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Macroinvertebrates of brooks and rivers of Martinique II. The family Leptophlebiidae : systematics, biogeography and ecological distribution [Ephemeroptera]

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Keywords : *Hagenulopsis*, new subspecies, *Terpides*, comparative morphology, ecological distribution, Martinique, French Guiana, chloride cells, conductivity, bioindicators.

Two species belonging to the family Leptophlebiidae occur in Martinique, both new records : *Hagenulopsis traverae marginata* n. ssp. new subspecies of *H. traverae* (Peters, 1971), described from Dominique island, and *Terpides jessiae* Peters & Harrison, 1974, described from St Vincent. Morphology of adults and last-instar larvae of *H. traverae marginata* was compared to *H. traverae traverae* and to *H. guadeloupensis* Hofmann & Peters, 1999, described from Guadeloupe. Only chromatic differences and a variation in the number of cross-veins in anterior wings were visible, according to a gradient Martinique-Dominique-Guadeloupe, an argument rather in favour of three subspecies of the same species.

Larval morphology of *H. traverae marginata* was also compared to *H. minuta* Spieth, 1943 from French Guiana. Among other differential characters, this latter species bears chloride cells on labrum, an adaptation to the very low water conductivity in Guiana. The female imago of *Terpides jessiae*, so far unknown, is described. Morphology of larvae is compared to *T. guyanensis* Demoulin, 1966.

In Martinique, *H. traverae marginata* is replaced downstream by *T. jessiae*, less alticolous and less rheophilic, but clearly more tolerant of anthropic disturbances. *H. traverae marginata* is among the most sensitive lotic bioindicators of Martinique ; but the survival of *T. jessiae*, living only in low elevation streams and rivers, is even more threatened, in particular due to catastrophic agricultural practices. In French Guiana, *Hagenulopsis minuta* and *Terpides guyanensis* (respectively vicariants of the two latter species) are seldom sympatric.

Macroinvertébrés des ruisseaux et rivières de Martinique.
II. La famille des Leptophlebiidae. Systématique, biogéographie et répartition écologique [Ephemeroptera]

Mots clés : *Hagenulopsis*, sous-espèce nouvelle, *Terpides*, morphologie comparée, répartition écologique, Martinique, Guyane Française, cellules à chlorure, conductivité, bioindicateurs.

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La famille des Leptophlebiidae compte deux espèces en Martinique, où elles sont des citations nouvelles : *Hagenulopsis traverae marginata* n. ssp., sous-espèce nouvelle d'*H. traverae* (Peters, 1971) décrite de l'île de la Dominique, et *Terpides jessiae* Peters & Harrison, 1974, décrite de l'île de Saint-Vincent. La morphologie des larves au dernier stade et des adultes d'*H. traverae marginata* est comparée à celle d'*H. traverae traverae* et à celle d'*H. guadeloupensis* Hofmann & Peters, 1999, décrite de l'île de la Guadeloupe. Seules quelques différences chromatiques et une variation du nombre de certaines nervures alaires transverses ont pu être mises en évidence, selon un gradient Martinique-Dominique-Guadeloupe, ce qui peut laisser à penser qu'il s'agit plutôt de trois sous-espèces d'une même espèce. La morphologie des larves a aussi été comparée à celle d'*H. minuta* Spieth, 1943, décrite du Surinam (sur la base de spécimens de Guyane française); les deux espèces se distinguent par plusieurs caractères : en particulier, *H. minuta* est la seule à posséder des cellules à chlorure sur le labre, une adaptation à la très faible conductivité des eaux guyanaises. L'imago femelle de *Terpides jessiae*, inconnue jusqu'ici, est décrite. La morphologie des larves de cette espèce est comparée à celle de *T. guyanensis* Demoulin, 1966.

En Martinique, on observe de l'amont vers l'aval le remplacement d'*H. traverae marginata* par *T. jessiae*, à la valence écologique plus étroite, mais nettement plus tolérante vis à vis des influences humaines. *H. traverae marginata* est l'un des bioindicateurs lotiques les plus sensibles de Martinique ; mais la survie de *T. jessiae*, espèce inféodée aux cours d'eau de basse altitude, est encore plus menacée, en particulier par des pratiques agricoles catastrophiques. En Guyane Française, les deux espèces *Hagenulopsis minuta* et *Terpides guyanensis* (vicariantes des précédentes) ne vivent que rarement en sympatrie.

1. Introduction

The present paper is part of a series devoted to the lotic macroinvertebrates of Martinique island, located over Cancer Tropics (14°25' to 14°53' N, and 60°49' to 61°14' W) at 120 km from Guadeloupe, 40 km from Dominique, 110 km from Saint-Vincent, 2300 km from Florida, 420 km from Venezuela. Coastal length 350 km, area 1090 km^2, length 65 km, and maximum width 35 km. 381,427 inhabitants in 1999.

Two seasons : wet (usually June to November) and dry (December to May). Annual average temperature : 25°C, with only a difference of 3°C between the hottest and the coldest months. Annual rainfall averages about 1500 mm in the Southern region, 3500 to 4500 mm in the middle part of the island, and 6000 mm in the Northern region, over Piton du Carbet and Montagne Pelée.

70 independent rivers flow in Martinique, but many catchments do not exceed 10 km^2, and the rivers are short : maximal length = 33 km (Lézarde river).

Humid tropical forest is present only in the Northern part of the island, and above 1000 m elevation it is replaced by grassland. Water temperature is high everywhere : between 20.0° and 29.7°C all over the territory during our study.

A preliminary account of the program can be found in THOMAS et al. (1997).

The quantitative importance of mayflies in running waters of Martinique, in comparison with the other zoological groups, is considerable. For instance, this order of insects accounted for 14054 individuals over a total of 32509 macroinvertebrates collected and studied in 1996, e.g. 43 % (CESAC report, 1997); or also 45 % of total aquatic insects sampled during the study program carried out in 1994, 1996 and 1999 (LALA 2003).

Two genera of Leptophlebiidae live in Martinique : *Hagenulopsis* and *Terpides*. Their main differential morphological characters are summarized hereafter (Table 1).

	Genus *Hagenulopsis* Ulmer	Genus *Terpides* Demoulin
ADULTS		
Hind wings	Absent	Present (Photo 3)
Tarsal claws	1 hooked, 1 blunt (Fig. 19)	2 hooked (Fig. 43)
First segment of forceps	Widened at mid-length (Figs 23, 24)	Widened at base (Fig. 45)
Penis	Long, rectilinear, slender (Figs 23, 24), hooked inwards near to apex (Fig. 23 a)	Shorter, somewhat conical (Fig. 45), no subapical hook inwards
Female VIIth sternum	Well developed ovipositor (Figs 21, 22)	No protruding ovipositor
Female IXth sternum	Emargination narrow, V-shaped	Emargination broad, rounded (Fig. 44)
LARVAE		
Head	Prognathous (Fig. 2), slightly narrowed anteriorly	Hypognathous (Fig. 25), clearly narrowed anteriorly
Labrum	Sides rounded (Fig. 1) with proximalmost bristles at base	Sides subparallel (Fig. 26) with proximalmost bristles at mid-length
Median lingua of hypopharynx	With lateral and parasagittal processes (Fig. 4)	More rectangular and without such processes (Fig. 29)
Glossae	Not curved over ventrolaterally (Fig. 6)	Curved over ventrolaterally (Fig. 31)
Apical segment of labial palpus	Narrowed distally (Fig. 6)	Rounded distally (Fig. 31)
Hind wingpads	Absent	Present
Forecoxae	Wide apart (Fig. 14)	Contiguous (Fig. 38)
Anterior margin of femur 1	No proximal row of short bristles	1 proximal row of short bristles (Fig.32)
Femora 2 and 3	Wider and curvesided	Rectilinear and parallelsided
Tarsal claws	1 set of denticles progressively longer from base to subapex (Fig. 9)	2 sets of denticles separated by a larger median denticle (Figs 33, 35, 37)
Posterolateral projections on abdominal segments	VI, conspicuous on VII-IX	III-VI or V-VI according to species, and VIII-IX (none on VII)
Posterior marginal denticles on abdominal segments	VII-IX	V-IX
Thorax and abdomen	Main tracheal trunks not pigmented	Main tracheal trunks pigmented
Gills	Bifid, long and slender, tracheae unbranched (Fig. 17)	Bilamellae, lanceolate, tracheae branched (Fig. 42)
Caudal filament and cerci	No lateral rows of dense setae	Lateral rows of dense setae, paddle like

Table 1. Main differential characters between the genera *Hagenulopsis* and *Terpides*.
Tableau 1. Principaux caractères différentiels opposant les genres *Hagenulopsis* et *Terpides*.

2. The genus *Hagenulopsis* Ulmer, 1919

2.1. Introduction

ULMER (1919) established the genus *Hagenulopsis* for the species *diptera*, from Southern Brasil (Santa Catharina), of which only the adults are known. SPIETH (1943) described *H. minuta* from Surinam without illustrations, on the mere basis of one female imago only. Fortunately TRAVER (1946) described from British Guiana the male imago of this latter species, and recently both the adult and larval stages were studied in detail by PETERS & DOMINGUEZ (2001). All other known species within the genus are also neotropical : *H. guadeloupensis* Hofmann & Peters, 1999 (Guadeloupe island); *H. ingens* Lugo-Ortiz & Mc Cafferty, 1996 (Costa Rica); *H. ramosa* Lugo-Ortiz & Mc Cafferty, 1996 (Costa Rica); *H. traverae* (Peters, 1971) (Dominique island).

Only one species of *Hagenulopsis* lives in Martinique. We were able to compare the present material with larvae of the species present in Guadeloupe (C. Bosca and A. Thomas leg.) and also with larvae of the only species found so far in French Guiana (C. Bosca, V. Horeau and A. Thomas leg.).

2.2. *Hagenulopsis traverae marginata* Thomas & Boutonnet n. ssp.: description

a) Last-instar larva

General coloration medium to dark brown dorsally. Long bifid and lanceolate gills.

HEAD

Somewhat flattened and square-shaped, especially in the female, only slightly narrowed forward. Mouthparts prognathous (Fig. 2).

Male compound eyes with upper portion pale brown to reddish brown, and lower portion black. Female eyes black.

Labrum (Fig. 1 t m) : anteromedial emargination with two large denticles and remnants of one to three small denticles (the instability of this character was pointed out by HOFMANN et al. 1999, see fig. 181 a). Dorsally, two submarginal transverse rows of bristles. Fine hairs scattered on dorsal surface and marginally. Ventrally, bristles of external edge becoming longer and stouter forward; the submarginal anterior parasagittal bristles are sharp (d), contrary to *H. minuta* where these bristles are spatulate (Fig. 1 m d').

Right mandible (Fig. 3 R) : basal set of incisors with two main denticles and up to three shorter ones; distal set with three denticles and up to five shorter ones. Prostheca with long setae extending towards mola, some of these setae being pectinate. Fine preapical setae down below the mola. Rows of setae on dorsal surface, and hairs scattered laterally. Numerous chloride cells intermixed laterally with setae.

Left mandible (Fig. 3 L) : basal and distal sets of incisors with three denticles each, and up to four shorter ones. Prostheca with a bifid bristle and some long and sometimes pectinate setae extending towards mola. Rows of setae on dorsal surface, and hairs scattered laterally. Numerous chloride cells are present.

Hypopharynx (Fig. 4) : median linguae with fine hairs and well developed lateral processes. Superlinguae with numerous long, simple setae.

