CYTOLOGY, TAXONOMY AND ECOLOGY OF SPECIES IN THE GENUS <u>HELLICHIELLA</u>

(DIPTERA: SIMULIIDAE)

By

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"Truth is one, the sages
speak of it by many names"

The Vedas

"The fact that something is clearly stated in writing
does not significantly improve its chances of being
understood, remembered, believed or not used against you"

Maurice Yacowar

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ABSTRACT

The relationship among simuliid species in the genus _Hellichiella_ from Europe and North America was studied on the basis of their salivary gland chromosomes, morphology and ecology. The banding pattern of polytene chromosomes of eight species was examined and compared with that of _H. congareenarum_ defined by Dunbar (1967) as the standard. Species studied for the first time are _H. rendalense_ (from Norway), _H. latipes_ (_subexcisum_ syn. from Britain) and _H. saccai_ (from Italy) and the undescribed "Opinaga" (from Quebec) and "near dogieli" (from Norway). _H. congareenarum_, _H. anatinum_ and _H. innocens_ were restudied. These species were found to differ from the standard by a minimum of one and maximum of three fixed inversions. It is concluded that the sibling distinction between _congareenarum_ and _congareenarum_ 'b' proposed by Dunbar (1967) is not valid and that _H. anatinum_ differs from standard by only one inversion.

The genus _Hellichiella_ Riv.&Card. is redefined and distinguished from _Eusimulium annulum_ group sensu stricto. Described for the first time are the larva, pupa and male of both _H. rendalense_ and _H._ near _dogieli_ and the pupa of _H. fallisi_. The close relationship of these species is confirmed both chromosomally and morphologically.

The immature stages of _H. rendalense_ s.l. were discovered in shallow seepages with water current 1-30 cm/sec and temperature 10°-16°C in sloping sedge-_Sphagnum_ bogs. This habitat is the source of larvae

of these simuliids and the origin of first order streams which are secondarily colonized by these and other bog species. The occurrence of related species in similar habitats in the Nearctic and Palaearctic regions estabilishes that sloping Sphagnum bogs, primarily in the Boreal region, are the main source of Hellichiella species. Thus species of this taxon, some of which are known vectors of Leucocytozoon, are linked ecologically with Anopheline mosquitoes and Ceratopogonid flies. The theory is proposed that the breeding habitat of these vectors of haematozoa is the unifying factor in the epizootiology of Haemosporidia.

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the thesis.

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INTRODUCTION

In a study of the phylogeny of several species of Simuliidae
in the genus _Eusimulium_ Roubaud 1906 (sensu lato), Dunbar (1962) and
Wood (1963) recognized that several groups of closely related species
in the Nearctic had similarities to others in the Palaearctic. Within
this taxon Rubtsov (1959-64) recognized seven species groups: _annulum_
Lundström, _montium_ Rubtsov, _alpinum_ Rubtsov, _batoense_ Edwards, _latipes_
(now _vernum_ Macquart), _angustitarsis_ Lund., _aureum_ Fries and the genus
Schönbaueria Enderlein. Subsequently, Rubtsov (1974) gave generic
rank to most of these groups, except the _annulum_-group. In the Nearctic,
Wood (1963) and Dunbar recognized six species groups, of which the first
three, _rivuli_ Twinn, _baffinense_ Twinn and _euryadminiculum_ Davies,
correspond to Rubtsov's _annulum_-group.

In order to accommodate a number of species in the _annulum_-
group, Rivosecchi and Cardinali (1975) erected the genus _Hellichiella_
with _H. saccai_ Rivosecchi, 1967 as type species. Distinctive features
of the immature stages of _Hellichiella_ as larvae are: shallow gular
(postgenal) cleft; elevation of the lateral hypostomial teeth above
the median tooth; relatively long antennae which, in most species,
except _rivuli_ and _excisum_ D. P. + W., have the second segment
subdivided into four or more annuli. The pupae have one long
anteromedial projection on the cocoon, and the pupal respiratory
filaments number from four, six, eight, ten and twelve per side.

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However, specific identification is rendered difficult invariably by the close similarity of other morphological characters of larvae, pupae and adults.

This difficulty can be circumvented by comparative analysis of the banding pattern of the salivary gland chromosomes of such closely related species, as shown by Rothfels (1956) and Dunbar (1962,1967) and for other groups of simuliids by Professor K. H. Rothfels and his other students over the past thirty years. This method of relating cytospecies to corresponding morphospecies of simuliids provides a reliable and predictable determination and elucidates phylogenetic affinity among sibling and group species, as pioneered with vector species of Anopheline mosquitoes (Jucci 1952).

Since Dunbar's (1962;1967) initial study of Nearctic species now ascribed to Hellichiella, the question to be resolved is: How closely related are species of this taxon from Europe and North America? This question will be investigated by a study of the taxonomy, including analysis of the polytene chromosomes, and ecology of most of the species listed below.

Palaearctic Region

Hellichiella

dogieli Usova

fallisi Golini

latipes Meigen
(subexcisum syn.)

rendalenseGolini

saccai Rivosecchi

yerburyi Edw.

Nearctic Region

Hellichiella

anatinum Wood

congareenarum Dyar & Shannon

congareenarum 'b'

excisum Davies, Peterson & Wood

innocens Shewell

minor Dyar & Shannon

rivuli Twinn

Two of these species, H. rendalense and H. fallisi were described initially from adult females found biting ducks in Norway (Golini 1970; 1975), but their other developmental stages and ecology remained unknown. Indeed, the initial primary objective of the present study was to find and describe the larvae, pupae and male of one or both species, and determine their affinities to other species of Hellichiella. The discovery of the breeding habitat of these simuliids in 1979 and 1980 led to a further study of their ecology. This has resulted in understanding the ecology and distribution of other species of Hellichiella in relation to their potential as conveyors of haemosporidia to birds.

The results of this study are reported below under the following chapters:

1) Cytology. Comparison of the polytene chromosome banding pattern of some Palaearctic and Nearctic species of Hellichiella.

2) Taxonomy. The subgenus Hellichiella and description of species from Rendalen. Diagnosis of other species.

3) Ecology and Geographical Distribution of Hellichiella species.

Chapter 1

CYTOLOGY

Comparison of the Polytene Chromosome Banding Pattern of
Some Palaearctic and Nearctic Species of <u>Hellichiella</u>

GENERALITIES

In his study of the salivary gland chromosomes of six closely
related species of _Hellichiella_, Dunbar (1962;1967) identified the
following cytological segregates: _congareenarum_ which he designated
as the standard due to the centrality of its chromosome banding pattern
which is generally shared among the other segregates; _congareenarum_ 'b',
anatinum and _innocens_. Chromosomally, these species differ by a minimum
of one and maximum of two fixed inversion steps from the standard, and
morphologically they have in common secondary annuli on the second
segment of the larval antenna and 12 respiratory pupal filaments except
innocens which has 10. Dunbar placed these segregates together in the
congareenarum subgroup A; he differentiated them from _rivuli_ and
excisum which differ from the standard by about 15 different fixed
inversion steps and hence placed them in subgroup B. Morphologically
these last two species lack annuli on the second segment of the larval
antenna and have respectively 4 and 6 pupal respiratory filaments.

General Features of Salivary Gland Chromosomes

Polytene chromosomes of Simuliidae may be distinguished, in
addition to specific banding patterns, by general morphological features
common within certain species groups. The species of _Hellichiella_
considered in this study have the typical simuliid diploid chromosome
complement 2n=6 (n=3), each chromosome pair being numbered I, II and III

in order of decreasing length, as in other simuliids (Rothfels 1956,
1980). The chromosomes are metacentric; the centromere dividing the
short arm IS from the long arm IL in a ratio near 1: 1.1; chromosomes
II and III have arm ratios of 1: 1.5 and 1: 1.8 respectively (Dunbar
1967). In all species of the congareenarum subgroup A the homologous
chromosomes are loosely paired, with the maximum separation occurring
in latipes and saccai; this is a useful feature which facilitates
detection of inversion linkages. More compact, or ectopic pairing,
occurs invariably at the centromere region where a denser centromere
band is readily detected. Another feature distinguishing chromosome I
from the other two is the occurrence of an expanded region associated
with the centromere. In the second and third chromosomes the expanded
region consists of a small bulge near the centromere. The first
chromosome contains also the nucleolar organizer (NO), located on IL
near the centromere (in subgroup B it is on IS). In anatinum the NO
is relatively large and causes the expanded region to flare out as if
exploded; in saccai the NO may be expressed in only one of the two
homologues.

The Ring of Balbiani (RB), similar to that of the
fly genera Bibio and Chironomus, is located on IIS, as in other
species of Simuliidae (Rothfels and Dunbar 1953). Near the RB is a
slightly expanded band-free segment referred to by Dunbar (1967) as
"double bubble" which, together with the RB, helps to identify the
orientation of this portion of IIS. The para-Balbiani, similar to,
but smaller than the RB, is found on IIL. The third chromosome, being
the shortest, is also distinguished by the comparatively expanded or
frazzled end of IIIS. The above landmarks are represented in salivary
gland chromosome idiograms of the six species studied (Figs. 1-6).

MATERIALS AND METHODS

The initial work of Dunbar (1967) will provide the reference maps for comparison of the chromosome banding pattern of the additional species of the congareenarum subgroup A studied for this thesis. The larvae analysed in this study include species of H. rendalense sensu lato collected in Rendalen, Norway by the author; H. latipes (syn. subexcisum) from Knebworth Wood, Herts. and Dorset, southern England collected by R. W. Crosskey and J. A. Bass respectively; H. saccai from Lazio province, Italy collected by L. Rivosecchi; H. anatinum from Opinaga on the eastern side of James Bay, Quebec collected by C. Back; H. anatinum from Algonquin Park, Ontario and H. innocens from Valens marsh, near Dundas, southern Ontario collected by the author. H. congareenarum larvae were re-analyzed lately while writing this thesis. A sample of 12 larvae of this species was collected from Sussex County, Delaware, U.S.A. by R. W. Lake. A summary of these larval collections is shown in Table 1.

The larvae were fixed in the field in Carnoy solution (1:3 glacial acetic acid to 95% or absolute ethanol); in the laboratory salivary gland chromosomes were stained by the Feulgen method and prepared on glass slides by a standard method (Rothfels & Dunbar 1953; Dunbar 1958) and analysed in Dr. Rothfels' laboratory. The gonads of each larva were also preserved on slide with the chromosomes to determine

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the sex of the specimen; male larvae were distinguished by the spherical

testis and female larvae by the elongated ovary. The carcass of each

larva, after removal of the salivary glands, was preserved in alcohol

in a microvial corresponding with its particular chromosome slide

preparation. These larval carcasses, primarily of the Rendalen

collection, were subsequently analysed for morphological differences

which could be associated with different cytotypes related to morpho-

species. Whenever possible only penultimate and last instar larvae with

developing respiratory filament histoblasts were squashed for optimal

chromosome preparations.

Mapping of the salivary gland chromosomes follows the

convention developed for simuliids (Rothfels and Dunbar 1953; Rothfels

1956; Dunbar 1958, 1967; Basrur 1962; Bedo 1977). Referring to the

congareenarum standard (Dunbar 1967), the entire complement of all three

chromosomes is divided into 100 major, approximately equal sections

based on total complement length (%TCL). These sections are numbered

sequentially from 1 to 100, beginning at the tip of IS and to the end

of chromosome I, continuing through chromosome IIS to the end of IIL

and IIIS through to the end of IIIL. Each major section is subdivided

sequentially into sections A, B, C within which are identified

individual bands.

Photographic maps of chromosomes are used to show sections

and subsection limits with inversion break points. Inversions are

indicated by brackets; those for interspecific or fixed inversions

lie generally below or on the left, those for intraspecific or floating

(polymorphic) inversions lie generally above or on the right of the

chromosome. Fixed paracentric inversions are numbered in sequence of their discovery, independent of the species in which they are found and denoted by plain numerals, e.g. IIS-3 or IIIL -1. Overlapping inversions are denoted by numbers separated by commas, e.g. IS-1,2 indicates IS-1 is overlapped by IS-2, and by overlapping brackets. Floating inversions are placed in brackets, e.g. (IIS-3), and/or they are specified by an epithet of the species (Basrur 1962) in which they occur, followed by the inversion number, e.g. (IIIS ana-1) is a floating inversion in the short arm of chromosome III of H. anatinum. Chromosomes with inversions occurring specifically in either male or female larvae, i.e. sex linked inversions, are designated as sexually differentiated and denoted by X or Y usually followed by a subscript; hence, X_1:IIS-5 and X_2:IIS-5,6 represent two differentiated X chromosomes with linked inversions; sexually undifferentiated chromosomes are designated X_o and Y_o.

RESULTS

Generalities

All the species of this group have n=3 metacentric chromosomes with the standard arm association (Rothfels, 1980 p. 216). Pairing is relatively loose in all species except for H. innocens where it is quite tight. The nucleolar organizer (NO) in all members of the group is in chromosome I, probably always in the same position in the base of IL next to the centromere, though the extreme "looseness" of the expanded region makes this localization less than certain in some species (latipes, saccai). Following Dunbar (1967), the banding sequence of H. congareenarum as standard was retained because of the centrality of its arrangements in all six arms. The idiograms in Figs. 1-6 include an amended version for H. anatinum and diagrams for the five newly studied taxa. Dunbar (1967) includes idiograms for H. innocens and H. congareenarum. All idiograms are patterned on Dunbar's figure for H. anatinum; no attempt was made to represent the expanded centromere I regions of the various species realistically. For ease of reference, limits of fixed and floating inversions cited in the text are given in Tables 2 and 3.

