar to that of the *Chimarra* species : one species *(bivittata)* is by far the most frequent and abundant, inhabiting — often in very large populations — especially IIIrd and IVth order streams in the Northern Range of Trinidad and in the Tobago hills, but also the calm water courses of Central and South Trinidad (less often also smaller streamlets of higher zones). Quite different is the situation of *tobada* and *anomala* (and certainly *bulara* Flint and Denning, 1989, too ; this last species not found by us) : not only are they clearly much less frequent and abundant, but they also show a tendency towards smaller, fast flowing water courses (orders I-III) in the Northern Range of Trinidad and in the Tobago hills (*bulara* presently known only from the Northern Range), being never found in the Trinidad lowlands. Several cases of coexistence are presently known : *bivittata* with *tobada*, *tobada* with *anomala*, *bulara* with *anomala* and possibly with *tobada*. The situation of the Trinidad and Tobago *Smicridea* species shows similarity in some respects, and apparent differences in other respects, with that of the four Jamaican congeneric species (Boon, 1988) ; in this publication the importance of microhabitat specialization for the distribution of the various species is stressed ; a similarly thorough study would probably give interesting results in Trinidad and Tobago, too.

Xiphocentron (Antillotrichia) sp. (spp. ?)

The larval galeries of *Xiphocentron* were seen — often in enormous numbers — on rocks, stones, logs, on wet rock surfaces above water level, in almost all localities in Trinidad and Tobago sampled in 1991, with the probable exception of a Vth order river : lowest course of Guanapo River. Unfortunately, no specific identification was possible, no adults having been caught, but only larvae. It may be supposed that during building of their long, sinuate galeries fixed on the substrate and with hemispherical lumen, the larvae actively graze on algae and FPOM.

Leptoceridae

The larvae of at least some *Oecetis* were found to be "true" predators — a trophic category poorly represented in the Trinidad and Tobago caddisfly fauna. *Oecetis avara* (Banks, 1895) is relatively well represented in IIIrd and IVth order streams in the Northern Range of Trinidad (accompanied by a congeneric species in the lower course of order IV streams).

The larvae of *Nectopsyche* belong to another trophic category, being collectors of FPOM and eaters of superior plant tissue (according to our observations : especially grazing on ooze on the surface of dead leaves accumulating near stream banks in slowly running water). The habitat spectrum of *N. gemmoides* Flint, 1981, is remarkably similar to that of *Oecetis avara*, the sampling localities being mostly the same (but this is one of the very few species also

extending downstream to the Vth order of running water). *N. cupreosquamosa* Botosaneanu, 1993, was found in a single locality : lower reach of a IVth order stream.

It is clear that both *Oecetis* and *Nectopsyche* are absent from the smallest water courses. Exactly the opposite is true for *Amphoropsyche multispinosa* Botosaneanu, 1993, exclusively found by a minute Ist order trickle in the Northern Range of Trinidad.

Calamoceratidae

Phylloicus angustior Ulmer, 1905

Supposedly this species, one of the two largest in Trinidad, is quantitatively underrepresented in our samples, no much effort having been done for collecting larvae in the deposits of dead leaves near the banks of streams, and the adults being possibly not attracted in large numbers by artificial light. The larvae not only use large amounts of dead leaves for buildings their conspicuous flat cases, but also for feeding : they are possibly the only typical shredders in Trinidad. Inhabited are streams of IInd, IIIrd, and IVth orders.

Helicopsychidae

Helicopsyche margaritensis Botosaneanu, 1959

H. maculisternum Botosaneanu, 1993

The *Helicopsyche* species — with their typical helicoidal larval and pupal cases — belong to the trophic guild of grazers. *H. margaritensis* is, by far, the most widespread and abundant representative of the genus in the Northern Range of Trinidad, sometimes forming large populations especially in swiftly flowing order III streams; but, being a rather tolerant species, it also inhabits the lower reach of IVth order streams, and the water courses of Central (and certainly South) Trinidad. In contrast, *H. maculisternum* is much less frequent and abundant, and with a tendency towards the upper reaches of water courses, being found not only in IIIrd order streams but also in IInd order streamlets and in a spring with madicolous habitats. Coexistence of the two species is only exceptionally observed.

DISCUSSION

By far the richest association of caddisflies is found in pristine order III + upper reaches of order IV streams, in more or less heavily forested areas (roughly : Meta + Hyporhithral) where certainly also the highest biomasses are attained by many species. In such water courses at least 40 caddisfly species are found in Trinidad and Tobago. In a "good stream" of the Northern Range of Trinidad belonging to this category, at least 21-24 species can coexist (e.g. in the Blue Bassin River, in Maracas River, or in Guanapo River). In similar situations in the Tobago heights (e.g. : Argyll River below the waterfall) 17 species were identified.