Maxillae (Fig. 5) : numerous chloride cells at base of palps. Segment one short, segment three 1.15 longer than segment two, segment four half the length of segment three. Segment four with long hairs. Galealacinia is wide, with a dense apical tuft of long setae. At base of this latter a sub-

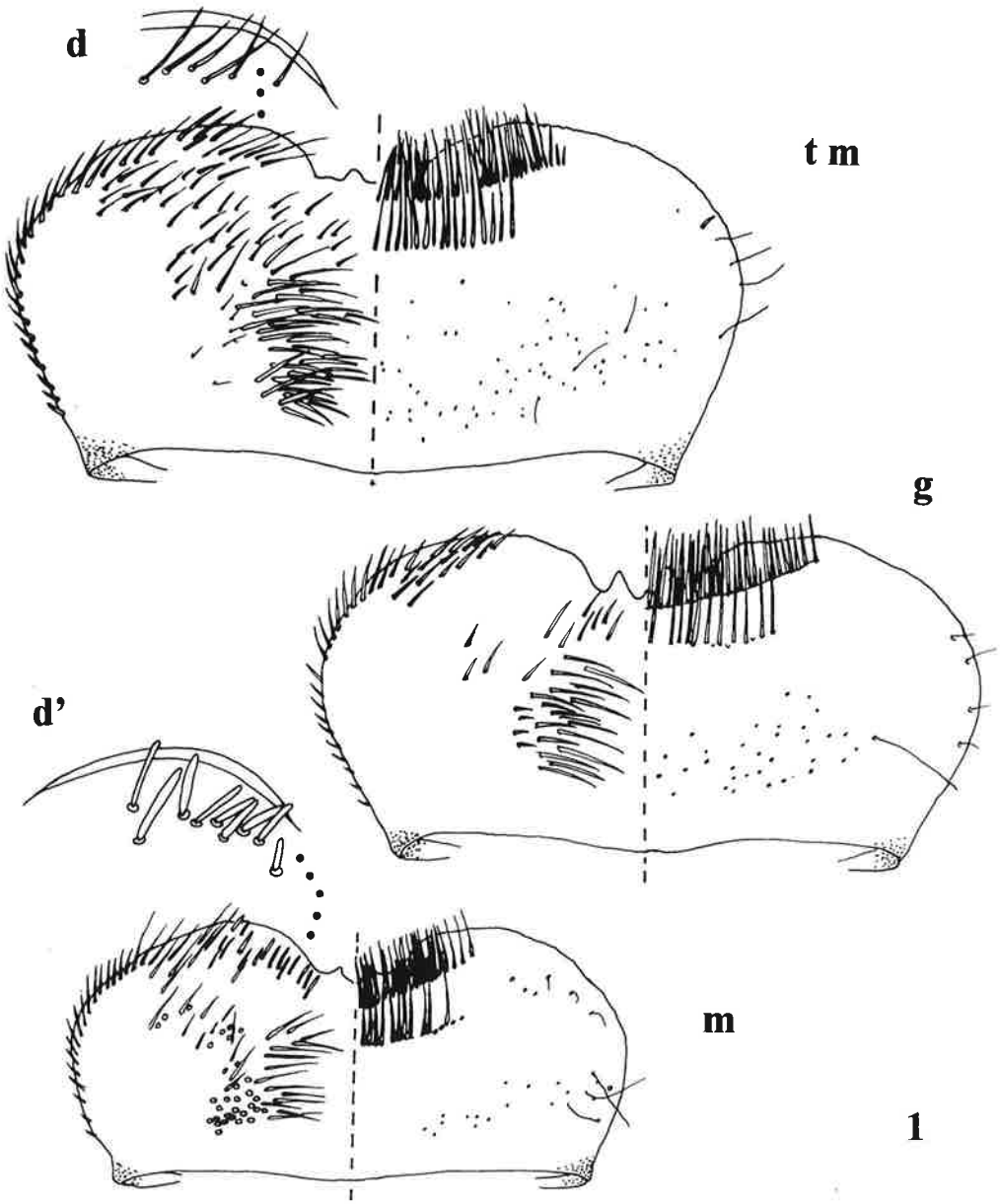


Plate I : Fig. 1. Larval structures (last-instar) of *Hagenulopsis* spp. t m : *traverae marginata* n. ssp.; g : *guadeloupensis*; m : *minuta*. Left : ventral ; right : dorsal.

1 : labrum; d-d' : detail of submarginal anterior parasagittal bristles.

Planche I : Fig. 1. Structures larvaires (au dernier stade) d'*Hagenulopsis* spp. t m : *traverae marginata* n. ssp.; g : *guadeloupensis*; m : *minuta*. A gauche : vue ventrale ; à droite : vue dorsale.

1 : labre; d-d' : détail des fortes soies sous-marginales antérieures parasagittales.

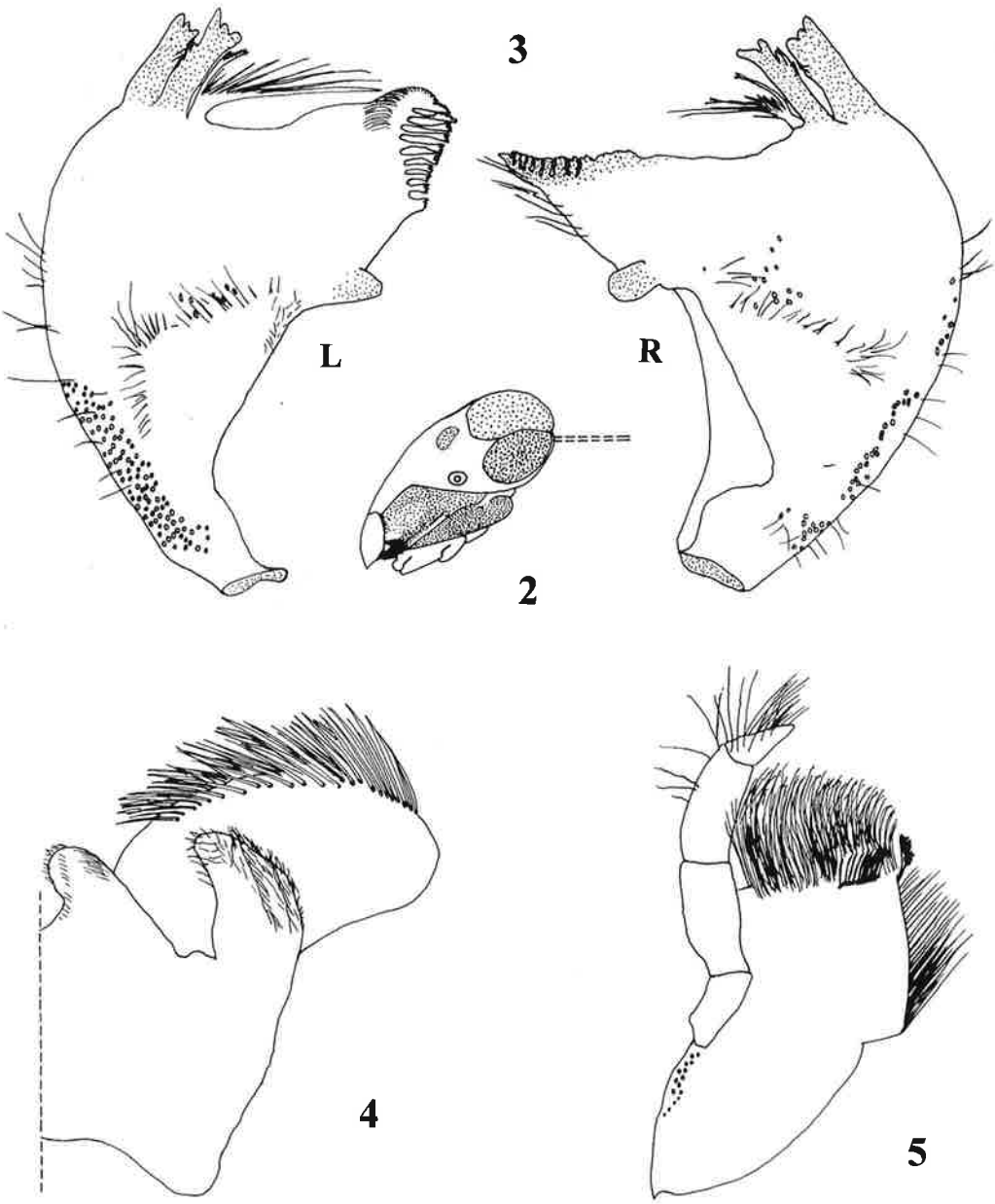


Plate II : Fig. 2-5. Larval structures (last-instar) of *Hagenulopsis traverae marginata* n. ssp.

2 : Head and body axis, lateral view (same scale as Fig. 25). 3 R : right mandible. 3 L : left mandible. 4 : hypopharynx, ventral view. 5 : maxilla.

Planche II : Fig. 2-5. Structures larvaires (au dernier stade) d'*Hagenulopsis traverae marginata* n. spp.

2 : Tête et axe du corps en vue latérale (même échelle que la Fig. 25). 3 R : mandibule droite. 3 L : mandibule gauche. 4 : hypopharynx en vue ventrale. 5 : maxille.

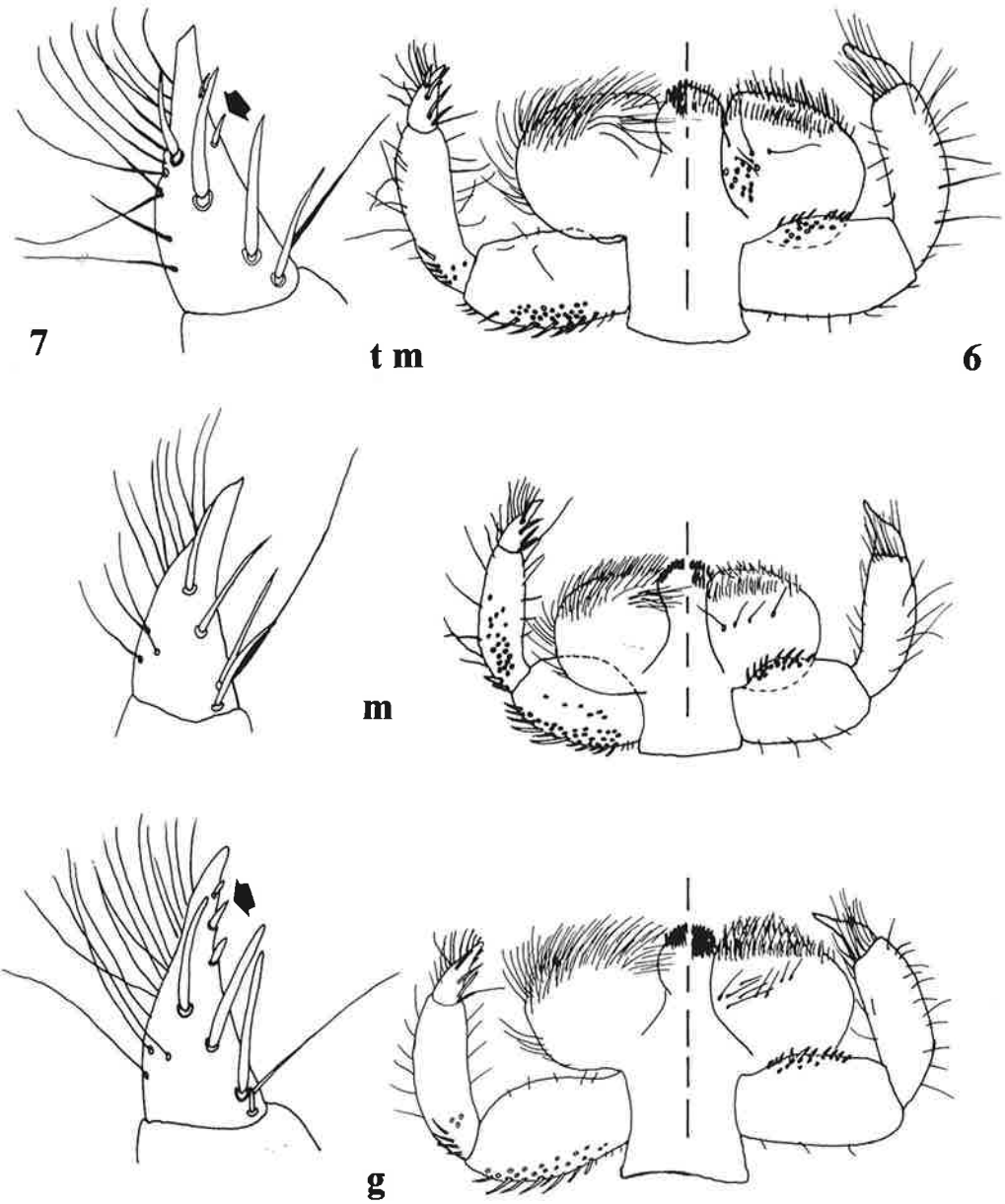


Plate III : Fig. 6-7. Larval structures (last-instar) of *Hagenulopsis* spp. t m : *traverae marginata* n. ssp.; g : *guadeloupensis*; m : *minuta*. Left : dorsal view ; right : ventral view.

6 : labium. 7 : apex of labial palp.

Planche III : Fig. 6-7. Structures larvaires (au dernier stade) d'*Hagenulopsis* spp. t m : *traverae marginata* n. ssp.; g : *guadeloupensis*; m : *minuta*. A gauche : vue dorsale ; à droite : vue ventrale.

6 : labium. 7 : apex du palpe labial.