Helichiella congareenarum

Dunbar distinguished H. congareenarum 'b' (Bruce Peninsula, Ontario) from H. congareenarum proper (one sample each from N. and S.

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Carolina). H. congareenarum 'b' was characterized by the fixed

overlapping inversions IIIL-6,7 and by the floating inversion IIL-3.

No sex chromosomes were noted but as the single sample of 12 larvae

was not sexed, conceivably there were only females. H. congareenarum

proper is standard in IIIL as well as in all other arms (by definition),

but has a very common inverted sequence in III (IIIL-1,50%) as well as

predominant IL inverted sequence (IL-4 98%) with IL-2 and IL-3 as rare

additional inversions. All males are heterozygous for a small

pericentric inversion IS-3 of the Y chromosome which is also anucleolate

(Dunbar 1967, Fig. 30). Both taxa have a pronounced secondary nucleolus

in IL, section 36, but, on the basis of their differences, Dunbar proposed

H. congareenarum 'b' as a distinct sibling of H. congareenarum. The

pupae are morphologically distinguished by the branching pattern of the

filaments (see Taxonomy section), those from the Carolinas having the

12 respiratory filaments essentially oriented forward and parallel, those

from the Bruce being arrayed over 180°, with some curving backwards.

The new small sample from Delaware supports the alternative interpretation

conceded as possible by Dunbar, namely, that H. congareenarum and

H. congareenarum 'b' are merely cytotypically differentiated populations

of one and the same widespread species. Of 11 larvae from Delaware

seven were homozygous IIIL-6,7/6,7 like congareenarum 'b'; the remaining

four were heterozygous st/6,7. More significantly all six males but

none of the five females had the sex differential segment IS-3 of true

congareenarum. No other heterozygous inversions were found in any of

the Delaware larvae, specifically neither the common IIIL-1 of

H. congareenarum nor IIL-3 of H. congareenarum 'b'. However all 11

larvae were homozygous for IL-4. Thus, the Delaware larvae combine features of H. congareenarum and H. congareenarum 'b', namely the predominance of IIIL-6,7 of 'b' with the sex chromosome system and prevalence of IL-4 of H. congareenarum. Especially the extensive heterozygosity for the alleged fixed inversion differences in IIIL indicates intermediacy of the Delaware population. The likeliest interpretation of these findings is that all four samples of H. congareenarum so far studied belong to one and the same species which exhibits gradients in floating inversions, IIIL-6,7 achieving fixation in the North, the standard IIIL sequence becoming fixed in the South with heterzygotes occurring in intervening populations. Likewise, the other floating inversions are distributed along clines, but the differentiated Y chromosome is probably common to the males of all populations; though, this remains to be proved for the Bruce Peninsula. Additional collections should substantiate this interpretation and eliminate H. congareenarum 'b' as a separate taxon. They should also clarify whether there really are consistent morphological differences in Northern and Southern pupae. In Fig. 38 pro tem. Dunbar's differentiation has been maintained.

Helichiella innocens

One additional sample of H. innocens was analysed. It conformed in all respects to Dunbar's description. It should be stressed that IIL of H. innocens is unique in having a wide band (center of section 60), instead of the single sharp one in what is otherwise the standard sequence (compare Figs. 29 and 30). All larvae shared the fixed IL-5 and IIIL-2,3 inversions. All 14 males had unpaired and complexly rearranged centromere

I regions with the anucleolate Y having the sequence illustrated by Dunbar (his Fig. 40) and interpreted as pericentric included (not contiguous) inversion pair, best represented as I-3.4. There is no doubt that the male sex chromosome configuration in our sample is identical to Dunbar's, but we have not attempted to verify in detail the stepwise derivation of Y nor the intermediacy of the H. congareenarum Y (I-3). In regard to floating inversions only Dunbar's IIIL-4 was seen. Seven larvae were st/st, 10 st/inv. and 2 inv/inv.

Helichiella anatinum

Dunbar (1967) describes H. anatinum as having fixed inversions in IIS (IIS-1), as having six floating inversions (IS-1, IS-2, IL-1, IIL-2, IIIS-2) and no identified sex chromosomes. Dunbar's records from Churchill, Manitoba and South/Central Ontario are supplemented by samples from the east side of James Bay and a few "workable" larvae from Algonquin Park, Ontario. These samples confirm the cytological description and documentation of Dunbar except for the following:

1) There is no fixed IIIS inversion. The standard sequence occurs (Fig. 27) and in fact is the predominant one in Quebec. There is a floating inversion (IIIS ana-1) with limits close to those shown by Dunbar for his fixed inversion (IIIS-1). His Fig. 51 shows the (in Quebec) rare inversion homozygote. His floating inversion IIIS-2 is spurious (i.e. it represents the standard sequence with slightly false limits). With respect to the IIIS polymorphism one Opinaga sample comprised eight st/st and seven st/inv zygotes.

2) In our samples, inversion IIL-1 (Fig. 29) of the standard sequence (Fig. 30) represents the X chromosome. In Opinaga all 17 scored

females were inv/inv, 9 males were st/inv and one male was sex
exceptional – inv/inv. Thus the standard sequence has been retained
as the Y and the inverted sequence is the X. In the Churchill
material Dunbar (1967) noted this inversion, but since he did not sex
these larvae, did not relate the inversion to sex. He did sex the
"Southern" populations with a total of 15 males and 21 females. For
these he recorded only five IIL-1 heterozygotes (sex not specified).
To the extent that the data are reliable it would appear therefore that
IIL-1 in Southern populations is at best a rare Y chromosome, if the
inversion is sex linked at all. The few Algonquin Park larvae consist
of two males st/inv and two females inv/inv. At Churchill, Dunbar (1967)
found in high frequency the overlapping sequence IIL-1,2 as well as
IIL-1 and standard (heterozygotes, scored only). Assuming that the
sex chromosome system in Northern populations (i.e. on both sides of
James Bay) is similar, we interpret IIL-1 as the basic (X_1) X chromosome
and IIL-1,2 as a derived X_2 type, so far, not observed outside Churchill.

3) Dunbar's documentation of a subterminal secondary NO in
IS (section 6) is indisputable (Fig. 7); a NO in this position occurred
homozygously, heterozygously and "azygously". In contrast in all the
analysed larvae from Opinaga and Algonquin Park, the secondary NO was
subterminal in IL (section 36) as in H. congareenarum and H. innocens,
and it was always homozygously expressed. Thus, it is possible that
populations differ with respect to position of the secondary NO and
that the IS site is characteristic of the Churchill population.

In regard to floating inversions in arms other than IIIS and
IIL, Dunbar recorded IS-1, IS-2 and IL-1, the last two being confined

to Churchill. We have observed IS ana-1 (Fig. 7) heterozygously in two

of the four Algonquin Park larvae and a new near – mimic IS-1 inversions

(IS ana-3, Fig. 7) in three of 25 Opinaga larvae scored in this regard.

IIS-1 (Fig. 16) remains as the sole fixed rearrangement of standard in

H. anatinum. As pointed out already by Dunbar it is of special

"directional" significance in that it is shared by a large series of

species in other groups of Eusimulium.

"Opinaga" Cytotype

Among the samples from James Bay identified as H. anatinum by

C. Back was one sample of six larvae (OP 101) which clearly represented

a different and new species both because it matures later in the season

(Table 1) and because of its cytological characteristics. It may seem

strange to base claim for new species status on a single small sample

of larvae; however, it is the nature of the cytological evidence that

makes such statements possible. The new species designated "Opinaga" is

chromosomally absolutely distinct in a number of ways. The IIS sequence

(IIS-2, Fig. 17) is diagnostic being a simple fixed inversion of standard

(Fig. 16) confined to this species. Likewise IIIL differs from standard

(Fig. 32) by a fixed rearrangement. The characteristic feature of this

IIIL-1 is the placement of the marker (M) region (95B - 96A) in reverse

orientation next to 90/91 (Fig. 35). This arrangement could be accounted

for by a simple fixed inversion, but there may be additional distal

changes, since the IIIL end of "Opinaga" could not be convincingly

homologized with standard. While the IIIL sequence is certainly diagnostic

for this species, its complete resolution would be very desirable. The

intriguing possibility exists that the inferred large/simple inversion

IIIL-1 of this species may be the first step in the derivation of the complexly rearranged IIIL of H. rendalense (see below). IIIS, IIL and IL are all standard (Figs. 26,30 and 31, 12). IS is the sex arm. There is a fixed inversion IS-1 (Fig. 7), and this sequence serves as the X chromosome. The Y chromosome is characterized by an additional overlapping inversion IS-1,2 (Fig. 7). The statement that these are sex differential segments can certainly be challenged on statistical grounds, there being only four males all XY and two females both XX. However, little doubt is felt that future larger samples will confirm this somewhat intuitive identification of the sex arm. A secondary NO is in IL in the standard position (section 36). No heterozygous autosomal inversions were noted in the small sample. To emphasize, the new species differs from H. anatinum in lacking IIS-1, by having the fixed inversions IIS-2, the rearranged IIIL, the sex arm IS (anatinum IIL) with one fixed inversion IS-1 in the X and an additional one in the Y, and by lacking floating inversions characteristic of H. anatinum. To find a sample, even of only six larvae, homogeneous for all these features among populations of H. anatinum, without any indications of hybridity, certifies species status on chromosomal evidence alone. Its later seasonal development supports its distinctiveness from H. anatinum which apparently is univoltine and certainly develops much earlier (Table 1). Unfortunately, none of the larvae was mature, and therefore the number of respiratory filaments could not be determined.

Hellichiella near dogieli

In bog seepages and bog drainage streams in Norway two species were found that cytologically belong to subgroup A of Dunbar's group 1.

Larval morphology (histoblasts with 12 respiratory filaments per side,

four or more annuli per second antennal segment supports this assignment

(see Taxonomy Chapter).   The first of these species is provisionally

designated H. near dogieli since the larval morphology differs from that

of H. dogieli in several important respects. Specifically, in H. dogieli

the mean ray number in the primary head fan is 63 in H. near dogieli it

is 73; in H. dogieli the gular cleft is longer than wide, in H. near

dogieli it is wider than long (see Taxonomy section). Authentic (?)

dogieli (as Greniera) was examined chromosomally by Chubareva and

Petrova (1979) but no details have been published to my knowledge.

All arms of H. near dogieli are standard (see Fig. 38, IIIL)

except IIS which is fixed for the simple inversion IIS-3 (comp. Figs. 19

and 20). This sequence is also the Y chromosome of H. rendalense (Figs.

20 and 21). The sex arm of H. near dogieli is not known with certainty,

most slides being rather poor, but there is a strong suspicion that

non-pairing of the centromere I region is preferentially or exclusively

found in males, and in some there is also a suggestion of a IS base

heterozygous arrangement. There is no conspicuous secondary NO. There

are floating inversions, particularly a small one that disrupts the IIIL

marker (M) segment, but the details have not been worked out.

Hellichiella rendalense

The second species of group 1 subgroup A in Norwegian bogs is

rendalense. In this species the IS, IL (Fig. 14), IIL (Fig. 30) and

IIIS arms are standard, and the secondary NO is always found homozygously

in IL section 36 (Fig. 14).

The diagnostic features of this species are in IIIL and IIS.

In IIIL (Fig. 34) three major rearranged segments have been identified approximately as follows:

-91A1.97C4-97A1.91A2-91B4.96C5-91B5.97C5-

conveniently symbolized as 1.7-6.2-3.5-4.8. The position and orientation of these segments indicate a minimum of three steps from standard and therefore the existence of two cryptic (i.e. small undetected) rearranged segments or a number of coincident breaks in separate inversion steps. A reasonable derivation of rendalense IIIL from standard is:

standard   1.2-3.4-5.6-7.8

Hypo 1   1.5-4.3-2.6-7.8

Hypo 2   1.7-6.2-3.4-5.8

rendalense   1.7-6.2-3.5-4.8

However, it should be noted that this derivation is not unique in any step, for all permutations of the order of the three inversions would give the sequence observed in H. rendalense. The derivation given above is interesting in a phylogenetic context, because, as already suggested in the "Opinaga" section, hypothetical step 1 may be identical with the large simple inversion IIIL-1 stipulated for "Opinaga". If this is so, "Opinaga" would have to be placed on a common lineage with H. rendalense. Regardless of the stepwise interpretation of the origin of H. rendalense IIIL, the sequence is entirely diagnostic for this species, most conspicuously in position and orientation of the marker (M) segment, corroborated by the placement of the conspicuous double band in 97B.

IIS is the sex arm of this species. The basic X and Y chromosomes differ by independent simple inversions from standard (Fig. 16). The X inversion (IIS-5) has limits shown in Fig. 18; the Y sequence (IIS-3)

is identical to the IIS sequence of <u>H.</u> near <u>dogieli</u> (Fig. 20). There
is a rarer derived Y_2 inversion (IIS-4) overlapping IIS-3 (Fig. 21)
which is found in about 20% of the males. There is also a second X
chromosome (X_2:IIS-6) derived by an included (in X_1) inversion (Figs. 16
and 18) which is readily recognized by the reversal of a segment including
the Balbiani ring. This X_2 chromosome predominates; it was found, in
17 of 20 males, and contributed 68 constituents in 84 X chromosomes
identified in females. Thus about 20% of the X chromosomes are X_1,
the remainder X_2. The various sex chromosomes were associated at random
in both sexes, and there were no sex exceptions; all males were XY of
sorts and all females XX.