In the smallest water courses (roughly : Crenal + Epirhithral) no less than 26 species were found, but most of them are present, too (and often in larger, or much larger, numbers) in order III + upper reach of order IV streams, and sometimes even further downstream. Only 5 species *(Centromacronema pygmaeum, Leucotrichia limpia, Ochrotrichia favus, Amphoropsyche multispinosa, Chimarrhodella tobagoensis)* may be considered — in the present state of our knowledge — as crenobiont and/or epirhithrobiont, and, in the Carribean, this is an interesting category. Maybe some more species belonging to this category will be found in the smallest water courses at elevations higher than 500-600 m.

In the lower reaches of order IV streams, outside the forest cover, the fauna is suddenly impoverished; 15-16 species were found in the reach of River Guanapo belonging to this zone. Moreover, the specific composition is mostly different from that in the upper reaches, and we even have the case of one species found only in such a habitat. Such water courses can be assimilated to the Epipotamal.

If there is somewhere a definite faunal change along the water courses of northern Trinidad, this is clearly between the eustatic order III + upper reach of order IV streams (inhabited, like the streams of lower orders, by a *"tropical warm-adapted montane pseudorhithronic fauna of rain-forested mountains"* : HARRISON and RANKIN, 1976), and the astatic (Epi) Potamal represented by the lower reaches of order IV + order V rivers; this change becomes really dramatic only with order V water courses. This is in agreement with the results in HYNES (1971). Possibly the decisive factors involved here are : faster/slower current speed, depending on higher/lower gradient; substrate (and turbidity) differences correlated with gradient and current speed; and more eustatic/more astatic character of temperature and flow regimes. In order V rivers the fauna is drastically impoverished : only *Leptonema albovirens* and *Nectopsyche gemmoides* were caught — in extremely small numbers — on the banks of the lowest reach of Guanapo River, at Tumpuna Road.

All this is in agreement with the "intermediate-disturbance hypothesis" as applied to lotic ecosystems (WARD and STANFORD, 1983; STANFORD and

WARD, 1983; according to these papers the hypothesis was first formulated by J. H. CONNELL, 1978; *non vidimus*) which predicts that biotic diversity will be greatest in communities subjected to moderate levels of disturbance (like in the middle reaches of a basin, region of greatest environmental heterogeneity), and reduced in stream habitats exposed to severe or frequent disturbances (like lower portions of rivers), as well as in habitats (like headwater reaches) with enhanced evironmental constancy, even if adverse conditions are not apparent.

The numbers of species mentioned above for a Trinidad (Northern Range) river, are clearly higher than those for a water course of the Lesser Antilles, probably similar to those for a greater Antillean island (like Cuba), and clearly lower than those for a river in continental Central America. Such important differences should be taken into account when comparing species richness of insects in tropical and in temperate streams!

In Table I we have assimilated the streams in the lowlands of Central and South Trinidad with the order V rivers — maybe not a wise decision. Anyway, we have found in these streams a strongly impoverished but not uninteresting fauna : *Neotrichia pequenita, N. intortigona, Hydroptila veracruzensis, Oxyethira tica, Macrostemum ulmeri, Smicridea bivittata, Helicopsyche margaritensis.*

As could be expected, there are no striking faunal differences between the various bassins fed by the Northern Range — or at least, between the well developed ones on the southern slopes of this Range (like Blue Bassin River, Maracas River, Arima River, Guanapo River...), most of them in the drainage area of River Caroni. These results are different, for instance, from those in BOON, JUPP and LEE (1986) who found important quantitative differences between two rivers on the opposite slopes of the Blue Mountains of Jamaica, or in FLOWERS (1991) where streams from four different drainage areas in northwestern Panamá were compared with the result that variation among streams within a tropical region is important.

The differences between the Northern Range, on one side, and Central and South Trinidad, on the other side, are very considerable, only a handful of eurytopic species being found in both.

There are, of course, differences between the fauna of the Northern Range of Trinidad, and that of the Tobago heights; these were enumerated in BOTOSANEANU and ALKINS-KOO *(in press)* and certainly have biogeographic — not ecological — reasons.