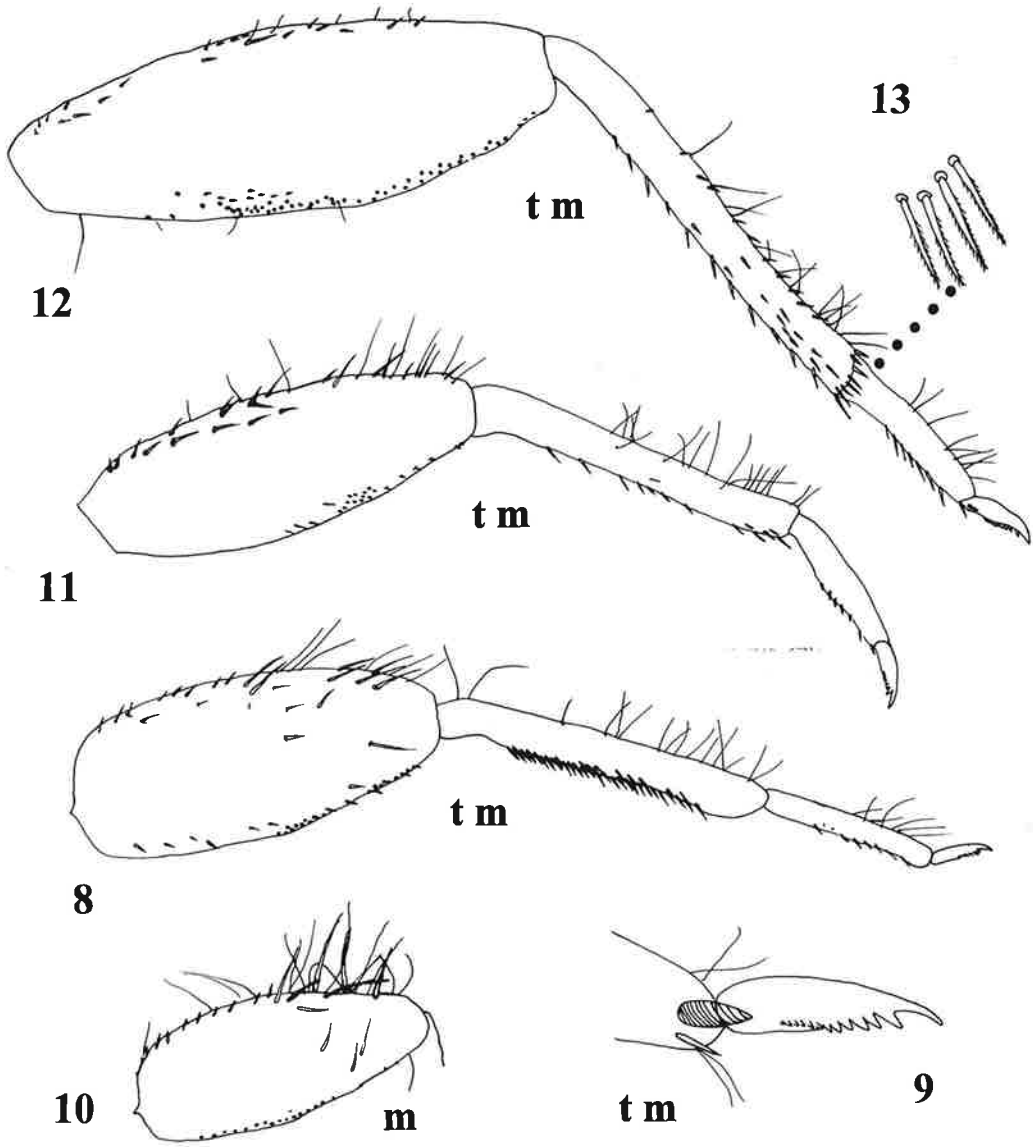


Plate IV : Fig. 8-13. Larval structures (last-instar) of *Hagenulopsis* spp. t m : *traverae marginata* n. ssp.; m : *minuta*.

8 : foreleg. 9 : foretarsal claw. 10 : forefemur. 11 : mid-leg. 12 : hind leg. 13 : apical pectinate bristles of hind tibia.

Planche IV : Fig. 8-13. Structures larvaires (au dernier stade) d'*Hagenulopsis* spp. t m : *traverae marginata* n. ssp.; m : *minuta*.

8 : patte antérieure. 9 : griffe tarsale antérieure. 10 : fémur antérieur. 11 : patte de la 2e paire. 12 : patte postérieure. 13 : soies apicales pectinées du tibia postérieur.

marginal row of 13-15 pectinate setae followed by another row of 5-8 on inner side. A bigger pectinate bristle at the apex of the galealacinia.

Labium (Fig. 6). Palp: segment one robust with short stout anteroventral and posterodorsal bristles, and some long fine hairs; chloride cells present, intermixed with bristles. Segment two narrower and longer than segment one, with an average of five basal bristles dorsally and some fine, long hairs laterally; chloride cells present, sometimes up to the proximal quarter of segment two (in *minuta* chloride cells always present all over the proximal half of the segment). Segment three short and narrowed distally (Fig. 7), dorsally four or three long bristles plus two or three short bristles (arrow) on inner side (no short bristles in *minuta* : Fig. 7 m, and see also PETERS & DOMINGUEZ 2001, fig. 16), ventrally some long fine hairs. Glossae with apical dorsal spatulate bristles. Paraglossae with long and fine setae laterally. Numerous chloride cells ventrally.

Remark : no unquestionable differential morphological difference could be found in mouthparts, between *H. guadeloupensis* and *H. traverae marginata*, and also with the figures 147, 156, 165, 175, 195 and 196 of *H. traverae* either (PETERS 1971).

THORAX

Light to medium brown. Anterior corners of pronotum with 5-6 relatively long pointed bristles. Hind wing pads totally absent.

Forelegs largely apart (coxae separated by a space equal to the length of foretarsi : Fig. 14). Femora (Fig. 8) with 8 to 10 long bristles dorsally near the posterior margin (distal ones are longer : about 1/5 as long as femora) and some short bristles scattered dorsally and ventrally. In *minuta*, marginal distal bristles are about 1/3 as long as femora (Fig. 10). Tibiae : posterior edge with about 20 long hairs, anterior edge with numerous pectinate bristles. Tarsi : posterior edge with long scattered hairs, anterior edge with 9 or 10 shorter bristles. Tarsal claws (Fig. 9) with one row of 12-13 denticles progressively longer from base to sub-apex (12 denticles in *H. traverae*, see fig. 203 in PETERS 1971; 11-13 in *H. guadeloupensis* Hofmann & Peters). Chloride cells present on femora and tibiae.

Mid-legs (Fig. 11) similar to forelegs except tibiae with more numerous and finer hairs along posterior margin, and about 8 short simple plus one or a few pectinate bristles on anterior margin. Tarsal claws with 12-13 denticles.

Hind legs. Femora (Fig. 12) with more than 20 dorsal bristles near the posterior margin, and some very short bristles on anterior edge followed by chloride cells. Tibiae with 14-20 simple bristles on inner edge, 10-15 pectinate bristles on ventral surface, 4-6 pectinate (Fig. 13) and 3 simple apical bristles, about 14-16 simple bristles of various length along outer margin intermixed with numerous hairs. Some scattered chloride cells. Tarsi similar to foreleg. Tarsal claws with about 13 denticles.

ABDOMEN

Brown dorsally, and grey brown ventrally.

Posterior edge of abdominal terga I to VI devoid of spiniform denticles (Fig. 16 t m); spines progressively longer from VII to IX, appearing laterally in VII-VIII (in *minuta*, posterior edge with wider triangular spines from I to VIII : Fig. 16 m). Chloride cells on lateral areas of all terga and sterna. Sternum IX (Fig. 15 t m) deeply cleft and relatively blunt at apex (acute in *minuta* : Fig. 15 m), preapical edge without denticles, contrary to *minuta*.

Gills 1-7 alike (Fig. 17), bifid, longer than two abdominal segments and slender, tracheae unbranched, with scattered chloride cells and short hairs.

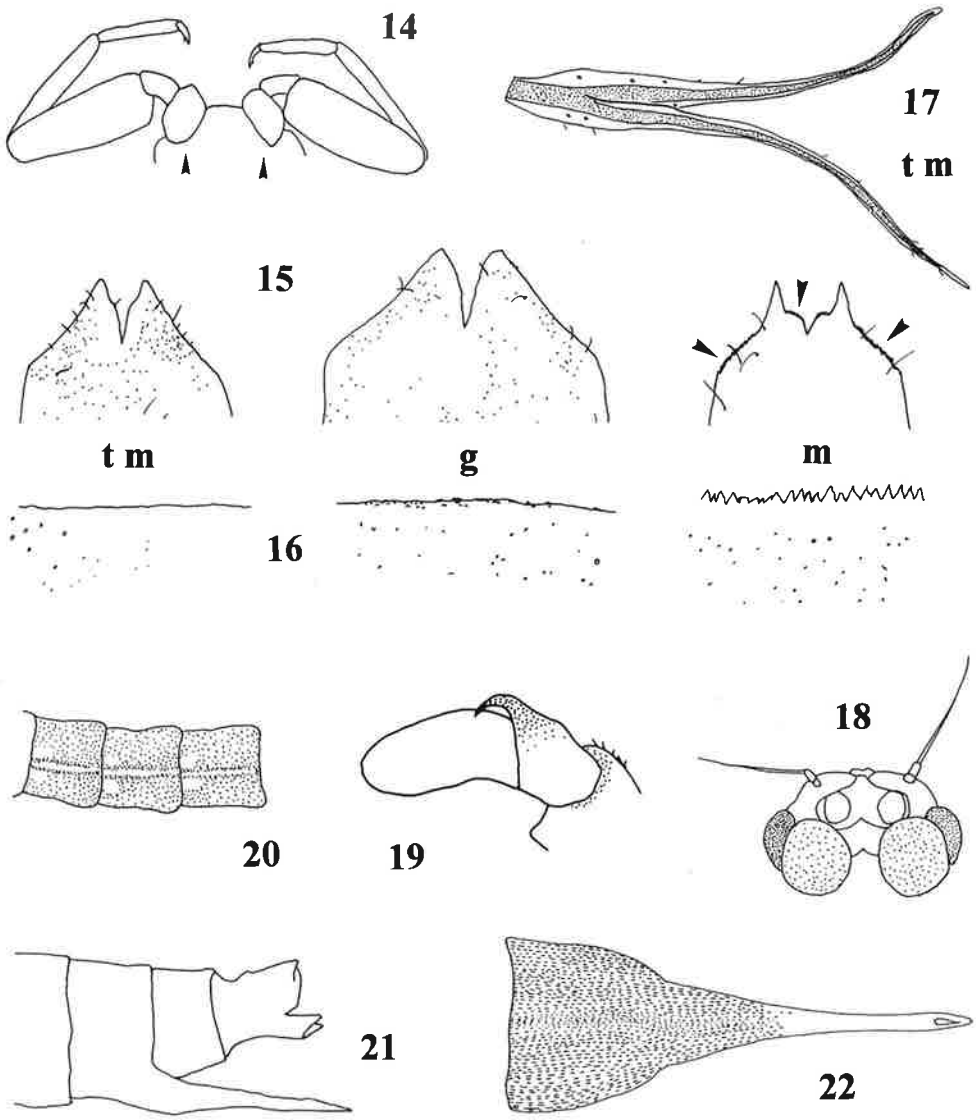


Plate V : Fig 14-22. 14-17 : larval structures (last-instar) of *Hagenulopsis* spp. t m : *traverae marginata* n. ssp.; g : *guadeloupensis*; m : *minuta*. 18-22 : adult structures of *Hagenulopsis traverae marginata* n. ssp.

14 : spacing of coxae (arrows), ventral view. 15 : apex of IXth sternum (arrows = denticles). 16 : posterior edge of IVth sternum. 17 : IVth gill. 18 : head of male, dorsal view. 19 : claws, male (same scale as Fig. 43). 20 : color pattern of terga IV to VI (male). 21 : abdominal segments VII-IX of female, lateral view. 22 : female ovipositor, ventral view.

Planche V : Fig. 14-22. 14-17 : structures larvaires (au dernier stade) d'*Hagenulopsis* spp. t m : *traverae marginata* n. ssp.; g : *guadeloupensis*; m : *minuta*. 18-22 : structures adultes d'*Hagenulopsis traverae marginata* n. ssp.

14 : espacement des coxas (flèches) en vue ventrale. 15 : apex du IXe sternite (flèches = denticules). 16 : bord postérieur du IVe sternite. 17 : IVe branchie. 18 : tête du mâle en vue dorsale. 19 : griffes du mâle (même échelle que la Fig. 43). 20 : coloration des tergites IV à VI du mâle. 21 : segments abdominaux VII à IX de la femelle en vue latérale. 22 : ovipositeur de la femelle en vue ventrale.

Caudal filament and cerci longer than the body. No lateral rows of dense setae on terminal filament and inner margin of cerci.

SIZE (last-instar larvae)

H. traverae marginata

Body length (without caudal filaments) : male = 5.3-5.7 mm; female = 5.7-6.3 mm.

Caudal filament (female) = 6.7-7.7 mm.

H. minuta

Body length (without caudal filaments) : male = 3.3 to 3.7 mm; female : 3.4 to 4.4 mm.

b) Male imago

HEAD

Antennae light brownish grey. Compound eyes : upper portion brick-red with a broad posterior brown strip ; right and left eyes separated on meson of head by a length subequal to maximum width of lateral ocellus, but without any inner bridge (Fig. 18), contrary to *minuta* (see PETERS & DOMINGUEZ 2001, fig. 5 and 6); lower outer portion of eyes black. Anterior ocellus greatly reduced. Lateral ocelli highly prominent, with dark brown base on inner side. Head : light brown laterally outside ocelli, and medially from antennae to eyes; dark brown between the eyes and between the ocelli.