There is a floating inversion in IS (Fig. 8) similar but not
identical to IS ana-1 or 3. It was seen heterozygously only five times
in 50 larvae.

<u>Hellichiella</u> <u>latipes</u>

<u>H. latipes</u> is the name now given to the former <u>subexcisum</u>
Edwards; <u>E. latipes</u> auct. being <u>E. vernum</u> Macquart (Crosskey and Davies,
1972). Larval samples from Sussex and Dorset, Britain, conformed to
each other. Chromosome arms IS (Fig. 9), IIS (Fig. 19), IIL (Fig. 31)
and IIIS (Fig. 28) are standard. IL has a simple inversion IL-1 (comp.
Figs. 15 and 13). The IIIL arm is complexly rearranged (Fig. 36).
Five rearranged segments have been identified as follows:

-91C7.97C4-98C1.93B1-95B5.100A2-98C2.93A5-92A1.97C3-95B6.100A3-

or more simply:

1.8-9.4-5.11-10.3-2.7-6.12

This sequence can be accounted for by three inversion steps from standard

without coincident breaks:

	standard	1.2-3.4-5.<u>6-7.8-9.10-11</u>.12
	Hypo 1	1.<u>2-3</u>.4-5.<u>11-10.9-8</u>.7-6.12
	Hypo 2	1.8-9.<u>10-11</u>.5-4.3-2.7-6.12
	<u>latipes</u>	1.8-9.4-5.11-10.3-2.7-6.12

The first step is mandatory but steps 2 and 3 are interchangeable having

an including-included relationship. Step 1 is of special interest since

it results in the IIIL end typical of <u>H. excisum</u> in subgroup B (comp.

Figs. 36 and 37). If Dunbar's postulated derivation of the <u>H. excisum</u>

sequence is correct, the second and third steps of <u>H. latipes</u> are not

shared by <u>H. excisum</u>, since Dunbar's second step displaces sections

89-91 that are in the standard position in <u>H. latipes</u>. Hypo 1 then is

the first step in the derivation of both the <u>latipes</u> and the <u>excisum</u>

sequences but is the only one shared by them, leading to the phylogenetic

pattern shown in Fig. 38.

All males of <u>H. latipes</u> are heterozygous for a non-pairing

region in the base of IIS (Fig. 22), the X chromosome relative to the

Y having some extra bands including a more or less deeply staining

hetero (H) band and a more compact centromere band. All females are

homozygous for the longer constituent (Fig. 23). In slides with poorly

banded chromosomes, consistent failure of pairing in the IIS base by

itself suffices to indicate a larva of male sex. Because of the

generally rather amorphous banding in the pericentric regions, it is

impossible to state unequivocally whether the X or the Y has the

standard sequence (Fig. 16) of <u>H. congareenarum</u> and <u>H. innocens</u>, but

it is probable that the H- band in the Y chromosome is deleted rather

than added in the X (see <u>H. saccai</u>). An inversion in IIIS was found

once and is shown heterozygously with standard (Fig. 28, upper constituent).
A second heterozygous inversion in IL (Fig. 15) was also found only once.

An incidental observation is of relevance in regard to the
status of the controversial species H. yerburyi from Britain. H. yerburyi
differs from H. latipes in the larva essentially only in having eight
respiratory filaments per side instead of six (Edwards1920; Davies 1966).
One of our H. latipes samples from Dorset included a pupa with eight
filaments enclosing a pharate male; more significantly, at least one of
the mature larvae sent as H. latipes also had eight respiratory filaments
on each side. It was a male and conformed to typical H. latipes in all
respects, including the details of the sex chromosomes. While this does
not exclude the possible existence of a truly distinct eight-filamented
H. yerburyi, the findings tend to reinforce the scepticism expressed by
others (Grenier 1953; Davies 1966; Crosskey, pers. comm.) regarding the
reality of H. yerburyi .

Hellichiella saccai

H. saccai (with 10 pupal filaments) and latipes (normally with
6 pupal filaments) are extremely closely related cytologically. They
share the basic sequence in all six arms, i.e. IS, IIS, IIL and IIIS
are standard, IL carries IL-1 (Fig. 15) and IIIL of H. saccai is
identical to the complexly rearranged one of H. latipes (Fig. 36). The
only clear difference is in the sex chromosome system. A IIS base H-band
polymorphism suggestive of and probably identical to the XY system in
latipes, exists also in saccai, but in this species it is strictly
autosomal, i.e. +/+, (Fig. 25) +/- (Fig. 24) and -/- occurs in equal
proportions in males and females. The numbers were 15, 16 and 2 for
males, and 7, 12 and 2 for females, with some indication of excess

heterozygotes. Parenthetically, occurrence of the -/- type supports
ancestrality of this sequence in that it eliminates the need to postulate
the viability of a deletion homozygote.

In H. saccai it is apparently the first chromosome that is sex
determining. The only manifestation of this is that in males the NO
is always expressed in one constituent only (+/-, Fig. 11) interpreted
to be the X, while in the female both NO are equally expressed (+/+,
Fig. 10). This of itself would not prove that the centromere I region
is sex determining – it could be a regulation phenomenon, one NO being
turned off in males – were it not for the fact that the Y is
characteristically anucleolate in a very large number of instances in
black flies where its identity can be certified by additional
rearrangements or inversion markers, as for instance in both
H. congareenarum and H. innocens of this paper. Where sex chromosomes
are not also nucleolar, the expression of NO is generally indentical
in males and females which 1) supports the above identification of the
H. saccai sex chromosomes and 2) suggests a functional significance:
an anucleolate Y chromosome is parsimonious in as much as the sperm does
not require ribosomal RNA. (Where the XY is not also the NO +/- pair, a
random assortment would cause the egg and sperm to be lacking in
ribosomal cistrons in equal proportions).

No heterozygous inversions were seen in H. saccai.

DISCUSSION

A summary of fixed rearrangements and sex differential segments relative to H. congareenarum as standard is shown for eight species of Helichiella in Table 4. This study amends the prior study of Dunbar (1967) in showing that in H. anatinum the standard sequence occurs in IIIS,.thus reducing the fixed differences from H. congareenarum to one (IIS-1) and in identifying the sex arm as IIL, the Y retaining the standard sequence, while the X has either a single inversion (IIL-1) or an overlapping pair (IIL-1,2). The idiogram for H. anatinum (Fig. 1) is modified accordingly.

The evidence of the present study suggests that Dunbar's distinction of congareenarum and H. congareenarum 'b' cannot be maintained since a population from Delaware contains features of both: though IIIL-6,7 of H. congareenarum 'b' predominates (considerable numbers of st/6,.7 heterozygotes are found), all individuals had IL-4 and all males the Y chromosome of true H. congareenarum. Accordingly, H. congareenarum as represented by the four cytologically studied populations is considered a unitary species with gradients in inversion polymorphisms. A revised idiogram should show the standard sequence for Helichiella, the Y differential segment (IS-3) as shown by Dunbar (1967) for H. congareenarum, with all other inversions, including IIIL-6,7 shown as floating.

The species studied here cytologically for the first time include an undescribed species designated 'Opinaga', known from a single

larval collection (James Bay, Quebec) with diagnostic IIS, IIIL and sex chromosome (IS) sequences. It matures later than the essentially sympatric H. anatinum and is evidently reproductively isolated from it.

Two species from Norwegian bogs were studied; the first H. near dogieli differed from standard only in a single fixed inversion (IIS-3) and probably in a sex differential segment based on the centromere region of chromosome I; the second, H. rendalense, differed from standard in a complexly rearranged IIIL arm and by X_1X_2, Y_1Y_2 polymorphic sex chromosome system based on IIS.

The fourth newly studied species H. latipes (subexcisum auct.) from Britain has the standard sequence in all arms except IL (IL-1) and IIIL which is again complexly rearranged but quite different from that of H. rendalense. IIS is the sex arm, the X chromosome having a number of basal extra bands not found in the Y and a tighter centromere band resulting in non-pairing in that region.

The fifth newly studied species, H. saccai, from Italy is cytologically identical to H. latipes in all six arms, but the IIS X and Y sequences of H. latipes are an autosomal polymorphism in H. saccai. Sex determination appears to be based on the centromere I region, the Y chromosome being anucleolate (females NO +/+, males NO +/−).

The cytological diagnoses of these eight species are further amplified by inclusion of data on inversion polymorphism, position of secondary nucleolar organizers, and features of the centromere regions. The essential diagnostic features of all newly studied species are shown in idiograms (Figs. 1-6). The complexly rearranged IIIL of H. rendalense and H. latipes/saccai are shown in toto in the photocomposites of Fig. 34 and 36. Similarly, the species differences

in all other chromosome arms are illustrated in Plates 1-4. The details given should be adequate to constitute a cytological description of each of the taxa (studied), and should enable others to identify cytologically larvae of all eight taxa, including the undescribed "Opinaga".

In a purely taxonomic context these findings have some bearing on the problem of the specific distinctness of H. latipes, H. yerburyi and H. saccai. With respect to H. yerburyi, the finding of an 8-filamented male larva which in all respects, including sex chromosome details, conforms to H. latipes males indicates the possibility that H. yerburyi does not exist as a distinct species. Likewise, with respect to the taxonomic distinction of H. latipes and H. saccai, cytology leaves us somewhat in limbo, since their chromosomal differences are confined exclusively to the presence of non-homologous sex chromosomes. There is taxonomic precedent at least in the Chironomiidae for considering populations with non-homologous sex chromosomes as conspecific, e.g. some populations of Chironomus tentans have sex determination based on chromosome I, others on II (Beermann, 1955) and yet others have even substituted female heterogamety for male heterogamety – yet they are all considered the same species and are crossable in the laboratory (Thompson and Bowen, 1972). In black flies in general it is considered that separate sex chromosome systems indicate different species, and a number of studies, notably those of Newman (in press) on sympatric Prosimulium onychodactylum sibling species with differing sex chromosomes, support this concept. Nonetheless, the derivation of these siblings, like those of Simulium vittatum, (Rothfels and Featherston , 1981) implies a plesiomorphic intraspecies polymorphism for non-homologous sex

chromosomes. As is generally the case, the taxonomic and cytogenetic problems should be settled by further – in between – sampling rather than by continued hypothesizing.

Beyond the cytological diagnoses it is desirable further to attempt to establish cytophylogenetic relationships within the subgroup and eventually to extend comparisons to Eusimulium and Simulium at large. A provisional chromosome phylogeny of the species studied in Helichiella is shown in Fig. 38. Failure to resolve the IIIL sequences of 'Opinaga' and H. rendalense completely leads to two alternative interpretations of 'Opinaga'. Our preference is to assume that IIIL of 'Opinaga' is independent of the IIIL rearrangement sequence leading to H. rendalense. However, the possibility is not excluded that the 'Opinaga' sequence leads to the H. rendalense one, which would place 'Opinaga' with the palaearctic species. For the present the phylogeny places the nearctic species of Dunbar's subgroup A on one side and the palaearctic ones on another without any common steps. Between subgroups A and B it is certain that H. latipes/saccai (A) share a common first step with H. rivuli/excisum (B). As already pointed out by Dunbar, the IIS-1 inversion, fixed in H. anatinum, is of special directional significance, in that it is characteristic of a large series of Eusimulium, including pugetense D. & S., vernum (latipes auct.), gouldingi Stone, croxtoni Nicholson and Mickle and others. The present study has extended the list of species sharing the IIS-1 sequence. On the other hand, Dunbar's inference of a simple inversion difference in IIS between H. anatinum and Cnephia dacotensis (Procunier, 1975), and therefore his postulate of a linear IIS series: Cnephia – anatinum – congareenarum, is erroneous. This situation is more complex and requires re-examination.

TABLE 1

Samples of larvae of <u>Hellichiella</u> species analyzed cytologically

	Sussex, Delaware, USA 5-V-1982
<u>congareenarum</u>	6 / 5

		James Bay, Opinaga, Quebec			Algonquin Pk., Ontario
		29-V-1978		26-VII-1978	8-14-V-1980
<u>anatinum</u>	♂ 4	8	2		2
	♀ 1	17	2		2
Opinaga	♂			4	
	♀			2	Valens Marsh, Dundas, Ontario
					7-V-1981
<u>innocens</u>	♂				14
	♀				6

		England			Italy
		Knebworth	Dorset		Lazio
	1981	28-III	29-III	9-III-82	10-III-1981
<u>latipes</u>	♂	14	4	67	
	♀	9	3	49	
<u>saccai</u>	♂				35
	♀				18

Rendalen, Norway

	1979	24-VI	26-VI	28-VI	1-VII	2-VII	11-VII
	N	93	96+99	111	123	131	145
<u>rendalense</u>	♂	2	2	32	8	6	8
	♀	5	8	47	14	22	13
near <u>dogieli</u>	♂	2	0	0	0	0	0
	♀	1	0	2	0	0	0

	1980	9-VI*	14-VI	25-VI	1-VII	2-VII*	6-VII	12-VII
	N	176-180	198	241	257	261	271	283
<u>rendalense</u>	♂	3	0	17	2	0	4	0
	♀	3	0	7	2	0	6	0
near <u>dogieli</u>	♂	10	2	5	0	-2	0	0
	♀	15	0	19	0	3	0	1

* Asmyrtjorna

TABLE 2   27

Interspecific inversions (H. congareenarum as standard).