Should be mentioned here the fact that we have in Trinidad several genera showing a similar pattern in their distribution : one species frequent and abundant in a variety of habitats, and 1, 2, or 3 congeneric species less frequent, less abundant, with more restricted habitat spectrum. This is the case of *Chimarra flinti* versus *C. spangleri* and *C. caribea*; of *Smicridea bivittata* versus *S. tobada, S. anomala,* and *S. bulara*; of *Helicopsyche margaritensis* versus *H. maculisternum.*

Concerning the distribution of representatives of various trophic guilds the following may be said — taking into consideration our imperfect knowledge of the exact trophic habits of the larvae of rather many species, and the fact that, too often in the bibliography, the limits between various "guilds" were certainly too sharply defined, many species belonging, in fact, to more than one guild (we suspect that rather many species are, or may become, generalists able to exploit several types of food, depending on availability of food, life cycle, etc.) and the limit between guilds being in some cases diffuse.

The "typical" predators (i.e. : "free" predators, without a "filtering net") are surprisingly underrepresented, without apparent reason : a genus definitely belonging to this category, *Atopsyche*, could certainly be expected in Trinidad and Tobago but was never found on these islands; the larvae of *Oecetis* are reputed predators, but they apparently do not form really large populations. A category very well represented is that of net-building larvae, filterers-gatherers of living or dead organic material (and certainly also, in some cases, more or less active predators!); here belong all Philopotamidae, Polycentropodidae, Hydropsychidae. A second very well represented category is that of grazers of bioderm (periphyton) and FPOM, either (or mainly) on stones — Protoptilinae, Leucotrichiini, *Xiphocentron, Helicopsyche* — or on dead leaves whose tissues are, too, used as food *(Nectopsyche)*. Some of the Hydroptilidae other than Leucotrichiini are certainly piercers-suckers of living algae (*Oxyethira*; possibly *Hydroptila* and *Ochrotrichia*) but others in this group are probably also — or, maybe, uniquely — scrappers *(Neotrichia)*. The only typical shredder (of CPOM), but a relatively important one from the quantitative point of view, is *Phylloicus.*

From our autecological observations (and from Table I) it is evident that all trophic guilds are represented in water courses of all stream orders — from I to IV — of a Northern Range basin. The very large populations of typical scrappers grazing on periphyton, like *Protoptila ignera, Mexitrichia simla, Helicopsyche margaritensis*, in streams of order III — upper reach of order IV, may appear somewhat surprising because these water courses are mostly in heavily forested areas with relatively low degree of exposure to direct sunlight. We find in the same streams the largest populations of species with net-building larvae, like *Chimarra flinti, Leptonema albo-*

virens, or *Smicridea bivittata*. The Vth order rivers with their extremely impoverished fauna, as well as — at the other extreme of the spectrum — the springs inhabited by a small number of species, are exceptions from the general situation outlined above.

An (empirical, of course, but rather careful) observation of the balance between trophic resources, on one side, and development of caddisfly populations, on the other side, leads us to the conclusion that in the running waters of Trinidad and Tobago — like in those of other Carribean islands — the food resources generally considerably exced the capacity of animals to process them, a very large part of these resources being simply left unused/carried away. A few examples will follow. In all larger streams (order III-upper reach of order IV) running from the southern slopes of the Northern Range through primary or secondary forest, invertebrate populations, periphyton on rocks, stones, and logs, FPOM and CPOM, are offering to the caddisfly fauna an amount of food which apparently very largely exceeds the processing capacity. When leaving the Oropuche Cave inhabited by a large colony of *Steatornis caripensis* (the Guacharo), River Cumaca (basin of R. Oropuche) carries away enormous amounts of dejections of these birds, but there is nothing in the composition of the caddisfly fauna which could lead to the conclusion that this considerable trophic resource is consistently used by aquatic insects. In the lower reach of a IVth order stream like R. Guanapo — outside the forest cover — the growth of filamentous algae on stones is very impressive; moreover the stones are covered by a well developed periphyton, and along the banks there are important accumulations of dead leaves carried from upstream during the frequent spates; and yet the caddisfly fauna found on stones, on the floating banks of filamentous algae, in the piles of dead leaves, was surprisingly sparse (April and July 1991), giving us a definite feeling of under-utilization of trophic resources.

All this would probably remain valid if the *entire* stream fauna would be taken into consideration, and it may be inferred that this situation is far from being characteristical for Trinidad and Tobago, or for the Caribbean islands. The question which arises is : *was not the importance of the trophic factor in the distribution* (or zonation; see — to take examples from the Caribbean — : HARRISON and RANKIN, 1975, 1976) *of animal populations along water courses too strongly stressed and generalized?* We foresee here an exciting field for rigorous research for the future.

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