THORAX

Pronotum light brown, with dark brown outline and parasagittal pattern. Mesonotum : scutum entirely light brown, scutellum darker. Metanotum light brown, darker medially and peripherally. Sternites dull medium brown, darker in prothorax. Pleurae dull brown with a dark brown membranous area under the pronotum, in prolongation of the costal sector.

Forelegs : femora dark brown, tibiae greyish with dark brown apex, tarsi greyish. Length ratios of segments, from femur to tarsus : 1; 2.08; 0.65; 0.49; 0.23; 0.13. Tarsal claws asymmetrical (one hooked, one blunt : Fig. 19).

Mid-legs entirely whitish with the exception of femora, dark brown at apex.

Hind legs : femora dark brown with a narrow longitudinal white line, tibiae and tarsi whitish.

Forewings (Photo 1, page 106) : membrane slighly brownish, costal and sub-costal sectors clearly darkened from base to apex, contrary to *H. guadeloupensis* (transparent, « slightly smoked in pterostigmatic area ») and *H. traverae* (darkened in apical third only). S, Sc and R1 dark brown, Rs medium brown, other veins lighter. About 14-18 cross-veins in costal sector, but only those located in pterostigmatic area (8-11) are conspicuous (in comparison : 8 in *traverae* -see fig. 72 in PETERS 1971- and 9-12 in *guadeloupensis*), the other ones in proximal half of wing being vestigial or appearing as a diffuse trail of pigment.

ABDOMEN

Terga dark brown with two small anterior parasagittal light spots and a faint mediodorsal light line on segments II-VII (Fig. 20). Anterior corners of terga lighter. Sterna lighter in anterior and posterior areas. On the whole, abdominal coloration is similar to *minuta* (see fig. 7 and 8 in PETERS & DOMINGUEZ 2001).

Genitalia

Forceps (Fig. 23, 24). Penis (Fig. 23, 23 a, 24, 24 d) very long and slender, hooked inwards near apex.

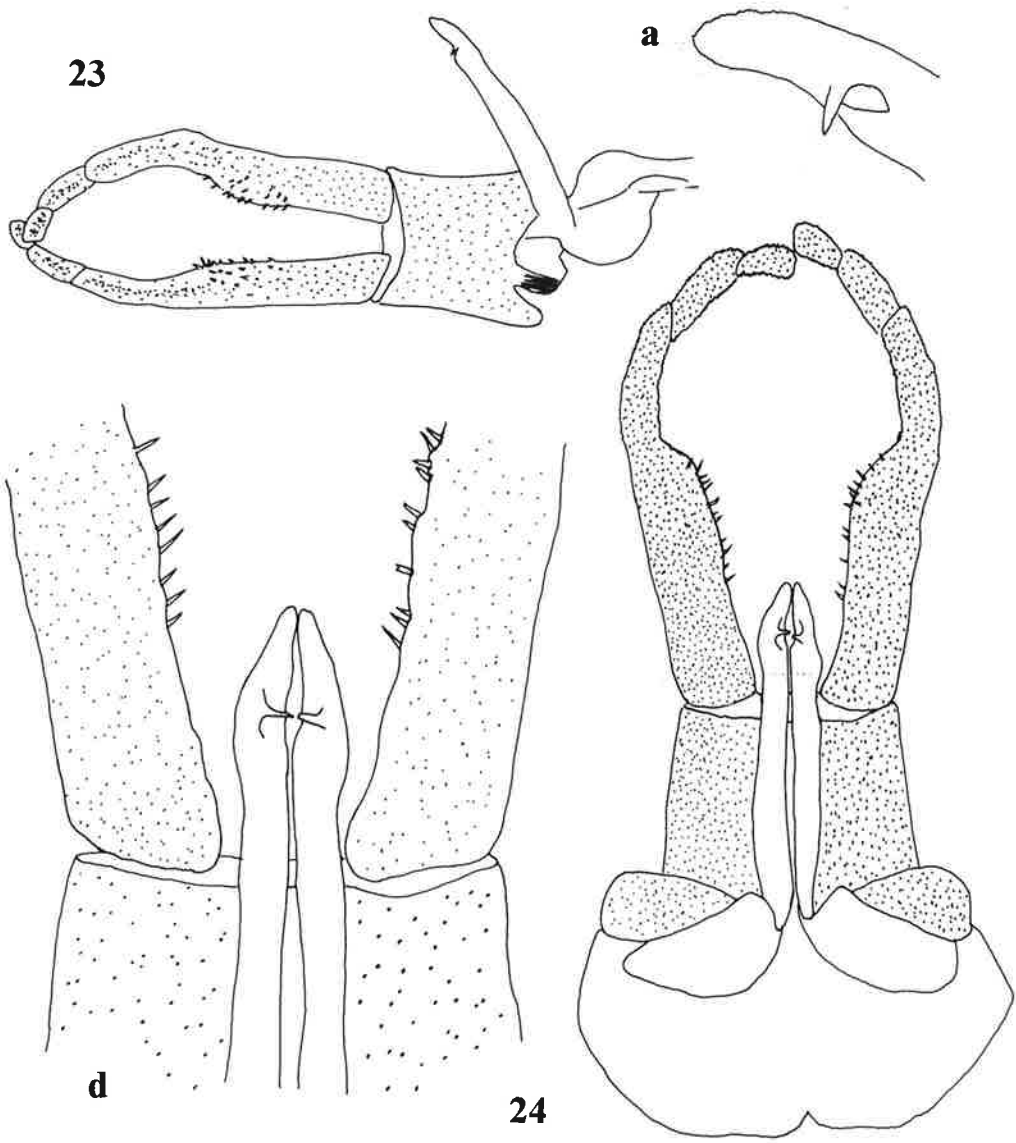


Plate VI : Fig. 23-24. Male imago structures of *Hagenulopsis traverae marginata* n. ssp.

23 : genitalia, oblique view ; a : apex of penis, inner side. 24 : male genitalia, dorsal view ; d : detail of penis and proximal part of forceps.

Planche VI : Fig. 23-24. Structures de l'imago mâle d'*Hagenulopsis traverae marginata* n. ssp.

23 : genitalia en vue oblique; a : apex du pénis, du côté interne. 24 : genitalia mâles en vue dorsale; d : détail du pénis et de la partie proximale des forceps.

Caudal filament and cerci pale with dark brown articulations.

SIZE

Wing length : 4.8 to 5.3 mm.

Body length (including genitalia) : 5.7 to 6.3 mm.

c) Female imago

Coloration similar to the male, lighter and relatively dull.

Femora lighter, in particular the internal side, whitish with dark brown apex.

Abdomen much lighter, largely yellowish all over midregion. A very long ovipositor (Fig. 21, 22), extension of VIIth sternum. IXth sternum clearly cleft.

SIZE

Wing length : 5.2 to 5.6 mm.

Body length : 5.4 to 5.8 mm.

d) Subimagos

Generally similar to imagoes, in particular regarding maculations, but lighter on the whole and dull brown greyish. Costal and subcostal sectors conspicuously dark, remainder of wing greyish brown.

e) Etymology

The sub-specific epithet *marginata* is an allusion to the conspicuous brown coloration all over the costal and subcostal sectors.

f) Types designation and deposition

HOLOTYPE : a male imago from Carbet river below the Saut du Gendarme, 550 m elevation, 22-VIII-1996, mounted in Canada balsam, together with many paratypes in Canada balsam or in alcohol.

ALLOTYPE : a female imago, same reference, mounted in Canada balsam.

Holotype and allotype are deposited at the Naturhistorisches Museum, Wien, and three paratypes at the Museum National d'Histoire Naturelle, Paris.

2.3. Discussion

Adults of the genus *Hagenulopsis* lack hind wings, and females bear a long ovipositor on sternum VII. EDMUNDS et al. (1976) proposed the following combination of larval characters : labrum narrower than width of head capsule and with denticles in median emargination; glossae with spatulate bristles ; apical segment of labial palpi narrowed distally (Fig. 7); abdominal gills 1-7 alike (Fig. 17), bifid, long and slender; posterolateral projections present at most on abdominal segments VI-IX.

TRAVER (1938) established the genus *Borinquena*, and PETERS (1971) the subgenus *Australphlebia* for the type-species *traverae* from Dominica and an undescribed species from St-Lucia (PETERS & DOMINGUEZ 2001). THOMAS et al. (1997) did not find any differential character between *Hagenulopsis* and *Borinquena (Australphlebia)*. PETERS & DOMINGUEZ (2001) synonymized *Borinquena (Australphlebia)* with *Hagenulopsis*. Figures 72, 96, 103, 110, 120, 147, 156, 175, 195, 196, 203 and 210 in PETERS (1971) allowed a morphological comparison between larvae from Dominique and from Martinique.

On a morphological basis, we were unable to find any substantial differential feature between the three taxa from Martinique, Dominique and Guadeloupe (Table 2). In particular, male and female genitalia are practically identical (see respectively : present paper Fig. 23-24; PETERS 1971 fig. 96; and HOFMANN & al. 1999 fig. 196). The only consistent difference was noticed on wing coloration, and cross-venation : presence of a dark brown coloration all over the costal and sub-costal sectors in specimens from Martinique (Photo 1), coloration lighter and limited to the pterostigmatic area in Dominica (PETERS 1971, fig. 72), and pterostigmatic area only slightly smoked in Guadeloupe (HOFMANN et al. 1999, fig. 194). Also the number of some cross-veins seems to regress according to a gradient Martinique-Dominique-Guadeloupe. This appears rather in favour of three subspecies of *H. traverae*. We hope the study of the material from St-Lucia, where is a species of *Hagenulopsis* still undescribed, will be materialized in the future (see PETERS & DOMINGUEZ 2001); it could help in this matter.

Chloride cells and conductivity of the water

Chloride cells are present on different parts of the body of *Hagenulopsis* larvae. In mayflies, such cells occur in the hypodermis of nearly all body parts (KOMNICK & ABEL 1971, WICHARD & KOMNICK 1973); in particular, this kind of cells involved in osmoregulation is « normally concentrated on tracheal gills as well as lateral areas of abdominal sternites and tergites » (KOMNICK 1977). We found also such cells on labium, mandibles and legs in the three examined taxa of *Hagenulopsis*, and also on the labrum of *H. minuta*. Chloride cells appear to absorb sodium and chloride ions in order to compensate for salt losses through excretion of water in excess by the Malpighian tubules (KOMNICK et al. 1972, KOMNICK 1977). Experimentation conducted by WICHARD et al. (1973) has shown the long-term adaptation of the individuals to a decrease or an increase in ionic concentration of the water. When ionic concentration increases, the number of chloride cells decreases, and on the contrary if concentration decreases, the number of these cells increases. But insects can handle low concentrations of external electrolytes better than high ones. A long-term adaptation to diluted fresh water causes a significant increase in the number of chloride cells. On the contrary, the gradual increase in concentration of fresh water to the hemolymph ionic concentration, within a period of 15 days, led to approximately 50 per cent mortality, and a significant reduction in chloride cells number in the survivors of *Callibaetis coloradensis* (WICHARD et al. 1973).

Considering the location and relative number of chloride cells, *H. minuta* bears a higher number than *H. traverae marginata* and *H. guadeloupensis* do. Average conductivity of brooks and rivers where *Hagenulopsis* spp were found :

- *minuta*, in French Guiana : 32.5 $\mu S.cm^{-1}$ (σ = 10.6), and weighted average taking into account the abundance of populations : 28.7 $\mu S.cm^{-1}$ (data from GLEMET 2003);

- *traverae marginata*, in Martinique : 171.9 $\mu S.cm^{-1}$ (σ = 130.12), and weighted average : 162.3 $\mu S.cm^{-1}$ (data from LALA 2003).

This confirms WICHARDS et al. (1973 and 1975) observations : the higher the conductivity is, the fewer the chloride cells are. In other words, *H. minuta* appears a priori better adapted to streams with a very low conductivity (due to extremely low ionic content) than *H. traverae marginata* is.

2. 4. Study material

See annex pages 111-112.