Species	Inversion	Sequence
innocens	IL-5*	-31A4.42C3-31A5. 42C4
	IIIL 2,3*	-90C.92C-91C1.95C4-93A1.91A1-91B5.96A1 -
anatinum	IIS-1*	-48C1.53A4-48C2.53A5
Opinaga	IS-1	-6C.16B-7A1.16C1-
	IIS-2	-50C.53B3-50C.53B4
	IIIL-1	-91A1.96B1-91A2.96B2 plus rearranged end?
near dogieli	IIS-3	-48B1.54A3-48B2.54A4
rendalense	IIIL-4,5,8	-91A1.97C4-97A1.91A2-91B4.96C5-91B5.97C5-
latipes and	IL-1	-31A2H. 34C-31A3. 34C
saccai	IIIL-9,10,11	-91C7.97C4-98C1.93B1-95B5.100A2-98C2.
		.93A5-92A1.97C3-95B6. 100A3-

*Cited from Dunbar 1967

TABLE 3

INTRASPECIFIC   INVERSIONS

28

Species	Inversion	Sequence
congareenarum	IS-3*(Y)	-20A.23A-20B.23B-
	IIL-3	-61A3.67B-61A4.67C1-
	IIIL-1*	-92C5.96A5-93A1.96B1-
	IIIL-67*	-92B4.97C1-97A7.99C-97C2.92B5-97A6.100A1-
innocens	IS-3,4*(Y)	-19C1.28C1-23A.20C-22C.20B-19C.28C2**
	IIIL-2,3,4*	-94B5.96A4-96A1.91B5-91A1.93A1-94C1.96A5
anatinum	IIL-1*(X)	-64B7.70A3-64C1.70A4-
	IS-1*	-7B1.14B3-7B2.14B4-
	IS-3	-8A3.15B4-8A4.15B5-
	IIIS-1	-76A4.80C3-76A5.80C4-
Opinaga	IS-1,2(Y)	-5C.8A5-16B.6C1-6A.8A4-7A1.16C1-
near dogieli	Y	centromere I rearranged
rendalense	IIS-3(Y$_1$)	-48B1.54A3-48B2.54A4-
	IIS-3,4(Y$_2$)	-47A3.52A-54A3.48B1-47A4.51C-48B2.54A4-
	IIS-5(X$_1$)	-47C3.54B1-47C4.54B2-
	IIS-5,6(X$_2$)	-47C3.51C-51A.48B4-50C.48B5-47C4.52A-
	IS-1	-8A4.13C1-8A5.13C2-
latipes	IL-1	-38A.35C-38B.35C
	IIIS-1	-76C3.78B-76C4.78C

*Cited from Dunbar, 1967.
**Underlining indicates the relevant inversion step.

Table 4. Fixed inversions and sex differntial segments of Hellichiella spp. relative to congareenarum standard.

Species	IS	IL	IIS	IIL	IIIS	IIIL
congareenarum	Standard Y: I-3	Standard	Standard	Standard	Standard	Standard
innocens	Standard Y: I-3,4	IL-5	Standard	Standard	Standard	IIIL-2,3
anatinum	Standard	Standard	IIS-1	Standard X1: IIL-1 X2: IIL-1,2	Standard	Standard
Opinaga	IS-1 Y: IS-1,2	Standard	IIS-2	Standard	Standard	IIIL-1
rendalense	Standard	Standard	X1: IIS-5 X2: IIS-5,6 Y1: IIS-3 Y2: IIS-3,4	Standard	Standard	IIIL-4,5,8
near dogieli	Standard	Standard	IIS-3	Standard	Standard	Standard
latipes	Standard	IL-1	Standard X: Hb+ Y: Hb-	Standard	Standard	IIIL-9,10,11
saccai	Standard	IL-1 X: NO+ Y: NO-	Standard Hb+/Hb- (autosomal)	Standard	Standard	IIIL-9,10,11

Figs. 1-6. Salivary gland chromosome idiograms of

Hellichiella species. C, Centromere; R, ring of Balbiani; P, para-

Balbiani; F, frazzled end; N, nucleolus; N_2, secondary nucleolus; M,

marker indicating position and orientation of re-arranged segment on

IIIL (section 95B-96A). Fixed inversions: brackets on the left hand

side numbered consecutively from standard as in IIS-1. Floating

inversions: brackets on the right hand side singly numbered on the

appropriate idiogram or with abbreviated specific epithet and consecutive

numbering within the species as in IIIS ana-1. Y-chromosome differential

segments: dashed brackets; X-chromosome differential segment: dotted

brackets. Sex chromosomes are also designated as X_0Y_0 where cytologically

undifferentiated and as $X_1X_2\ldots$, $Y_1Y_2\ldots$ for sex chromosomes of increasing

complexity.

Figs. 7-37. Photographic maps of the six chromosome arms IS,

IL, IIS, IIL, IIIS, IIIL. S and L stand for short and long arms for I,

II and III. Each arm is subdivided into sections in sequence from IS

to IIIL totalling 100 in complement. Each section is subdivided into

subsections A,B,C within which bands may be enumerated and are thus

specified by a ternary designation. Section and subsection limits are

those of Dunbar (1967) for the group standard: congareenarum. For

each arm the standard (reference) sequence is reproduced from his paper,

courtesy of Dunbar. Novel arrangements are indicated either by brackets

or arrows on the standard sequence and/or the actual sequence is shown

especially where complexly different from standard. Floating inversions

are designated by a specific abbreviation followed by numbers which are

consecutive within species, e.g. IIIS ana-1. For a more complete description

see Bedo (1977, pp. 39-40).
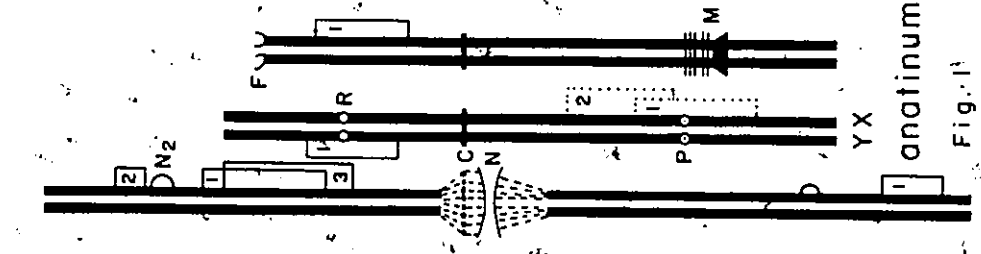
saccai Fig. 6

latipes Fig. 5

rendalense Fig. 4

nr. dogieli Fig. 3

opinaga Fig. 2

anatinum Fig. 1
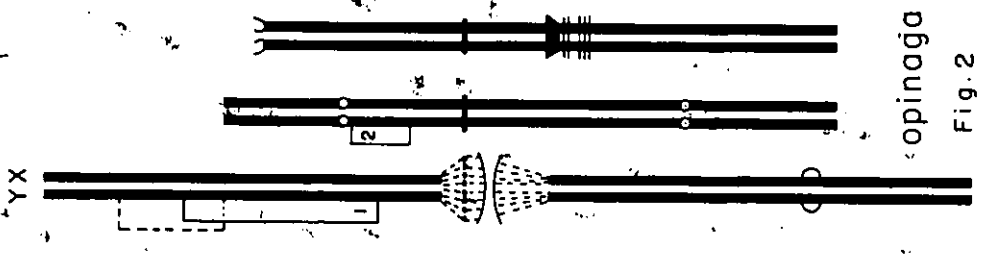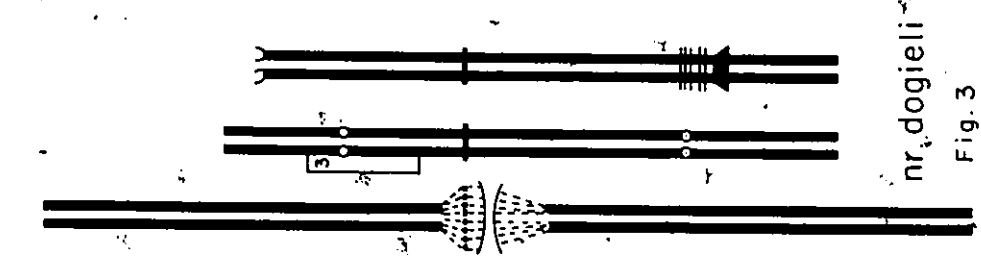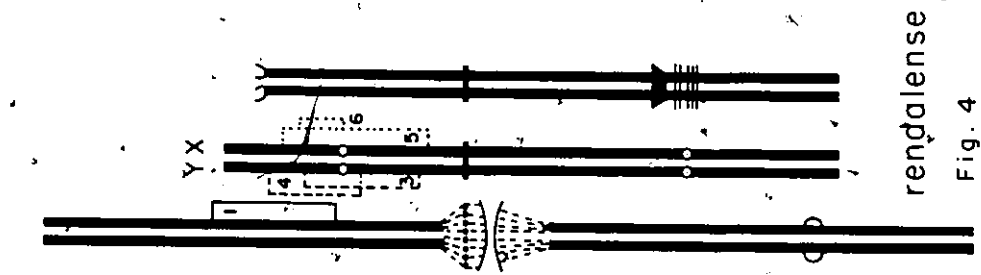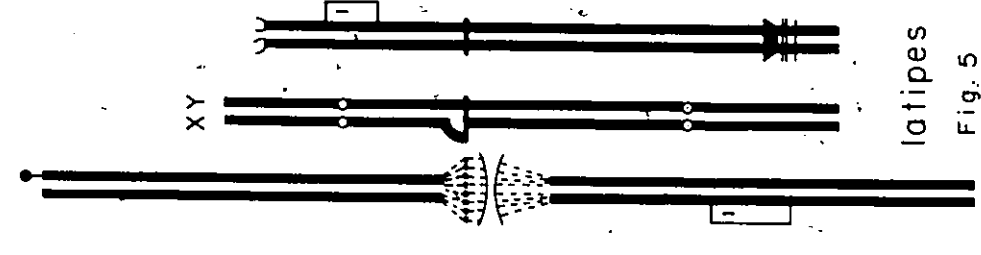
Plate I. Figs. 7-11. IS chromosome banding sequences.

Note: seven of the eight taxa of this paper have the standard sequence in IS (Figs. 7,8,9), though IS-3 and IS-3.4 serve as Y chromosome differential segment in _congareenarum_ and _innocens_, see Dunbar 1967, Figs. 30 and 40. "Opinaga" has a simple fixed inversion marking the genetic X chromosome plus an additional overlapping inversion marking the Y chromosome (brackets below Fig. 7). IS of _latipes_ occasionally has a heterochromatic end piece not shown in the plate, but shown in the idiogram Fig. 5.

Fig. 7. IS standard sequence as displayed in _anatinum_ (Dunbar 1967, Fig. 20), showing sections 1-19 (sections A, B, C, in most cases), the secondary nucleolus heterozygously expressed, and the floating inversions ana-1 (Algonquin Park), ana-2 (Churchill), ana-3 (Opinaga), as well as the fixed inversion IS-1 of Opinaga (=X_o) and the break points of its Y chromosome sequence.

Fig. 8. IS standard sequence in _innocens_ (Dunbar 1967, Fig. 21) with more representative details in sections 1-10, showing also the break points of the _rendalense_ floating inversion (ren-1).

Fig. 9. IS of _latipes_ (Dorset-Britain) showing sections and subsections conforming to standard sequence.

Fig. 10. IS of _H. saccai_ $NO^+/^+$ (homozygously expressed nucleolar organizer) characteristic of females.

Fig. 11. IS of _H. saccai_. $NO^+/^-$ heterozygously expressed nucleolar organizer) characteristic of males.

31

Fig. 7

Fig.8

Fig. 9

Fig.10

Fig.11

IS

IL

C

NO+/+

? Y NO−

NO+

Is

IL

C

C
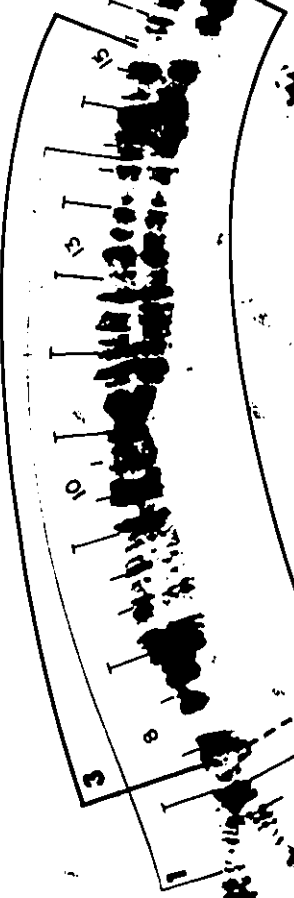
Plate II. Figs. 12-15. IL arm banding sequence.

Note: five of the eight taxa have the standard sequence in IL; exceptions are _innocens_ with the large inversion designated IL-5 (Dunbar 1967, Fig. 32), and _latipes_ and _saccai_ which have in common the fixed inversion IL-1.

Fig. 12. Dunbar's (1967) standard sequence of _anatinum_ showing the sections 25-44 and in general subsections A, B, C, and also the fixed IL-5 inversion of _innocens_.

Fig. 13. _H. innocens_ "synthetic" IL standard sequence. The fixed inversion sequence IL-5 has been rotated to simulate the standard sequence for better resolution and to facilitate comparison with IL-1 of _latipes_ (see bracket in Fig. 15).

Fig. 14. Photocomposite of the IL standard sequence of _rendalense_ showing the conspicuous secondary nucleolus (NO_2) characteristic also of _congareenarum_, _innocens_, Opinaga and some _anatinum_ specimens. Arrows connect homologous bands.