CHARACTERS / SPECIES	*traverae traverae*	*traverae marginata* n. ssp.	*guadeloupensis*	*minuta*
Author, date	Peters, 1971	Thomas & Boutonnet, 2004	Hofmann & Peters, 1999	Spieth, 1943
Reference description	Peters, 1971	Thomas & Boutonnet, 2004	Hofmann & Peters, 1999	Peters & Dominguez, 2001
Distribution	Dominique island	Martinique island	Guadeloupe island	Surinam, French Guiana (new record)
ADULTS				
Wings : costal and subcostal areas	Hyaline, darkened in the distal third	Brown throughout	Hyaline, slightly smoky in the pterostigmatic area	Hyaline (Spieth 1943)
Wing length of the male (mm)	5.2-5.6	4.8-5.3	5.3	3.9-4.0
Body length of the male (mm)	5.5-5.7	5.7-6.3	6.0	3.5-3.8
Body length of the female (mm)	6.0	5.4-5.8	5.1	3 (Spieth 1943)
LARVAE				
Eyes (male) : upper portion / lower portion	light brown / black	light brown / black	black / black	red / black
Labrum : chloride cells	Not mentioned	No	No	Present
parasagittal anteroventral bristles	Not mentioned	Acute	Acute	Spatulate
3rd segment of labial palpi	Not mentioned	2-3 dorsal short bristles (arrow in Fig. 7 t m)	3-4 dorsal short bristles (arrow in Fig. 7 g)	no dorsal short bristles
Bristles on hind tibiae : inner edge	Not mentioned	14-20	13	30+
outer edge	Not mentioned	14-16	12	30+
Bristles on hind tarsi : inner edge	Not mentioned	8	7	5-7
outer edge	Not mentioned	1	1	3-4
Location of chloride cells	Not mentioned	Mandibles, labium, legs, abdomen	Mandibles, labium, legs, abdomen	Labrum, mandibles, labium, legs, abdomen
Posterior edge of abdominal terga I to VI	Without denticles	Without denticles	Without denticles	With denticles
IXth sternum	-	Apex relatively blunt, no preapical spines	Apex relatively blunt, no preapical spines	Apex acute, preapical spines present
	-			
Body length (mm)	not mentioned	6.3	6.2	3.8-4.2

Table 2. Main differential characters between the Carribean and Guianese species of *Hagenulopsis*.

Tableau 2. Principaux caractères différentiels opposant les espèces d'*Hagenulopsis* de la région Caraïbe et de Guyane.

2.5. Key to the known species of *Hagenulopsis*

Last-instar larvae.

1 Emargination of labrum with 3 main denticles and remnants of small denticles 2

1' Emargination of labrum with only 3 denticles 4

2 Labrum with parasagittal anteroventral bristles spatulate, and with chloride cells (Fig. 1 m); 3rd segment of labial palpi without dorsal short bristles (Fig. 7 m); posterior edge of abdominal terga I to IV with denticles; sternum IX with preapical lateral spines (Fig. 15 m) .....*minuta*

2' Labrum with parasagittal anteroventral bristles acute, and devoid of chloride cells (Fig. 1 t m, g); 3rd segment of labial palpi with dorsal short bristles (Fig. 7 tm, g); posterior edge of abdominal terga I to IV without denticles; sternum IX without preapical lateral spines (Fig. 15 tm, g) 3

3 Male compound eyes with upper portion pale brown to reddish brown and lower portion black.....*traverae traverae* (Dominique island) and *traverae marginata* (Martinique island)

3 Male compound eyes with upper and lower portion black .....*guadeloupensis*

4 Presence of simple setae posterodistally on hind tibiae (fig. 18, Lugo-Ortiz & McCafferty 1996); presence of scattered long fine setae over the entire body; relatively large body size (8.0-9.2 mm), Costa-Rica .....*ingens*

4' Presence of branched setae on the distal end of hind tibiae (fig. 20, Lugo-Ortiz & McCafferty 1996); presence of relatively fewer long, fine, simple setae over the body; somewhat smaller body size (7.0-7.2 mm) .....*ramosa*

Discrimination between the subspecies *H. traverae traverae* and *H. traverae marginata* is possible only on imagoes, with the following character :

1 Costal and sub-costal sectors clearly darkened from base to apex .....*traverae marginata*

1' No such darkened sectors .....*traverae traverae*

3. The genus *Terpides* Demoulin, 1966

3. 1. Introduction.

Demoulin (1966) established the genus *Terpides* for the species *guyanensis*, description based upon 11 larvae collected in the Surinam River drainage. Peters & Harrison (1974) described the larva and male adult of *T. jessiae* from St-Vincent island, and Lugo-Ortiz & McCafferty (1996) the larva of *T. diadema* from Costa Rica. In Martinique only one species occurs, *T. jessiae*, which is to be compared to material of *T. guyanensis* from French Guiana. The *Terpides* lineage belongs to the subfamily Atalophlebiinae; it was isolated on the ancient Guiana and Brazilian shields (Savage 1986).

3.2. *Terpides jessiae* Peters & Harrison : complementary description

a) Last-instar larva

General coloration medium to light brown dorsally. Tracheal trunks conspicuously darkened, appearing as short parallel tubes in abdominal segments at base of gills. Relatively broad gills with finely branched tracheae.

HEAD

Narrowed and rounded anteriorly, not flattened; mouthparts hypognathous (Fig. 25).

Compound eyes : male with upper portion reddish brown, lower black; female : black.

Labrum (Fig. 26 j) : sides subparallel, with a shallow anteromedial emargination and 6 small denticles, these latter being larger in *guyanensis* (Fig. 26 g). Labrum is also proportionnally larger in this latter species. Dorsally, many hairs scattered all over the surface, and two submarginal transverse rows of long bristles, farther off in *guyanensis* than in *jessiae*. Ventrally, anterior half of external edge with bristles; scattered bristles on medial and anteromedial areas.

Right mandible (Fig. 27 R) : basal set of incisors with two main denticles, distal set with four. Prostheca with setae as long as the incisors, distalmost seta unbranched (arrow) contrary to *guyanensis* where this latter is pectinate (Fig. 28 R arrow). Central area of the mandible, with a row of bristles. Down below the mola, a marginal row of long simple bristles.

Left mandible (Fig. 27 L) : basal set of incisors with three main denticles, distal set with four. Prostheca with numerous long bristles extending towards mola. Central area of mandible with a row of long bristles.

Hypopharynx (Fig. 29) : lingua rectangular without lateral processes, superlingua with anterior rows of setae. General shape similar in the two species; proximal edge of lingua possibly more concav in *guyanensis*.

Maxillae (Fig. 30). Maxillary palp : segment one about 2/3 the length of segment two, segments two and three subequal, segment four 4/5 the length of segment two. Segment four with fine setae. Galealacinia large with a dense apical tuft of long parallel setae. A short submarginal row of pectinate bristles, and a larger pectinate bristle at apex of galealacinia.

Labium (Fig. 31). Palp : segment one about 1.4 the length of segment two, with a row of bristles and some fine scattered setae; chloride cells present. Segment two with some fine scattered setae and sometimes a few chloride cells. Segment three about 0.8 the length of segment two, not constricted, triangular, with a row of long bristles, and inner anterolateral margin (long arrow) with a row of 12-13 short bristles (15-18 in *guyanensis*). Glossae clearly curved over ventrolaterally (short arrow).

THORAX

Anterior corners of pronotum with 10-11 pointed bristles.

Mesonotum medium brown with two yellowish parasagittal maculae before the wing pads.

Hind wing pads present.

Forecoxae contiguous (Fig. 38). Forefemora largely covered by prothorax in dorsal view, and light brown except a large dark macula on both dorsal and ventral sides of mature larvae (Fig. 32 j, and PETERS & HARRISON 1974, fig. 17); in *guyanensis* a macula variable in size on dorsal side, a proximal and a distal maculae on ventral side (Fig. 32 g). Inner edge with a row of short simple bristles, and four short branched bristles (Fig. 32 j d); outer edge with some simple bristles. Tibiae with an inner row of simple bristles, two of these latter becoming much longer near to apex. Tarsi with two rows of simple bristles. Tarsal claws (Fig. 33 j) with a larger tooth in the middle, separating two sets of denticles (8-11 in all); denticles of distal set narrower. In *guyanensis* the largest tooth is a bit more proximal (Fig. 33 g).

Mid-legs (Fig. 34). Femora yellow to light brown; inner margin with a row of simple short bristles; simple scattered bristles (not figured) on dorsal surface. Tibiae with bristles on inner and outer margins. Tarsi with bristles on inner margin. Tarsal claws (Fig. 35) as in foreleg.

Hind legs (Fig. 36) similar to mid-legs, except tibiae and tarsi with more numerous short simple bristles on inner margin.

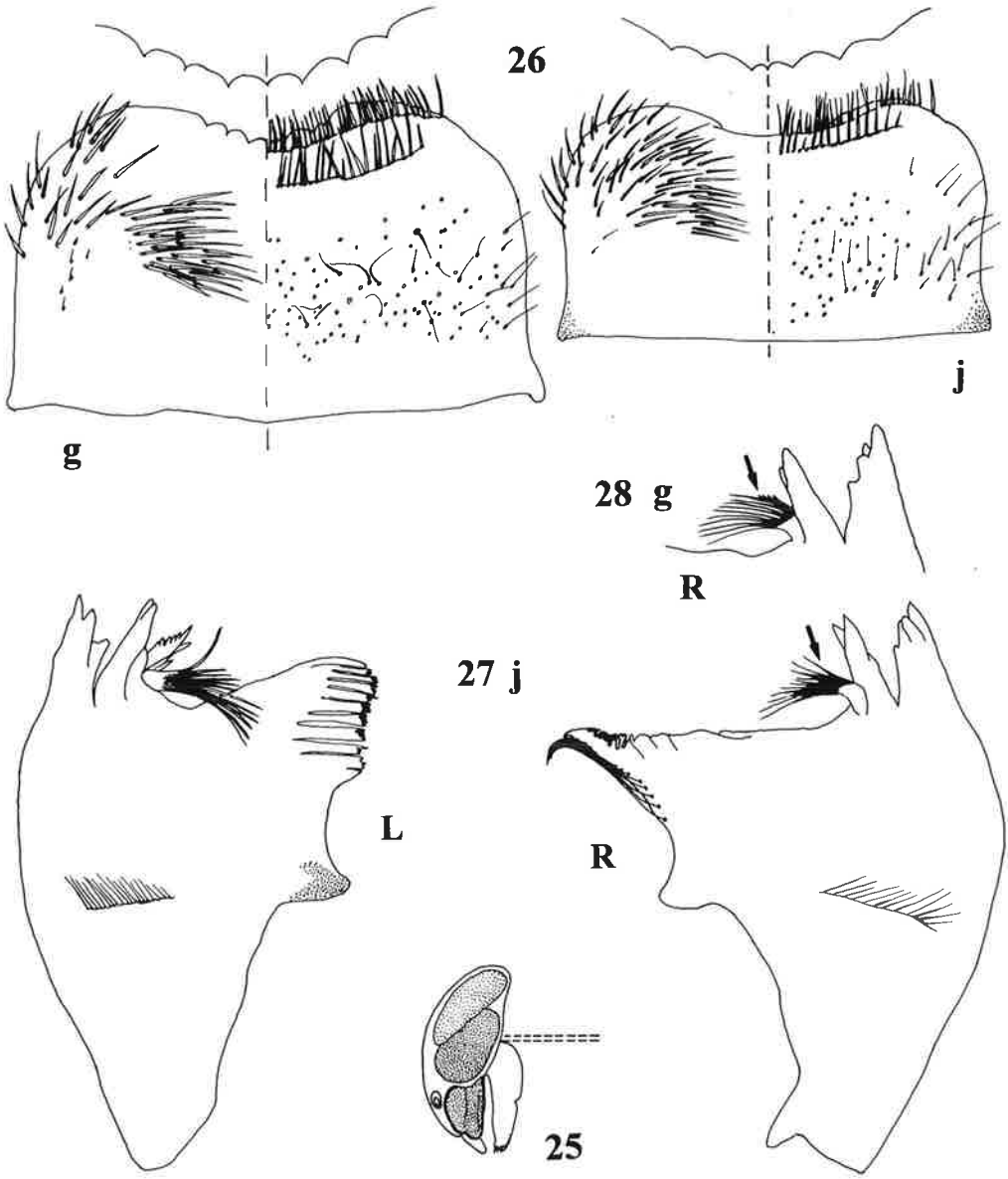


Plate VII : Fig. 25-28. Larval structures (last-instar) of *Terpides* spp. j : *jessiae*; g : *guyanensis*.

25 : head and body axis, lateral view (same scale as Fig. 2). 26 : labrum. 27 L : left mandible; 27 R : right mandible, 28 R : right incisors and prostheca.

Planche VII : Fig. 25-28. Structures larvaires (au dernier stade) de *Terpides* spp. j : *jessiae* ; g : *guyanensis*.

25 : tête et axe du corps en vue latérale (même échelle que la Fig. 2). 26 : labre. 27 L : mandibule gauche; 27 R : mandibule droite, 28 R : région incisive et prostheca droites.

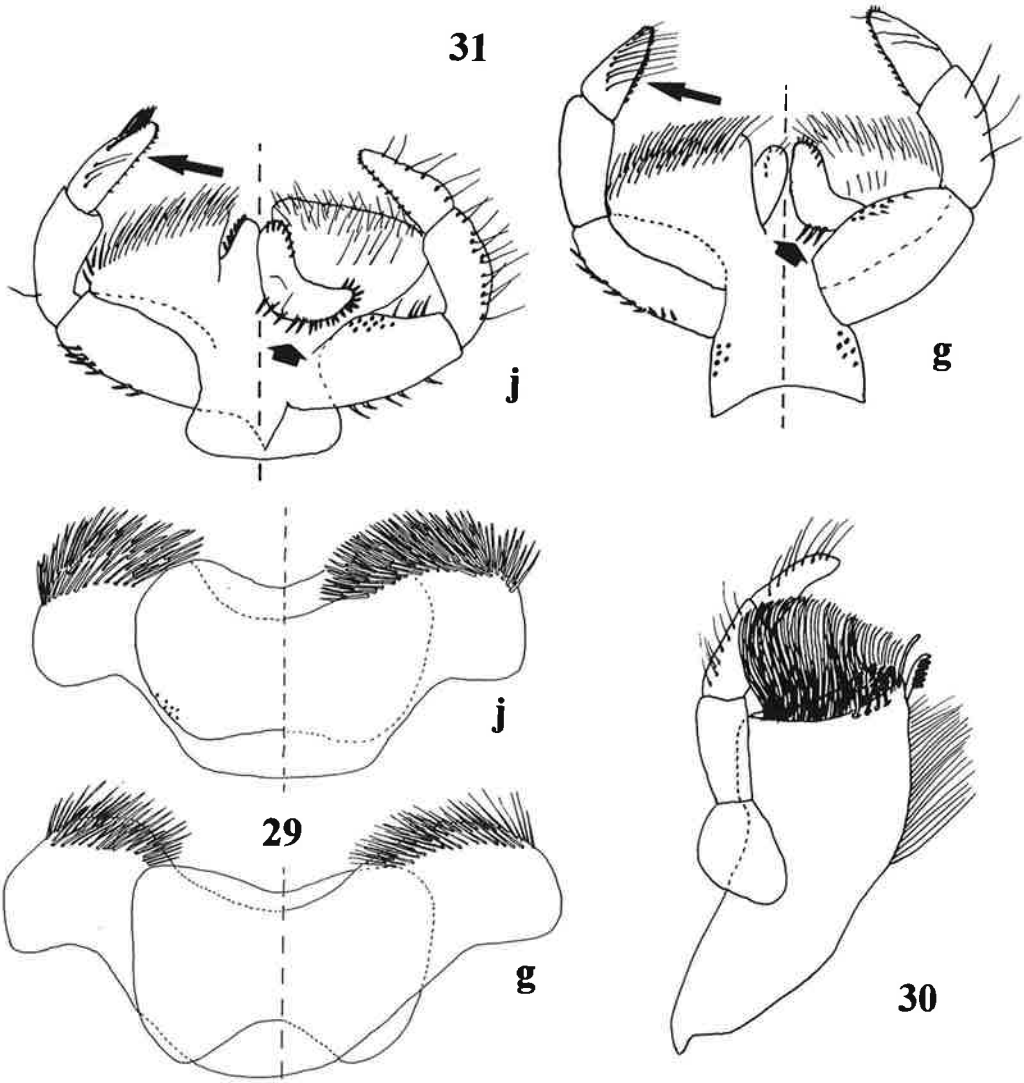


Plate VIII : Fig. 29-31. Larval structures (last-instar) of *Terpides* spp. j : *jessiae*; g : *guyanensis*.
29 : hypopharynx (left : ventral). 30 : maxilla. 31 : labium (right : ventral).
Planche VIII : Fig. 29-31. Structures larvaires (au dernier stade) de *Terpides* spp. j : *jessiae* ; g : *guyanensis*.
29 : hypopharynx (vue ventrale à gauche). 30 : maxille. 31 : labium (vue ventrale à droite).

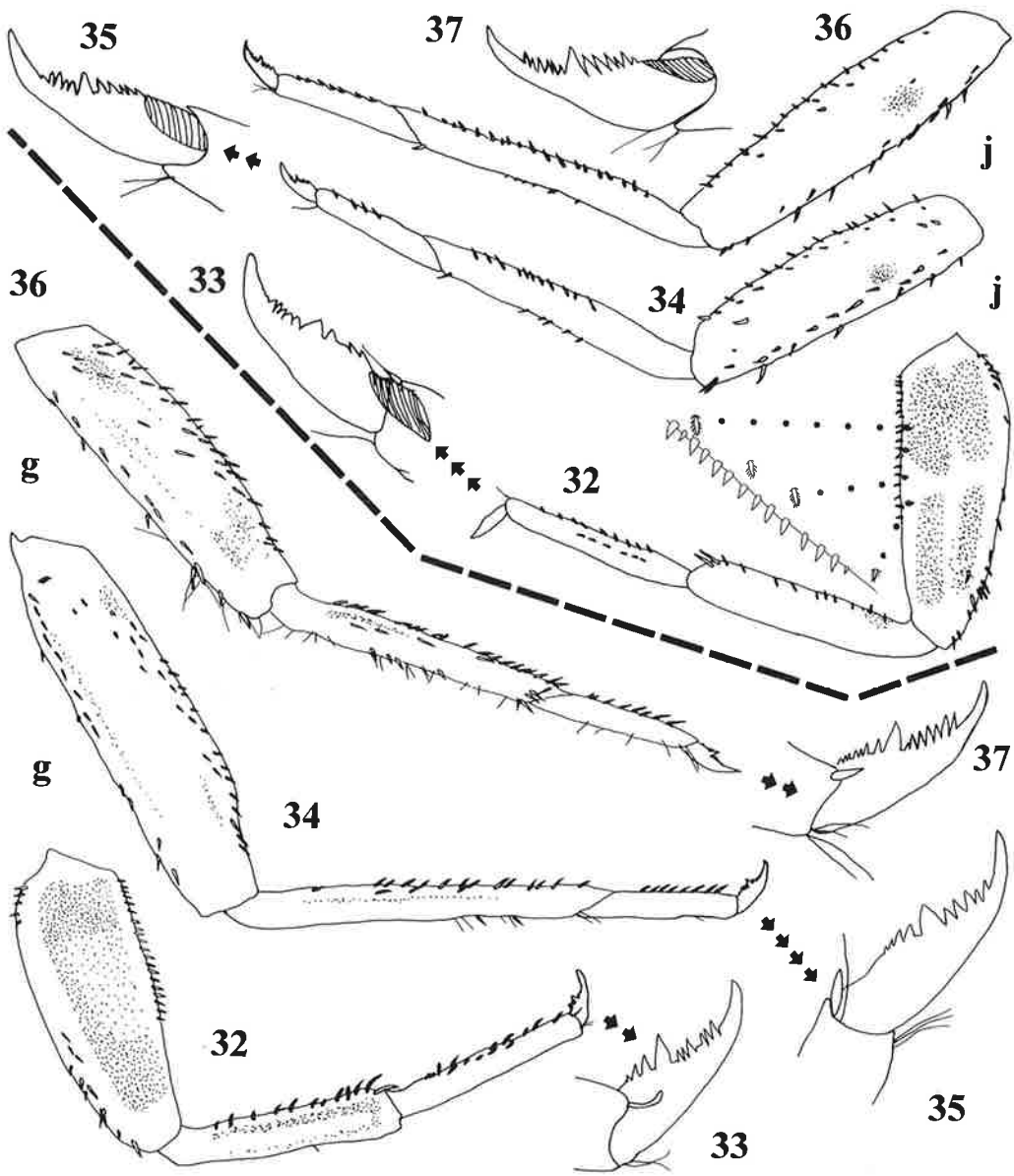


Plate IX : Fig. 32-37. Larval structures (last-instar) of *Terpides* spp. j : *jessiae*; g : *guyanensis*.

32 : foreleg; d : detail of branched bristles of inner edge of femur. 33 : fore tarsal claw. 34 : mid-leg. 35 : mid-tarsal claw. 36 : hind leg. 37 : hind-tarsal claw.

Planche IX : Fig. 32-37. Structures larvaires (au dernier stade) de *Terpides* spp. j : *jessiae*; g : *guyanensis*.

32 : patte antérieure; d : détail des fortes soies ramifiées du bord interne du fémur. 33 : griffe tarsale antérieure. 34 : patte de la 2e paire. 35 : griffe tarsale de la 2e paire de pattes. 36 : patte postérieure. 37 : griffe de la patte postérieure.

ABDOMEN

Dorsal color pattern as in Fig. 39 j.

Posterolateral projection present on terga III-VI (very short on III-IV) and VIII-IX (absent on VII); in *T. guyanensis* (Fig. 39 g) posterolateral projection only on terga V-VI and VIII-IX. Spines on posterior margin of terga V-IX (few very small spines on IV in *T. guyanensis*). Male : IXth sternum with a rounded medial posterior projection in *jessiae* (Fig. 40 j), and a broad emargination in *guyanensis* (Fig. 40 g). Female : emargination of IXth sternum U-shaped in *jessiae* (Fig. 41 j), V-shaped in *guyanensis* (Fig. 41 g).

Gills 1-7 relatively alike (Fig. 42), dorsal and ventral lamellae lanceolate; main tracheal trunks, especially 2-6, branched along median line of lamellae. Tracheae pigmented in black throughout, contrary to *guyanensis* (partly black, clearly contrasted : I, IV and VII g, arrows).

SIZE (last-instar larvae)

Body length (without caudal filament) : 5.0 to 5.7 mm (male) ; 6.2 to 6.8 mm (female).

Caudal filament : 3.8 mm (male) ; 4.0 to 4.5 mm (female).

b) Female imago

The female imago was unknown. Hereafter is its first description.

HEAD

Whitish with a conspicuous posterior transverse blackish strip between the eyes. Area between the ocelli darkened. Antennae yellowish with the exception of distal half of pedicel, dark brown. Ocelli with a basal black ring. Eyes black.

THORAX

Pronotum rather dull yellowish, darkened in the middle. All other sclerits rather bright, uniform dark yellow to light brown. Lateral membranous areas mottled with blackish, branched tracheal trunks particularly conspicuous, dark blackish purple.

Anterior wings hyaline (Photo 2), most of the cross-veins being dark purplish smoked. Posterior wings hyaline (Photo 3) with costal projection wide but moderately prominent.

Forelegs : femora largely blackish brown, with the exception of central part, yellowish ; tibiae and tarsi yellowish. Inner and outer tarsal claws alike, both hooked at apex (Fig. 43).

Mid-legs and hind legs : entierely yellowish, with a small dark brown spot on proximal third of femora.

ABDOMEN

Terga relatively light brown, with a darker posterior strip. Tracheation clearly visible.

Sterna dull light greyish yellow. VIIth sternum with two converging posterior black dots. IXth sternum deeply cleft, this emargination being broad and rounded (Fig. 44).

SIZE

Wing length : 5.5 to 5.7 mm.

Body length : 4.9 to 5.2 mm.

3.3. Discussion

The genera *Terpides* Demoulin, 1966 and *Fittkaulus* Savage & Peters, 1978 are nearly allied, sharing in particular the following characters (see also Savage 1986) :

- in larvae : head considered hypognathous [Fig. 25, see also fig. 10 a of Demoulin (1966), Sa-

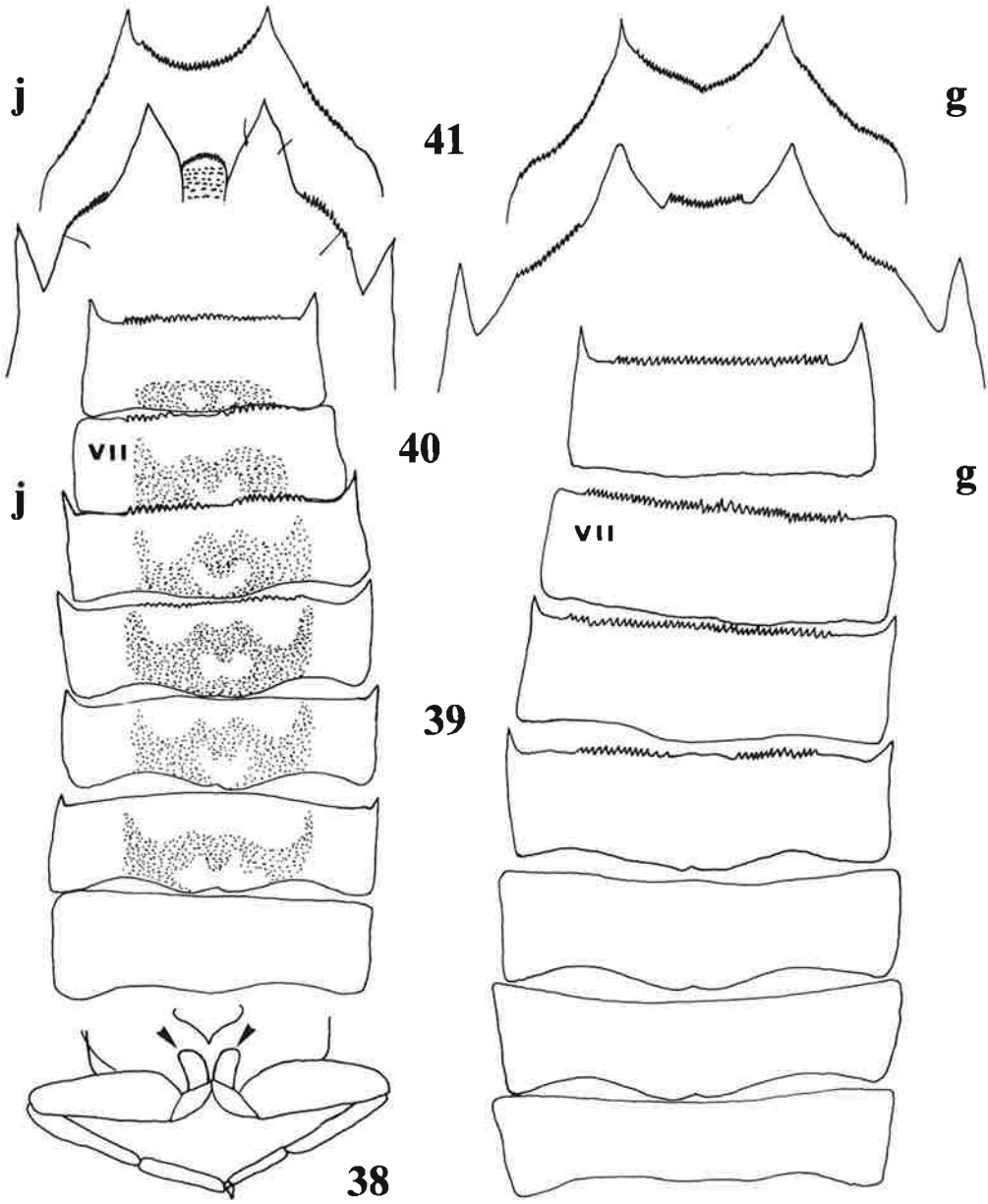


Plate X : Fig. 38-41. Larval structures (last-instar) of *Terpides* spp. j : *jessiae* (left); g : *guyanensis* (right).