Fig. 15. Photocomposite of the IL sequence of _latipes_ (Britain) showing the limits of the fixed inversion IL-1 of _latipes_ and _saccai_ and the absence of NO_2.
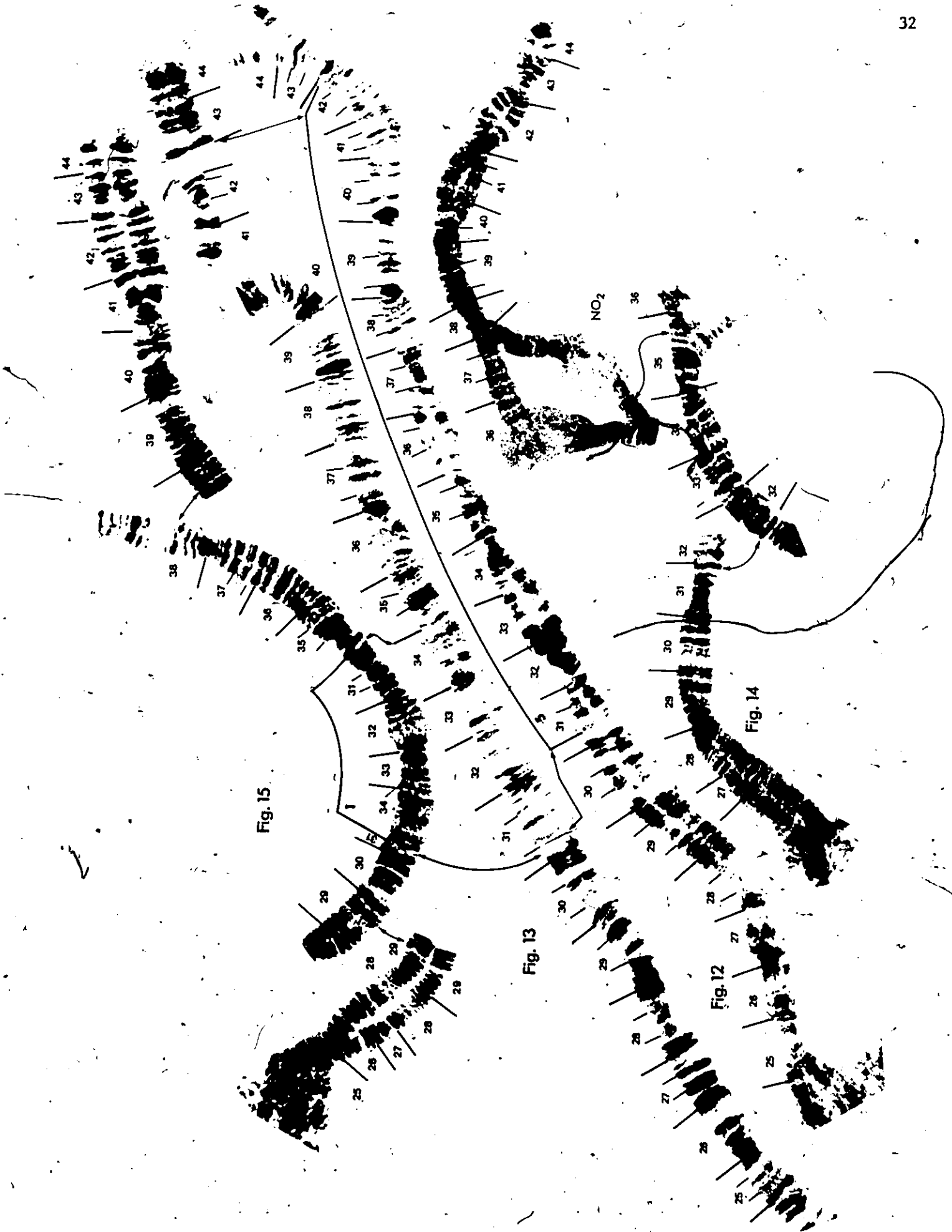
Fig. 12

Fig. 13

Fig. 14

Fig. 15

NO₂

Plate III. Figs. 16-25, IIS and Figs. 26-28, IIIS sequences.
Note: IIS is a rather diversified arm which exhibits the standard
sequence only in congareenarum (by definition), innocens, latipes and
saccai. In contrast, the standard sequence in IIIS occurs in all eight
taxa.

Fig. 16. IIS standard sequence of innocens (Dunbar 1967,
Fig. 42), showing arrowed IIS-2 of "Opinaga" and bracketed IIS-1 of
anatinum.

Fig. 17. "Opinaga" sequence showing the limits of the fixed
IIS-2 inversion relative to standard (Fig. 16).

Fig. 18. rendalense X_1X_2 heterozygote, showing above the X_1
(IIS-5) sequence, below the included X_2 inversion (IIS-5,6).

Fig. 19. The standard IIS sequence in latipes .

Fig. 20. The IIS sequence (IIS-3) of H. near dogieli which
is identical with the Y_1 sequence of rendalense (not shown separately).

Fig. 21. H. rendalense the X_1Y_2 sequence. The Y_2 (IIS-3,4)
sequence (above) shows the limits of IIS-4 versus IIS-3 ($=Y_1$) of H. near
dogieli (Fig. 20) and facilitates comparison of the basal sequence of
Y_2 and H. near dogieli.

Fig. 22. IIS base of latipes male showing lack of pairing
due to heterozygosity for the heteroband (Hb) constitution. Hb^+:X, Hb^-:Y.
Note also the more compact centromere of the X chromosome.

Fig. 23. IIS base of latipes female showing homozygosity for
Hb^+ (XX) sequence, compact centromeres and tight pairing.

Fig. 24. IIS base of saccai showing heterozygosity for the
Hb polymorphism that is autosomal in this species. Note also centromere
dimorphism.

Fig. 25. IIS base of saccai showing homozygosity for the Hb$^+$ sequence. (The X-linked Hb$^+$ sequence of latipes is probably identical with the autosomally polymorphic Hb$^+$ of saccai.)

Fig. 26. IIIS standard sequence of innocens (Dunbar 1967, Fig. 49) showing below the limits of the anatinum floating inversion (IIIS ana-1).

Fig. 27. IIIS standard sequence of anatinum showing limits of the floating inversion IIIS-1.

Fig. 28. H. latipes IIIS heterozygous for the floating inversions IIIS lat-1, the inverted sequence above (bracket) and the standard sequence below; arrows indicate the break points. Note particularly the identity of banding pattern in the standard constituents of Figs. 27 (anatinum) and 28 (latipes) in sections 74 through 80.

Fig. 16.

Fig. 17

Fig. 18

Fig. 19

Fig. 20

Fig. 21

Fig. 22

Fig. 23

Fig. 24

Fig. 25

Fig. 26

Fig. 27

Fig. 28
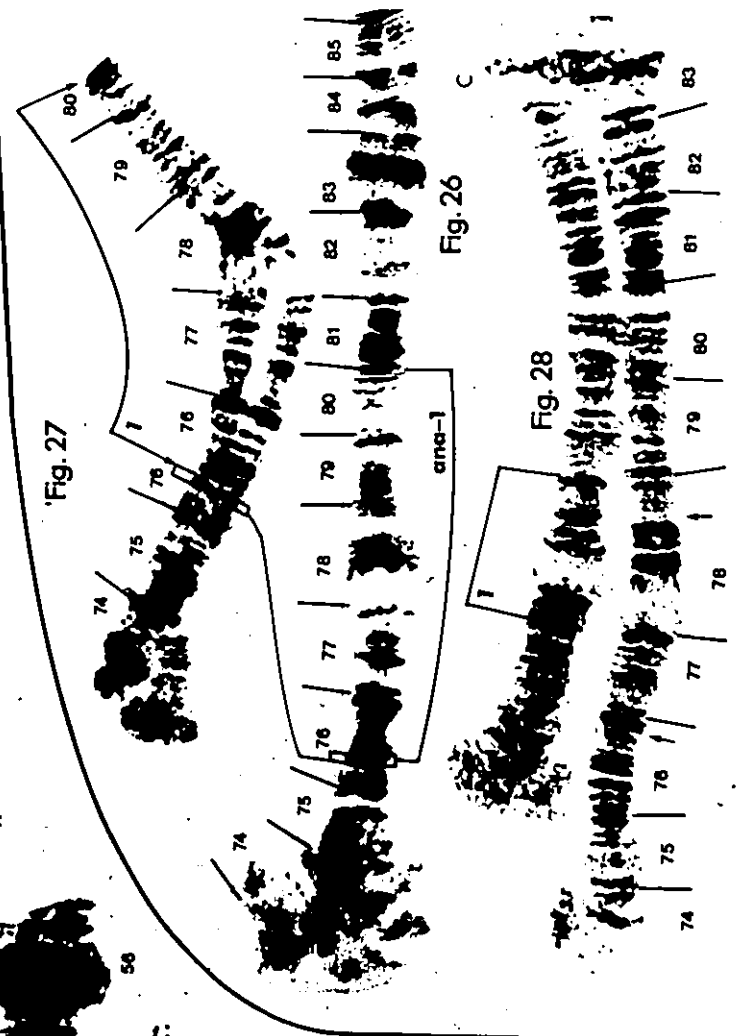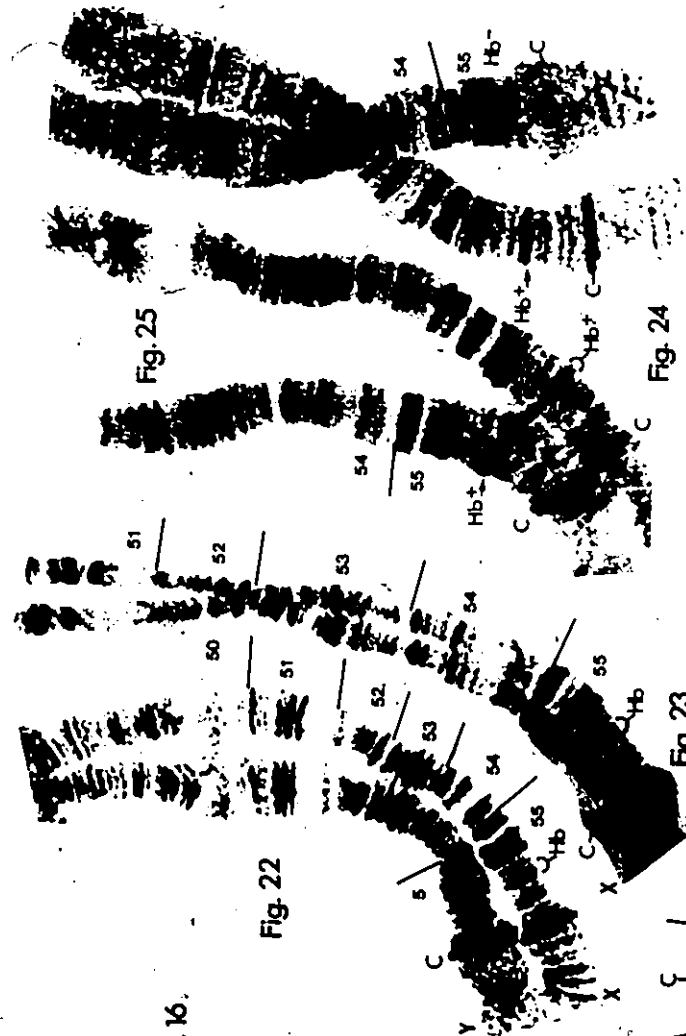
Plate IV. Figs. 29-31, IIL and Figs. 32-37, IIIL sequences. Note: all eight taxa are standard in IIL. IIIL is very variable and the standard sequence occurs in congareenarum (by definition), anatinum and H₂ near dogieli. The overlapping fixed inversion IL-2,3 of innocens is shown in Dunbar (1967) Figs. 56 and 57. Analysis of the IIIL sequence of "Opinaga" and rendalense is incomplete, but position and orientation of a marker segment (M) is diagnostic for each species.

Fig. 29. IIL standard sequence of innocens, a photocomposite of Dunbar (1967) Figs. 44a, b and 45. Limits of the anatinum X chromosome inversion (IIL-1) are shown. Note, the extra heavy band group at centre of section 60 is unique to innocens.

Fig. 30. H. rendalense IIL standard sequence. (Note the sharp center band of 60 characteristic of the seven taxa other than innocens.)

Fig. 31. H. latipes (Britain) IIL standard sequence.

Fig. 32. IIIL standard - composite of Dunbar (1967) Fig. 56 (innocens, centromere to 84/85) and Fig. 55 (anatinum, for remainder). Marker segment (M) is horizontally arrowed.

Fig. 33. H. near dogieli standard IIIL end. Note identity of M segment position and orientation with Fig. 32. Homology with standard extends through the entire arm.

Fig. 34. H. rendalense IIIL; three major re-arranged segments are recognized, but three inversion steps are required to place them in the observed position and orientation (see also text). Note reversed orientation and proximal shift of M segment.

Fig. 35. Opinaga IIIL base. Note that the M segment has the reverse orientation from standard and is close to the basal marker (section 89). The change from standard may be a simple inversion IIIL-1 (see text); however, the end also looks atypical.

Fig. 36. <u>H. latipes</u> IIIL sequence. Five resolved
rearranged segments are indicated. The sequence can be derived in
three inversion steps without coincident break points (see text). The
first step generated the IIIL end characteristic of subgroup B (<u>excisum</u>/
<u>rivuli</u>), see Fig. 37.

Fig. 37. <u>H. excisum</u> end (Dunbar 1967, Fig. 58) to substantiate
homology with <u>latipes</u> (Fig. 36).

Fig. 29
Fig. 30
Fig. 31
Fig. 32
Fig. 33
Fig. 34
Fig. 35
Fig. 36
Fig. 37
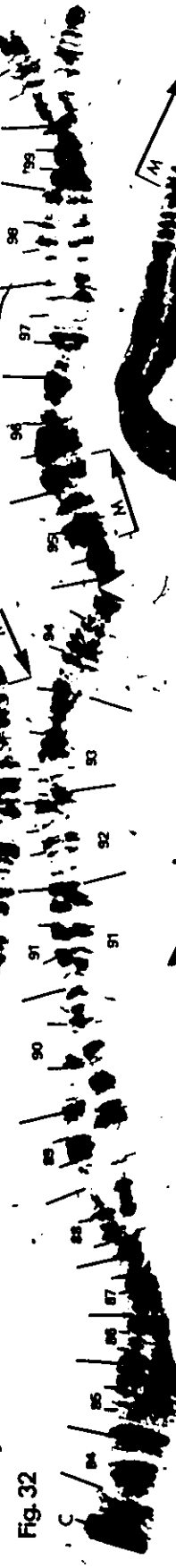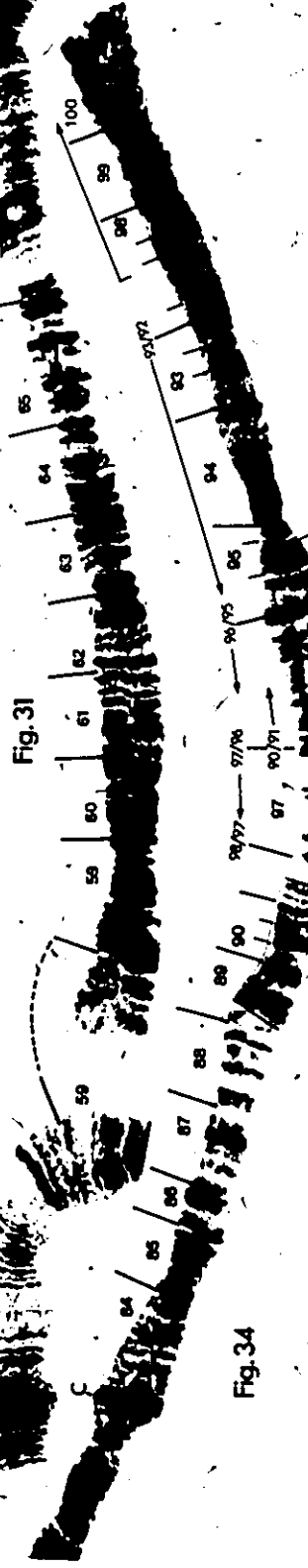
Fig. 38. Chromosome phylogeny of eight species of Hellichiella

with congareenarum as standard. Inversions listed between species names

are fixed or interspecific. Significant floating inversions are in

brackets. Sex differential segments, where known, are shown for each

species. No directionality is assigned, and the phylogeny is not rooted.

rendalense
$(x_1:IIS\text{-}5, x_2:IIS\text{-}5,6)$
$(Y_1:IIS\text{-}3, Y_2:IIS\text{-}3,4)$

latipes
(IIS base X–Y)

nr. dogieli

IIIL-4,5,8

(IIS-3)

IIS-3

saccai
$(X:NO^+, Y:NO^-)$

congareenarum 'b'

IIIL-6,7

(IIS-3)

IIIL-9

IL-1   IIIL-10,11

>14 rearr.

rivuli, excisum
(subgroup B)

opinaga
(Y:IS-1,2)

IIIL-1

IIS-2

IS-1

congareenarum standard
(Y:IS-3)

IL-5 IIIL-2,3

innocens
(Y:IS-3,4)

IIS-1

anatinum
$(x_1:IIL\text{-}1, x_2:IIL\text{-}1,2)$
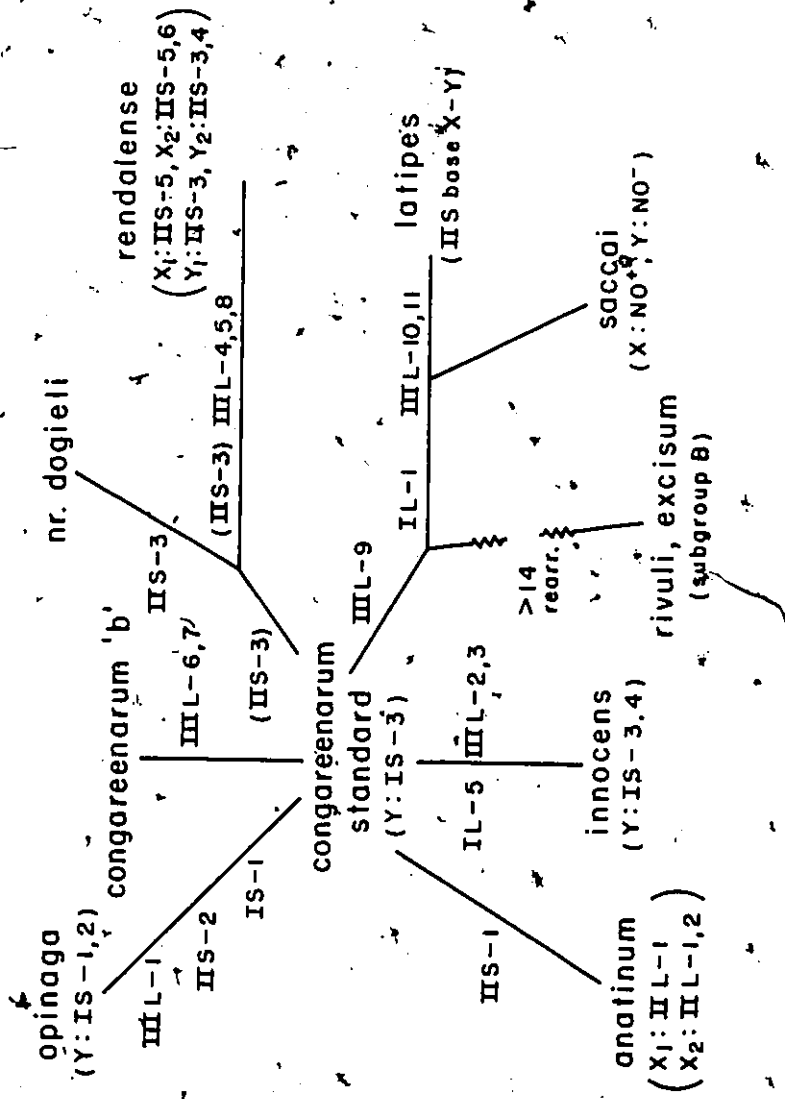
Fig. 38

Chapter 2

TAXONOMY

The Genus <u>Hellichiella</u> and Description of Species from Rendalen

Diagnosis of other Species

GENERALITIES

In the revision of the genus _Eusimulium_ Roubaud, 1906 sensu lato, Rubtsov (1974) gave generic status to several species groups previously included under this genus, and assigned them to the tribe Eusimuliini Rubtsov, 1974. In this revision, the genus _Eusimulium_ (s.s.) was restricted to the _aureum_ - group, while the group _annulum_ Lundström (Rubtsov 1959-64), which included the _subexcisum_ - group of Davies (1966), remained unrevised. Consequently, Rivosecchi and Cardinali (1975) erected the genus _Hellichiella_ based on the type species _Eusimulium saccai_ Rivosecchi, 1967 to represent the _annulum_ - group, and placed it in the tribe Cnephiini Grenier and Rageau, 1960. However, the inclusion of _Hellichiella_ in the Cnephiini is problematic since this taxon contains some characters shared by both Cnephiini and Eusimuliini; it is, therefore, a link connecting these two tribes.

The above two tribes are recognized by simuliidologists who generally use Rubtsov (1974) classification. Others, who generally adopt Crosskey's (1981) classification, recognize only two tribes in the subfamily Simuliinae, and thus include the genera of the Cnephiini with the Prosimuliini and those of the Eusimuliini with the Simuliini. Thus, Crosskey (1981) recognizes _Hellichiella_ as a subgenus in the Simuliini. While appreciating Crosskey's simpler classification, in this thesis the taxon _Hellichiella_ is treated as a genus in the Eusimuliini and redefined in relation to the _E. annulum_ group sensu stricto.

Separation of Hellichiella from the annulum - group sensu stricto

Although Hellichiella is defined by its type species E. saccai Rivosecchi, the taxon was initially described as a genus to replace the annulum - group sensu lato which includes the additional group of species strictly defined by E. annulum (Lundström). Rivosecchi and Cardinali (1975) did not differentiate between Hellichiella and the annulum - group sensu stricto which are sufficiently distinct morphologically and ecologically to justify separating them into two discrete taxa. Just as I was erecting a new subgenus for the latter group, R.W. Crosskey brought to my attention a recent publication by Rubtsov and Yankovsky (1982) who raised this group to generic rank under the name Boreosimulium I have re-defined the basic combination of characters distinguishing these two taxa as outlined below.

Hellichiella Rivosecchi and Cardinali, 1975

- Type species Eusimulium saccai Rivosecchi, 1967, Riv. Parasitol., 28, 63.

Morphological Characters

Adults, relatively small, with minute calcipala about 1/4 to 1/3 as wide as hind basitarsus at distal end, pedisulcus on hind tarsal segment vestigial, less than 1/3 as deep as its segment; hind basitarsus with parallel margins; wing with second basal cell present, base of radius haired, R_s simple; basisternum connected to proepisternum by a precoxal bridge. Females have tarsal claw with a large subbasal tooth and biting mouth-parts are serrated, except in crassum and baffinense. In males the ventral plate tapers posteriorly with a ventrally recurved lip, and a broadly concave anterior margin; dististyle tapered with one apical spine; parameres with numerous long and short spines. The pupae

cocoon slipper - shaped, loosely woven with a long anteromedial pro-
jection thicker only along the margins; respiratory filaments range
from 4 to 12 per side (in multiples of 2), diverging from petioles
of various length. The larva has long antennae, about 1.5 the length
of cephalic fan stalk, the second segment is usually subdivided into
secondary annuli, except in rivuli and excisum; the cephalic fan has
about 60 rays; hypostomial teeth are moderately long, lateral teeth on
two lobes generally elevated above median teeth, usually 3 setae on
each hypostomial row; postgenal cleft is shallow, subquadrate, about
1/5 to 1/4 the depth to base of submentum; two conical ventral papillae
on segment VIII well developed; rectal gills either simple or compound.

Biology

This study has established that immature stages of Hellichiella
species develop in small eurythermal seepages 5 to 20 cm wide and as
deep, with sluggish water current of 5 to 30 cm/sec, draining ombrotrophic
sedge - Sphagnum bogs (see Ecology section). Hibernation is in the
egg stage for northern species and in the larval stage for southern
species (see Discussion). Larvae and pupae are loosely attached to vege-
tation, usually decaying sedges, trailing in the water or on humus and
small stones on the stream bottom. Females have mouth-parts developed
for biting, and the bifid tarsal claws indicate that they feed on avian
blood (Shewell 1955), except for autogenous species, such as baffinense
and crassum. In species for which the host-seeking behaviour is known,
females are restricted specifically to aquatic hatitats where they feed
on water fowl at water level (Bennett 1960; Davies et al. 1962, Stone
and Snoddy 1969; Golini 1975); they are also known as vectors of avian

haematozoa (Bennett and Fallis 1960; Bennett 1961; Anderson 1968; Eide and Fallis 1972).

The genus <u>Boreosimulium</u> Rubtsov and Yankowsky, 1982, with type species <u>Melusina</u> <u>annula</u> Lundström, was erected as a genus to replace the <u>annulum</u>-group. The definition of this taxon, according to its authors, is identical to that which Rubtsov (1959-64) gave initially to the <u>annulum</u>-group sensu lato, without significantly differentiating it from <u>Hellichiella</u> Riv. and Card. The diagnostic differences between these two taxa, as given by Rubtsov and Yankowsky (1982) is as follows:

	<u>Boreosimulium</u>	<u>Hellichiella</u>
<u>Adults</u>		
calcipala & pedisulcus	absent or barely apparent	?
♂ anal sclerite	simple narrow plate slightly expanded basally	simple narrow plate strongly expanded basally
♀ frons	broad	narrow
mandibles & maxillae	usually without teeth	?
tooth at base of claw	smaller	larger
<u>Pupa</u>	3-8 filaments/side lacking anchor-shaped hooks on abdomen	10 filaments/side with anchor hooks
<u>Larva</u> antenna 2nd segment	long 5-7 annuli	long 5-7 annuli
<u>Biology</u> immatures	in small rivers, shallow swamp streams often in middle of swamps	?
adults	biting not recorded	?
<u>Distribution</u>	northern & central Europe, northwest Siberia, Yakutiya and Trans-Baikal	?

Other characters given for <u>Boreosimulium</u> include: Larva with large number, 50 or more, of primary head fan rays; gular cleft shallow, often with uneven shape; rectal "gills" branched, rarely simple. Cocoon is simple, with an anteromedian projection.

According to the above diagnosis, these two taxa are not significantly distinguished from each other. The difference in number of pupal filaments is not a significant character, since it is highly variable among species of <u>Hellichiella</u>, as shown in this thesis. Thus, the concept of <u>Boreosimulium</u>, as defined by its authors, is not differentiated from <u>Hellichiella</u> and does not distinguish the <u>annulum</u>-group sensu stricto, rather it includes both.