38 : spacing of coxae (arrows), ventral view. 39 : abdominal terga II-VIII. 40 : IXth sternum of male. 41 : IXth sternum of female.

Planche X : Fig. 38-41. Structures larvaires (au dernier stade) de *Terpides* spp. j : *jessiae* (à gauche); g : *guyanensis* (à droite).

38 : espacement des coxas (flèches) en vue ventrale. 39 : tergites abdominaux II-VIII. 40 : IXe sternite du mâle. 41 : IXe sternite de la femelle.

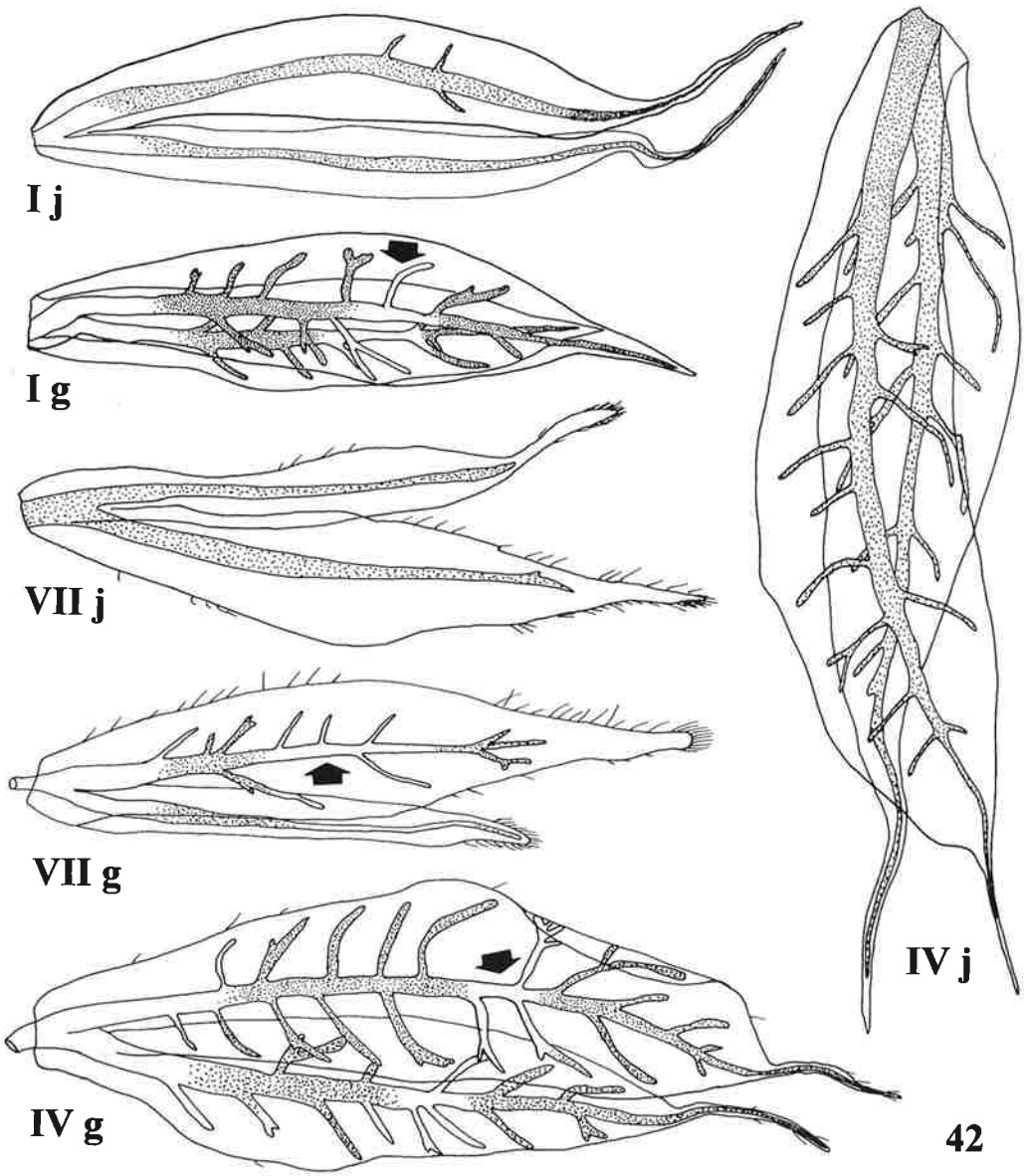
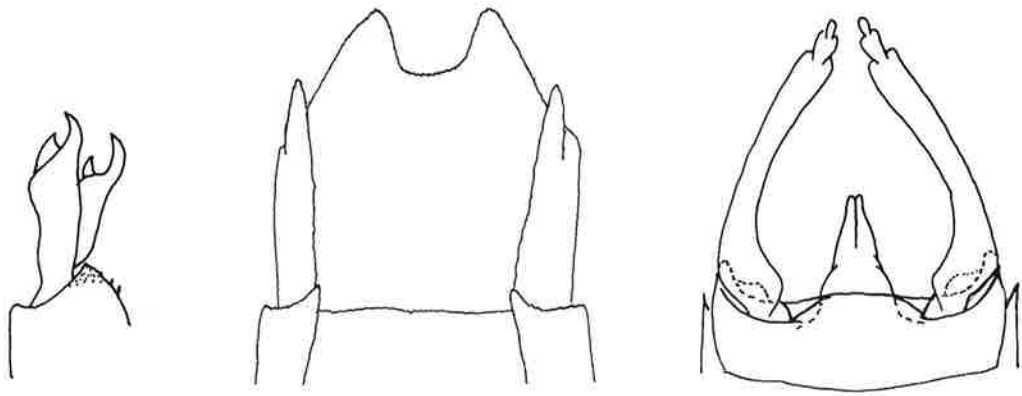


Plate XI : Fig. 42. Larval structures (last-instar) of *Terpides* spp. j : *jessiae*; g : *guyanensis*. 42 : gills I, IV and VII.

Planche XI : Fig. 42. Structures larvaires (au dernier stade) de *Terpides* spp. j : *jessiae*; g : *guyanensis*. 42 : branchies I, IV et VII.



43 44 45

Plate XII : Fig. 43-45. Adult structures of *Terpides jessiae*.

43 : fore tarsal claws of female (same scale as Fig. 19). 44 : IXth sternum of female. 45 : male genitalia, ventral view (redrawn from PETERS & HARRISON 1974).

Planche XII : Fig. 43-45. Structures adultes de *Terpides jessiae*.

43 : griffes tarsales antérieures de la femelle (même échelle que la fig. 19). 44 : IXe sternite de la femelle. 45 : genitalia mâles en vue ventrale (redessinés d'après PETERS & HARRISON 1974).

VAGE & PETERS (1978), SAVAGE (1986)], although PETERS & HARRISON (1974) wrote « head prognathous »; morphology of most mouthparts generally quite similar; lingua of hypopharynx rectangular and devoid of lateral processes; glossae clearly curved over ventrolaterally; posterolateral projections absent on abdominal segment VII; tracheae clearly branched in gills; cerci and caudal filament with longitudinal rows of setae;

- in adults : the claws of a pair both hooked; similar venation of forewing; and similar morphology of genitalia.

So far the two genera can be separated mainly by larval morphology (labrum, tarsal claws, gills) and costal projection of hind wing, much more prominent in *Fittkaulus* (see Photo 3, SAVAGE & PETERS 1978 p. 295, and SAVAGE 1986 p. 258).

Table 3 summarizes the main differential characters between *Terpides jessiae* and *T. guyanensis*.

3.4. Study Material

See annex pages 111-112.

3.5. Key to the known species of the genus *Terpides*

Last-instar larvae :

1 Segment 2 of labial palpi with 3 long bristles on medial margin; posterolateral projection on terga VIII and IX only ..... *diadema*

1' Segment 2 of labial palpi without long bristles on medial margin; posterolateral projection at least on terga V-VI and VIII-IX 2

2 Labium : segment 3 with 12-13 stout, short bristles on inner margin; gills with tracheae

black; forefemora brown with a small paler line in the middle and few branched setae; posterolateral projections on terga III-VI and VIII-IX ..... *jessiae*

2' Labium : segment 3 with 15-17 stout, short bristles on inner margin; gills with tracheae black only in part; forefemora brown without any pectinate setae; posterolateral projections on terga V-VI and VIII-IX ..... *guyanensis*

	Terpides jessiae	*Terpides guyanensis*
Author, date	Peters & Harrison, 1974	Demoulin, 1966
Distribution	St-Vincent island, Martinique island (new record)	Surinam, French Guiana (new record)
LARVAE		
Labrum	Anteromedian rows of setae closer Denticles of emargination smaller	Anteromedian rows of setae farther off Denticles of emargination bigger
Right mandible : prostheca	Distal seta simple	Distal seta pectinate
Labium : segment 3 of palpus	12-13 stout short bristles on anterolateral margin	15-18 stout short bristles on anterolateral margin
Forefemora	Brown with a small paler median line and few branched setae	Brown without paler median line and any pectinate setae
Foretibiae	With a small inner proximal brown dot	Apex and inner anterior edge brown
Abdomen	Posterolateral projections on terga III-VI (weak on III-IV) and VIII-IX	Posterolateral projections on terga V-VI and VIII-IX
	A brown pattern on terga II-IX	No brown pattern on terga II-IX
Gills	Tracheae pigmented throughout	Tracheae partly pigmented

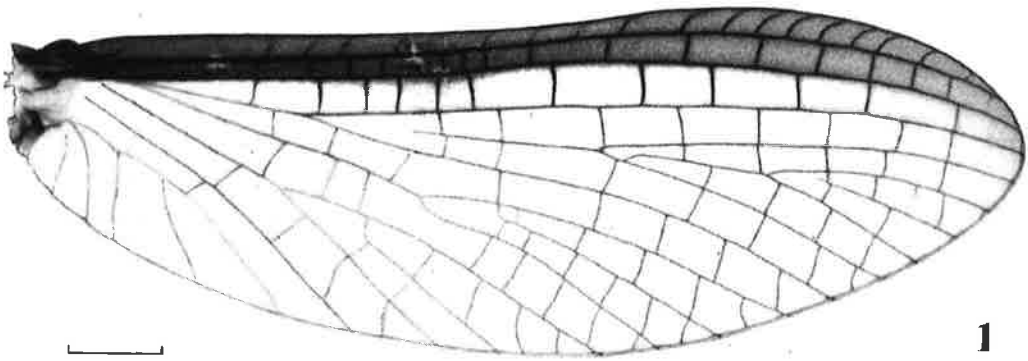
Table 3. Main differential characters between the Carribean and Guianese species of *Terpides*.

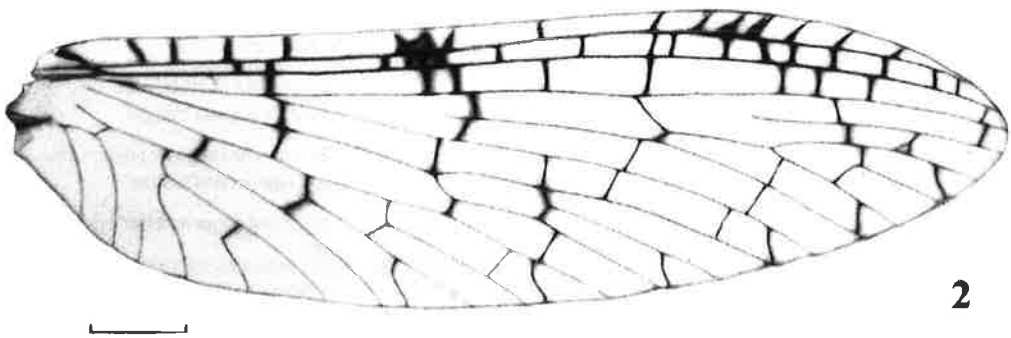
Tableau 3. Principaux caractères différentiels opposant les espèces de *Terpides* de la région Caraïbe et de Guyane.

4. Comparative ecology of *H. traverae marginata* and *T. jessiae*

43 sites were studied in Martinique between 1996 and 1999, within the frame of a water quality evaluation program, conducted by DIREN of Fort-de-France. From the beginning, the main difficulty was the great lack of knowledge regarding systematics of lotic fauna.

Frequency of occurrence of the two Leptophlebiidae species was relatively high : *H. traverae marginata* = 0.58 (present at 25 sites), *T. jessiae* = 0.40 (present at 17 sites). However, *H. traverae marginata* exhibits a clearly higher range of elevation, being found up to about 600 m a.s.l., against only 300 for *T. jessiae*. More alticolous than this latter, *H. traverae marginata* is also more rheophilic and in fact, beyond the frame of the program, we could record this species from almost every little brook in the northern mountainous area of the island, whenever elevation and slope prevent any agricultural or domestic activity.





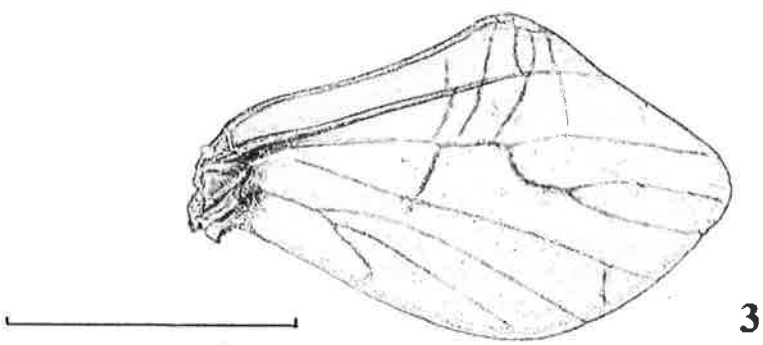


Plate XIII : Photos 1-3. Bar = 0.5 mm.

1 : anterior wing of *Hagenulopsis traverae marginata* (male). 2 : anterior wing of *Terpides jessiae* (female). 3 : posterior wing of *T. jessiae* (female).

Planche XIII : Photos 1-3. Echelle = 0,5 mm.

1 : aile antérieure d'*Hagenulopsis traverae marginata* (mâle). 2 : aile antérieure de *Terpides jessiae* (femelle). 3 : aile postérieure de *T. jessiae* (femelle).

The morphology of *T. jessiae* is well adapted to slow flowing water : orthognathous head, much less hydrodynamic than prognathous type; wide lamellar gills with highly branched tracheae, favourable to O_2-CO_2 diffusion in difficult conditions, but clearly unadapted to high or even moderate current speeds ; forelegs contiguous at base, not wide apart, inducing a relative instability of attitude on the substratum ; and above all presence of a caudal paddle (strong cerci held contiguous, with longitudinal rows of natatorial setae) indicating a swimmer behavior. More thermo-

	H. traverae marginata	*T. jessiae*
Abiotic parameters	range : min.-max.	range : min.-max.
Conductivity (µS/cm)	46 - 583	62 - 583
Cl- (mg/L)	4 - 74	6 - 75
Water temperature (°C)	22,4 - 29,9	24,6 - 29,9
pH	6,4 - 8,2	7,2 - 8,2
Slope at study sites (%)	0,1 - 26,6	0,1 - 6,2
Elevation (m)	4 - 570	4 - 298
Width (m)	0,5 - 15	0,8 - 15

Table 4. Range of several major abiotic parameters.

Tableau 4. Intervalle de variation de plusieurs paramètres abiotiques majeurs.

	Elevation (m)	*H. traverae m.*	*T. jessiae*
Lézarde river and tributaries			
Palourdes brook	570	+++	0
Blanche river at Alma	450	+	0
Lézarde Deux	180	++	0
Glotin	76	+	++
Soudon 1996	23	+	+
Soudon 1999	23	0	++
Carbet river			
Saut du Gendarme	550	+++	0
Fond St Denis	230	+	0
Fond Baise-Fond Savane 1996	40-25	+	+
Fond Baise-Fond Savane 1999	40-25	0	+++

Abundance classes : Cl 1 (+) : 2-5 ind. Cl 2 (++) : 6-20 ind. Cl 3 (+++) : > 20 ind.

Table 5. Distribution of the populations of Leptophlebiidae at some sites of two catchments (numbers of individuals per 0.2 m²).

Tableau 5. Répartition des populations de Leptophlebiidae à quelques stations de deux bassins-versants (effectifs par 0,2 m²).

philous also (Table 4), *T. jessiae* is better adapted to live in the downstream sectors of rivers, or at least in low slope streams ; this is particularly clear, considering the respective ranges of slope for the two species (Table 4). For example, two major catchments show the regression of *H. traverae marginata* from upstream to downstream sites (Table 5), contrary to the populations of *T. jessiae*.

Comparison of the requirements of the two species, as regards other main abiotic factors (pH, conductivity, Cl^- concentration), shows that *H. traverae marginata* exhibits a larger ecological range of tolerance than *T. jessiae*. However, population densities of *H. traverae marginata* considerably regress when conductivity exceeds 400 µS/cm (Fig. 46); on the contrary, *T. jessiae* hardly tolerates low values of conductivity, and is rare below 100 µS/cm, a situation probably relevant to the low number of chloride cells observed in this species.

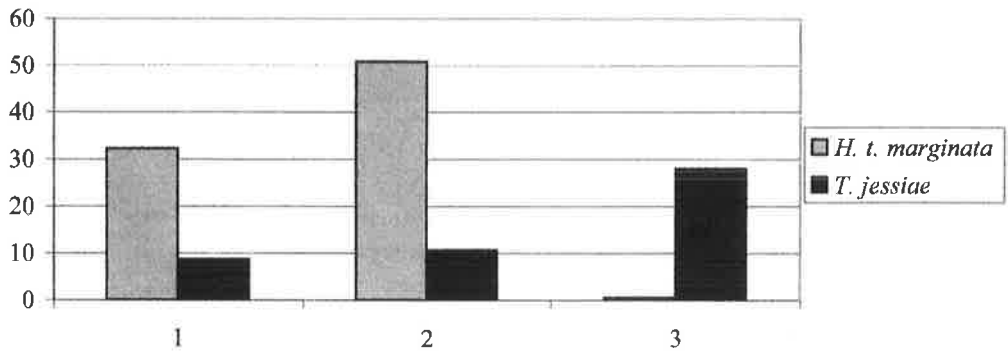


Fig. 46 : Average numbers of individuals of Leptophlebiidae collected per station, in function of conductivity.

Fig. 46 : Effectifs moyens de Leptophlebiidae récoltés par station en fonction de la conductivité.

T. jessiae tolerates human disturbances much better than *H. traverae marginata* does. Thus, only one station out of 25 colonized by *H. traverae marginata* (e.g., 4.0 %) is located in diffuse urban environment, in comparison with 5 stations out of 17 colonized by *T. jessiae* (29.4 %).

Between 1996 and 1999, the Lézarde river at Soudon was increasingly impacted by NH_4 and NO_3 wastes (respectively 0 and 1.7 mg/L as maximal values measured in 1996 to be compared to 0.35 and 4.95 mg/L in 1999, according to our data). Within the present limits of our study, *H. traverae marginata* is a particularly sensitive bioindicator among the lotic insects of Martinique : it disappeared from this station, while the population of *T. jessiae* increased from abundance class 1 to class 2. Another example, in the downstream sector of the Carbet river, following diverse fittings on the banks and in the stream bed, the population of *H. traverae marginata* disappeared, whereas that of *T. jessiae* evolved from abundance class 1 to class 3. In other words, anthropic influences presently increase the natural ecological upstream-downstream replacement of *H. traverae marginata* by *T. jessiae*.

On the contrary, an example of recolonization was observed in Grand Rivière at Stadium between 1996 and 1999 : as a consequence of the improvement of water quality (mainly NH_4, NO_3 and O_2 concentrations), the population of *H. traverae marginata* increased steadily, from abundance class r (rare : 1 or 0 individual per sample of 0.2 m^2) to class 2.

Remark : a first survey of Guianese species (after ORTH et al. 2000, and GLEMET 2003) shows that *H. minuta* and *T. guyanensis* generally do not cohabitate : only one station is colonized by both species whereas 22 are colonized by one of these species only.

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(appeared in Septembre 2004)

Stations (elevation a.s.l.)	**Species** (numbers of larvae / 0.2 m2) *	
MARTINIQUE	*H. traverae marginata* n. ssp.	*T. jessiae* (new record)
Study program 1996		
Grand Rivière, amont stadium	1	
Riv. Capot, Petite Cécile, 380 m	142	
Riv. Lorrain, 563 m	1	
Affl. Riv. Lorrain, 560 m	1	
Riv. Lorrain, Séguineau, 10 m		1
Riv. Oranges, 95 m	7	
Ravine Digue, 80 m	33	
Ravine Morne Cabrit, 70 m	27	
Riv. Couleuvre, 15 m	74	
Riv. Carbet, Saut du Gendarme, 550 m	324	
Riv. Carbet, Fond-St-Denis, 230 m	3	
Riv. Carbet, aval	5	2
Riv. Galion, amont, 298 m	28	2
Rav. Palourdes, affl. Lézarde, 570 m	30	
Riv. Lézarde, Lérarde Deux, 180 m	13	
Riv. Lézarde, Glotin, 76 m	4	18
Riv. Lézarde, Soudon, 23 m	2	2
Riv. Blanche, Alma, 450 m	1	
Riv. Salée, Peter Maillet, 25 m		14
Riv. La Nau, La Suin, 48 m	1	18
Riv. Grande Pilote, Cassis Germont, 35 m	1	25
Riv. Petite Pilote, Desmartinières, 120 m	257	8
Riv. Petite Pilote, Concorde, 15 m	1	1
Riv. Simon, aval, 8 m		55
Study program 1999		
Grand Rivière, amont stadium	7	
Riv. Lorrain, Séguineau		1
Riv. Ste-Marie, Lassale	2	27
Riv. Carbet, aval		64
Riv. Galion, Grand Galion, 4 m	2	27
Riv. Lézarde, Soudon, 23 m		16
Riv. Dumauzé, usine Didier, 221 m	58	75
Riv. Case-Navire, Fond Rousseau, 23 m		2
Riv. Petite Pilote, Concorde, 15 m	2	1
Riv. Oman, Dormante, 10 m	43	25

Annex (1st part) : Martinique.
Provisional results : main study sites and material. * : mesh size = 0.3 mm.

Annexe (1e partie) : Martinique.
Résultats provisoires : principales stations et récoltes. * : vide de maille = 0,3 mm.

Stations (date)	**Species** (numbers of larvae / 0.2 m2) *	
GUADELOUPE	*H. guadeloupensis*	
Grand Rivière, Vieux Habitants, 05/96	19	
Riv. Ecrevisses, 12/05/96	2	
FRENCH GUIANA	*H. minuta* (new record)	*T. guyanensis* (new record)
Oyapok catchment :		
Riv. Camopi, amont Camopi, 03/11/98		1
Kaw mountain :		
Cr. St-Martin, route de Kaw, 02/09/96	25	
Cr. affl. Approuague, marais, 04/09/96	30	
Mahury catchment :		
Cr. Fourgassié (affl. Orapu), 28/06/96	16	
Outskirts of Cayenne :		
Cr. Mancellière, 30/08/96	37	
Cr. Innominée, 30/08/96	6	
1e cr. sur mont Matoury, 07/96	2	
2e cr. sur mont Matoury, 29/06/96	1	
Dév. Lac des Américains, 06/09/96	5	
Sinnamary catchment :		
Cr. du Muséum, 28/06/99		1
Riv. Kourcibo, saut Koumarou, 25/11/99		3
Riv. Kourcibo, racines aériennes, 29/06/99		2
Riv. Kourcibo, île, 27/11/99		1
Cr. affl. Kourcibo, 25/06/99	9	
Cr. Louée, aval Petit Saut, 04/12/99	1	
Cr. Roténone, aval Petit-Saut, 04/12/99	1	
Cr. Venus, aval Petit-Saut, 03/09/96	2	
Maroni catchment :		
Petit Inini, aval, 20/06/98		2
Inini, aval confl. Gd-Petit Inini, 20/06/98	1	
Maroni à Langa Tabiki, 03/06/99		1

Annex (2nd part) : French Guiana.
Provisional results : main study sites and material. Stations : ORTH et al. (2000).
* : mesh size = 0.3 mm.

Annexe (2e partie) : Guyane Française.
Résultats provisoires : principales stations étudiées et récoltes de matériel.
Stations : ORTH et al. (2000).
* : vide de maille = 0,3 mm.