To clarify this confusion, <u>Hellichiella</u> is differentiated in the present study from the <u>annulum</u>-group sensu stricto which was initially represented by Wood (1963) under the species group name <u>euryadminiculum</u> Davies. This group is redefined below as a genus of Eusimuliini.

<u>Parahellichiella</u> gen. n.

Type species: <u>Simulium euryadminiculum</u> Davies, 1949. Can. Ent., <u>81</u>: 45-49.

<u>Morphological Characters</u>

<u>Adults</u>, calcipala moderately developed, about 1/3 distal width of hind basitarsus, pedisulcus moderately developed, about 1/3 to 1/2 the depth of its second hind tarsal segment; basitarsus of fore leg slender, cylindrical; hind basitarsus of males wider than that of females; pleural membrane bare; basisternum not connected to proepisternum by a precoxal bridge; wing, basal cell vestigal or absent, base of radius

haired dorsally. <u>Female</u>, frons moderately broad, or with parallel sides, length: broadest width about 1.5:1, length to narrowest width about 3:1; genital fork usually with broad terminal plates and two well-developed apodemes at base of terminal plates; cerci generally subquadrate, broadly rounded apically, as long as anal lobe; tarsal claw with large subbasal tooth. <u>Male</u>, ventral plate broadly subrectangular with margin concave posteriorly and convex anteriorly; paramere usually with several small teeth, some being modified into a long spicule; dististyle slender, tapering with one apical spinule. <u>Pupa</u> with four respiratory filaments/side, diverging moderately (ca 30°) in two petiolate pairs, ventral petiole twice as long as, and filaments slightly thinner than dorsal petiole; cocoon slipper - shaped- lacking an anteromedial projection. <u>Larva</u>, head capsule light yellow, positive head spots arranged in a cross; antenna relatively short about 1.2 the length of cephalic fan stalk, second antennal segment subdivided into 3 to 5 (average 4) annuli; hypostomial setae 2 or 3 in a row per side; hypostomial teeth small and parallel, lateral teeth not elevated above tooth; postgenal cleft usually square, moderate in size, with depth 1/3 to 1/2 the distance to base of submemtum; primary cephalic fan with relatively few, 40 to 50, short rays; abdominal segment VII with two conical ventral papillae; anal gills compound.

Biology

Immature stages normally develop in rivers of moderate size, 3 to 6 m wide, with water current 50 to 100 cm/sec and temperature 8°- 10°C, originating from lake outlets; hibernation is usually in the egg stage (Rubtsov.1959-64; Usova 1961, Davies <u>et al</u>. 1962), although Usova (1961) reports <u>E. annulum</u> to hibernate as larvae. Adult females have well- developed biting mouthparts and a bifid tarsal claw and feed primarily

on avian blood. Some species, whose feeding behavior is known, are

host specific, being attracted to their avian host uropygial gland

extract (Lowther and Wood 1964; Fallis and Smith 1964). Its distribution

is boreal holarctic.

Species belonging in Parahellichiella include:

Palearctic	Nearctic
annulum Lund.	canonicolum D. & S.
olonicum Usova	euryadminiculum Davies
annuliforme Rubtsov	emarginatum D. P. & W.
	johannseni Hart
	duplex Shewell & Fredeen

Hellichiella and Parahellichiella are, therefore, separated

both morphologically and ecologically. The immature stages of Hellichiella

spp. occur in bog seepages in water current of 5-30 cm/sec and 12°-18°C;

those of Parahellichiella occur in medium sized streams, 3-6 m wide, in

water current of 50-100 cm/sec and 8°-10°C, originating from lake outlets.

Observations during this study indicate that the development of aquatic

stages and adult emergence of most species, in both taxa, are correlated

with the spring reproductive period of their avian hosts. The morphological

differences of species distinguishing these two taxa are summarized in

Table 1.

Table 1. Morphological differences between <u>Hellichiella</u> Riv. & Card.
and <u>Parahellichiella</u> gen. n.

	Hellichiella	Parahellichiella
Adults		
calcipala & pedisulcus	both present but poorly developed	both moderately developed
wing basal cell precoxal bridge	complete complete	incomplete or vestigial incomplete or vestigial
♀ frons	normally narrow	normally broad
subbasal tooth on claw	usually large, occasionally reduced	large
plates of genital fork	broad, occasionally with basal apodemes	broad with basal apodemes
♂ hind basitarsus	uniformly cylindrical as in females	large and swollen, about twice as thick as that of females
ventral plate	normally tapering posteri'oly, anterior margin concave	uniformly wide, anterior margin usually convex
parameres	several small and large teeth	1 or 2 large spines and several small teeth
Pupa numbers of filaments	4 to 12 per side	4 per side
cocoon	with a long anteromedian projection	simple, slipper-shaped, without anterior projection
Larva hypostomium	3 groups of 9 teeth, lateral teeth elevated above middle ones	9 parallel teeth, lateral ones not elevated
postgenal cleft	subquadrate, small, length 1/5 - 1/4 to tip of submentum	subquadrate, larger, length ca 1/3 to submentum

Continued...

Table 1 continued

Larva

antenna	long, ca 1.5 longer than head fan stalk	short, 1.1-1.3 length of head fan stalk
2nd segment	with 4-7 annuli	4-5 annuli
primary head fan	50-80 rays	40-50 rays

Rivosecchi and Cardinali (1975) initially included in the genus Hellichiella the following species: saccai Riv., latipes Mg. (their subexcisum Edw.), annulum Lund. and innocens Shewell.

The species now included in Hellichiella, as revised in this thesis, are listed on p. 2, with the possible addition of the following: crassum Rubz., arctium Rubz., tsheburovae Rubz., barabensis Rubz., acutum Patrucheva and baffinense Twinn.

Rubtsov and Yankowsky (1982) list in the genus Boreosimulium only the type species, annulum Lund.; although their genus description, which does not refer specifically to this species, implies the inclusion of other species which are placed in Hellichiella in this thesis.

For comparison, species included in Parahellichiella gen. n. are listed on p. 42. Rubtsov (1959-'64) include E. annuliforme Rubz. in the annulum-group, but adult morphological character   annuliforme (whose immature stages are unknown) indicate that thi   s belongs in the genus Cnephia (or possibly Metacnephia).

Historical Background of the Taxonomy of

<u>Hellichiella</u> Species from Rendalen, Norway

During July 1968 about 2500 female simuliids were captured
from CO_2 - baited traps and others as they fed on domestic ducks, <u>Anas</u>
<u>boschas</u> L., in Rendalen, Norway (Golini 1970; 1975). These simuliids
were initially referred to as <u>Eusimulium</u> sp. 1 and were considered
related possibly to <u>E. meigeni</u> Rubtsov and Carlsson, 1965 (in litt. to
Rubtsov, 1979). Further study revealed that the minute calcipala, shallow
pedisulcus and shape of the genital fork place <u>Eusimulium</u> sp. 1 closer
to <u>E. dogieli</u> (Usova 1959), hence in the <u>subexcisum</u>-group (L. Davies 1966),
now <u>Hellichiella</u>. To confirm their identity six females of <u>Eusimulium</u>
sp. 1, selected from a collection made in Rendalen on 16 July 1968,
were sent to Dr. I.A. Rubtsov in February 1969. The importance of identi-
fying these flies correctly was emphasized because they had apparently
not been reported previously from Norway and because <u>Eusimulium</u> sp. 1
was implicated as vector of <u>Leucocytozoon simondi</u> Mathis and Leger to
ducks (Eide and Fallis 1972).

In response, Rubtsov set out to revise the identity of species
related to the "<u>pygmaea</u>" group, and observed (in litt. 1969) that
although the former <u>E. pygmaeum pygmaeum</u> Zetterstedt (Rubtsov 1956:
768, fig. 203) is synonymous with <u>E. meigeni</u> Rubtsov and Carlsson 1965,
the genital fork of the holotype, "slide #4785", a female from the
Murmansk region was evidently distinct from that of Fig. 203 (op. cit.).

He related E. meigeni with Eusimulium sp. 1, and considered E. pygmaeum pygmaeum a new species. Originally Rubtsov and Carlsson (1965, p. 19) designated E. pygmaeum pygmaeum Zett. a new species under the name E. meigeni which they "distinguished as a distinct species on genital fork of females and male genitalia. It is described from Murmansk material, and probably meets the Scandinavian form in Karelia". The illustrations of this species have been redrawn in text Fig. 1. This shows that the name meigeni is preoccupied for one species of Eusimulium (Nevermannia) and therefore not transferable to another species of the same genus. Nevertheless, Rubtsov (1971) proceeded to redescribe E. meigeni from a new holotype #4875, a female from Murmansk; his illustrations have been redrawn in text Fig. 2. He considered this species similar to the specimens from Norway and placed it in the subexcisum - group, distinguishing it from E. curvans, which belongs in the subgenus Nevermannia Enderlein, but not from Hellichiella dogieli (Usova), its closest relative (see text Figs. 1,2).

This transferral of the name meigeni from one species to another resulted simply in mis-identification of the second species for the original E. meigeni. To clarify this confusion, Eusimulium sp. 1 was briefly described under the name E. rendalense (Golini 1970). Subsequent re-examination of females of this species showed two morphological entities formally described as E. rendalense and E. fallisi (Golini 1975); a third entity, E. near dogieli, was also identified, resembling closely E. dogieli (Usova). The morphological differences of females of these species have been outlined in Golini (1975), and in text Figs. 3 and 4 and in the Discussion of this chapter. Subsequently, Raastad (1979) synonymized E. rendalense with E. dogieli which he placed in Cnephia (Grenier),

and E. fallisi with E. meigeni which he placed in E. (Hellichiella).
To clarify this argument affinities remained to be scrutinized further,
pending the discovery of the other developmental stages of rendalense
and fallisi, a comparative analysis of their polytene chromosomes and
a study of their ecology. This objective has largely been achieved,
and additional questions raised, in the present study after the immatures
of Hellichiella were found in 1979 and 1980 in Rendalen where the
adult females were first discovered eleven years earlier.

· In particular, the taxonomic status of E. dogieli needs to
be resolved. The description of this species was reported initially
by Rubtsov (1956) who attributed authorship to Usova, based on his
citation of Usova's intention to publish the new species in the 1956
proceedings of the Leningrad Society of Naturalists. However, the
description of dogieli as new species by Usova was not formally published
until 1959 in a different journal (see Discussion section).

Aside from the confusion in authorship of this species, there
are significant character differences between dogieli of Rubtsov (1956)
and dogieli of Usova (1959) which indicate that these are two different
entities. Usova's (1959) description of dogieli was analysed in
translation from Usova (1961, English ed. 1964); her illustrations are
reproduced in this thesis text Fig. 4b. Since the first description
of dogieli by Rubtsov (1956) is available only in Russian, a translation
into English was obtained specifically for the present study and
reproduced literally below. The species was redescribed, with supplemental
illustrations, by Rubtsov (1963); his illustrations are also reproduced
for comparative study in text Fig. 4a. This species is treated further
in the Discussion and in Table 9.

Fig. 1   Eusimulium pygmaeum pygmaeum (Zett.), renamed
         Eusimulium meigeni Rubzov and Carlsson, 1965.
         Redrawn from Rubzov (1959-64)., p. 341, Fig. 230.

Fig. 2   Eusimulium meigeni Rubzov and Carlsson, 1965 sensu
         Rubzov, 1971. Redrawn from Rubzov (1971), p. 103,
         Fig. 8. Known only in the female. (Dimensions in mm)
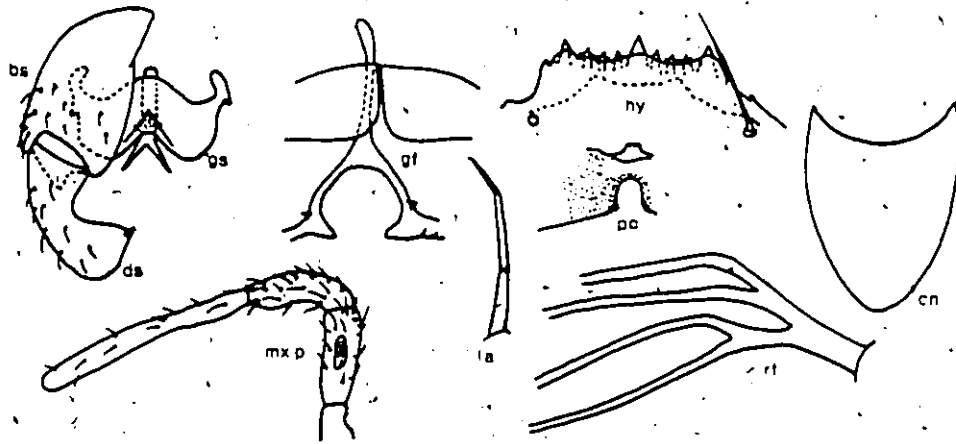
Fig. 1
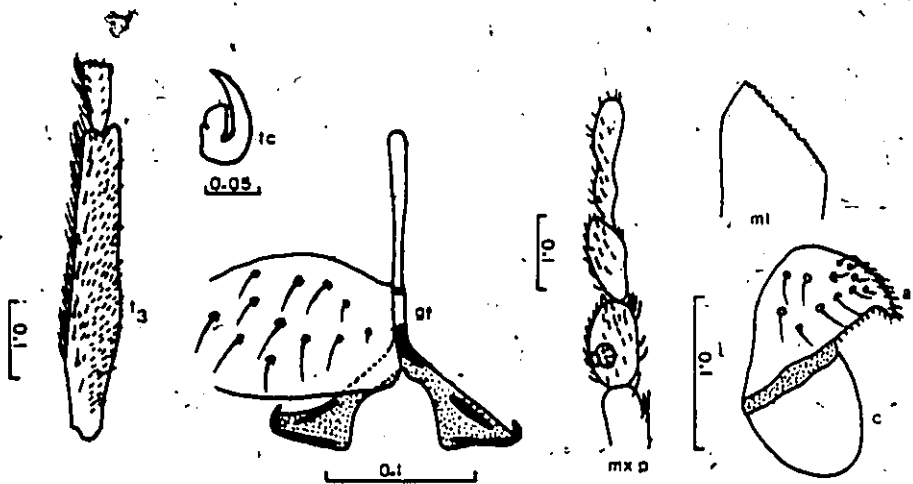
Fig. 2

Fig. 3. Hellichiella rendalense (redrawn from Golini 1975) and the metathoracic leg l_{3d} of H. near dogieli These two entities were known initially only from females of the 1980 Rendalen collection and were separated by the variegated yellow and dark-brown colour of the legs of H. near dogieli and uniformly dark-brown legs of H. rendalense.

Fig. 4a. Hellichiella dogieli (Rubtsov) showing diagnostic characters of larva, pupa and adults. Reproduced from Rubtsov (1962) p. 281, Fig. 153a. Compare this figure with text Figs. 4b and 10, 11 and 12. Note: the 12 pupal filaments are parallel and point forward in one direction; larval antenna with 4 annuli on the 2nd segment; contour of basistyle opening (Gok); straight arms of sternum (Stern); narrow tip of gonofurka (Ga); sternum tapering to a point.
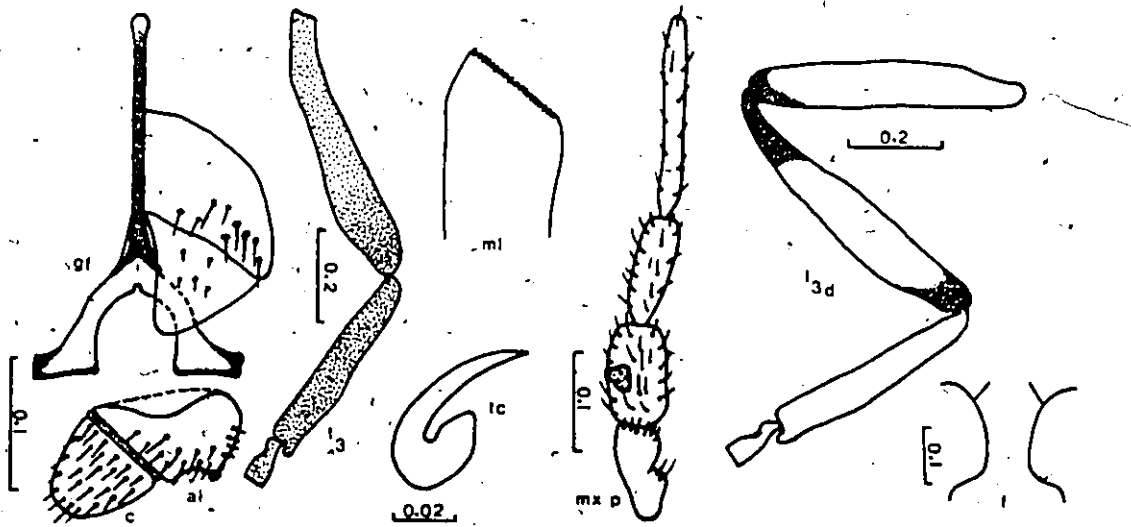
Fig. 3
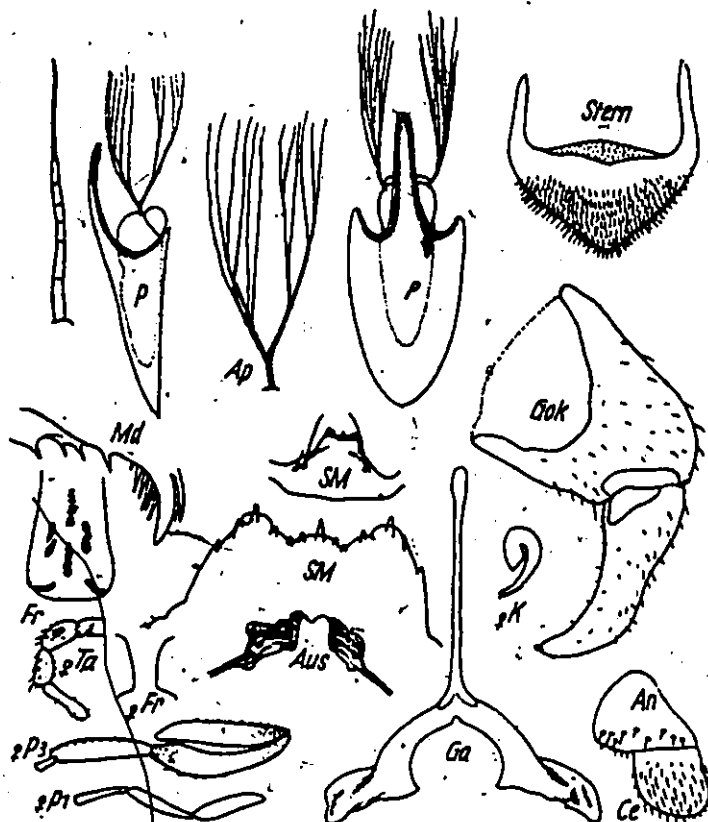
Fig. 4a

Fig. 4b. <u>Hellichiella</u> <u>dogieli</u> (Rubtsov after Usova) showing
diagnostic characters of larva, pupa and adults.
Reproduced from Usova (1961, in 1964) p. 78, Fig. 34.
Compare this figure with text Figs. 4a and 10, 11 and 12.
Note:The 12 pupal filaments (r.f.) flare out in all
directions; indistinct annuli on larval antenna consist
of 4 as stated by Usova (1961); ventral incision (v.i.)-
of the larva head capsule is longer than wide; contour of
basistyle opening; arcuate hind tarsal segment of female
(mt3); wider gonosternum (gste); 3 long spines of
paramere (pa).
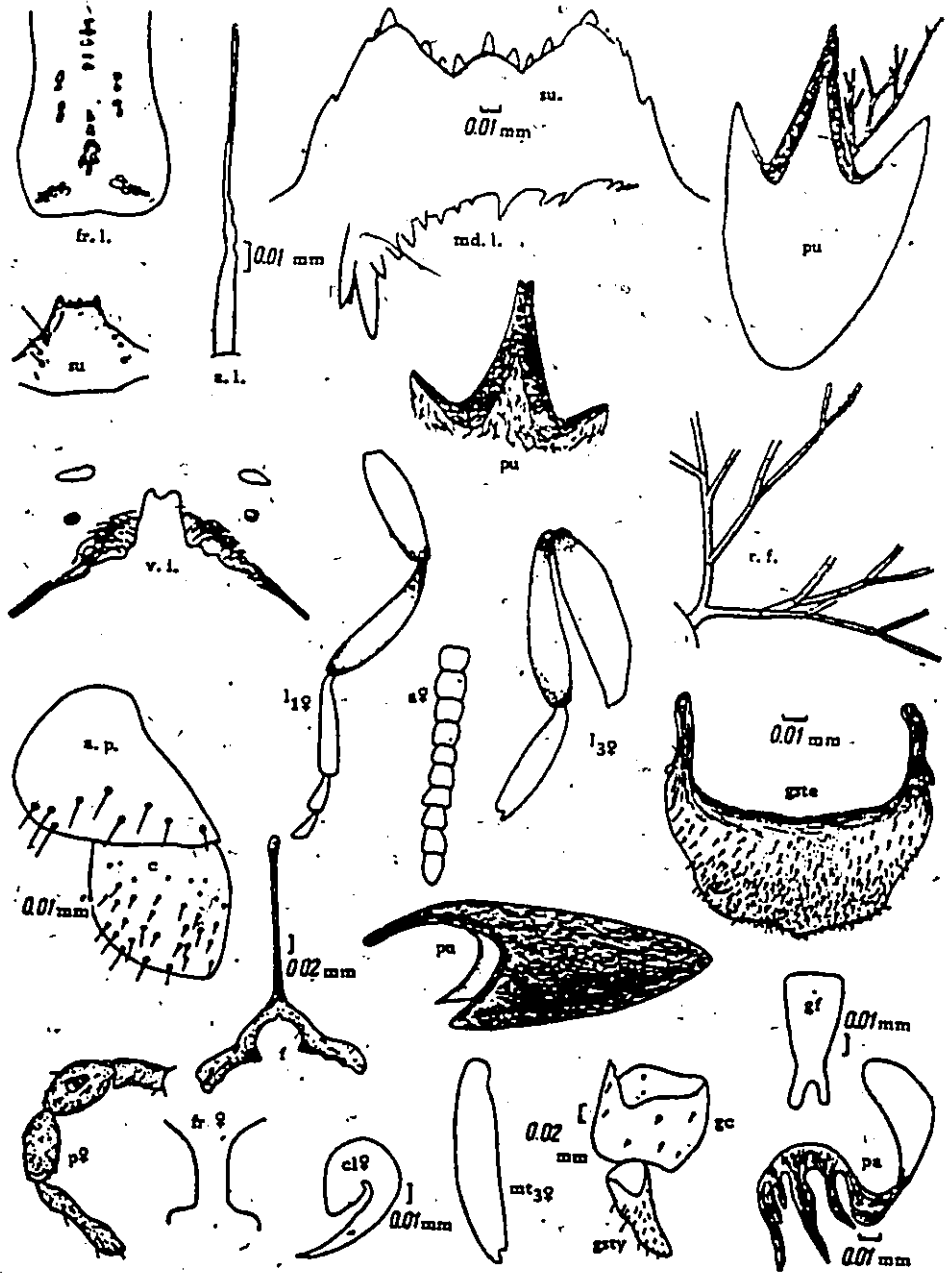
Fig. 4b

MATERIALS AND METHODS

Larvae, pupae and reared adults of Hellichiella species described below were obtained from Rendalen, Norway, in sedge – Sphagnum bogs, described in the Ecology section. Simuliid larvae were collected from two main habitats, Renadalen bog and Åsmyrthjörna bog, during June to August. Hellichiella larvae preserved in Carnoy solution were separated from the other simuliid species for chromosome analysis and their carcasses subsequently analysed morphologically. Morphometric measurements were made of various characters of last instar larval carcasses of H. rendalense and H. near dogieli, reported in the first section, using an ocular filar micrometer mounted on a Wild stereomicroscope. The number of analysed larval carcasses is shown in Table 2. Pupae, collected in the same habitats together with the larvae, were reared individually in the field (Golini 1981) so that each emerged adult remained associated with its exuvia and cocoon. Pupae and reared males and females were subsequently examined for morphological differences associated with different morphotypes related to larval cytotypes. Line drawings of larval, pupal and adult characters were made with the aid of a camera lucida mounted on a Wild (Heerbrugg) compound microscope. Drawings of larval characters were made from carcasses cleared automatically during chromosome preparation, while hypopygia excised from male and female specimens were cleared in 10% KOH for about 24 hours at room temperature. The cleared specimens were kept in glycerine on glass slides, usually without a coverslip, to facilitate viewing the specimen in different orientations.

RESULTS

Morphological Separation of Sibling Species

The caracasses of *Hellichiella* larvae from Rendalen examined
for morphological differences associated with Type I (*rendalense*) and
·YY (near *dogieli*) cytotypes (see Chapter 1) were differentiated
initially by the number of secondary annuli on the second antennal
segment and number of rays on the primary cephalic fan. Carcasses of
Type 1 sibling had a mean number of 5 annuli, with some occasional
specimens showing a re-subdivided basal annulus to form 6, and more
rarely 7 annuli; the number of fan rays, as shown by intact cephalic
fans mounted and spread in glycerine under glass cover slip on slides,
varied from about 60 to 75, with a mean number of 66. Carcasses of
the YY sibling had a constant number of 4 annuli; the number of fan
rays varied from 60 to 85, with a mean of 74 rays. These values were
found to apply only to mature or last instar larvae. Specimens with
mature or fully developed histoblasts were found to have normally 12
respiratory filaments per side. Last instar larvae were easily distinguished
by their developing histoblasts and fully separated cervical sclerites,
both of which are undeveloped in younger instars. Penultimate instars
of either sibling had one annulus less on the second segment of the
antenna and about ten fewer rays than the average in corresponding mature
larvae.

The frequency distribution of the number of cephalic fan

52

rays for Type 1 and YY siblings derived from carcasses of chromosomally

analysed last instar larvae are shown in Table 3 and Figs. 5a, b,

and from last instar ethanol-preserved whole larvae in Table 4 and

Fig. 6 a,b. Morphometric measurements differentiating these two siblings

are shown in Tables 5,6 and 7. The association of larval morphotypes

with their corresponding pupae and reared adults was made by the

identity of eight head capsules of last instar larvae of _Hellichiella_

remaining trapped among the respiratory filaments of _Hellichiella_ pupae.

Five of these pupae had trapped Type 1 larval head capsules; one emerged

as a female and the other four as males which were identified as _H. rendalense_.

The other three pupae had trapped head capsules of YY'type larvae; these

pupae produced two females and one male identified as _H. near dogieli_.

Association of larval types with pupae and reared adults was made also,

when applicable, by comparing the relative abundance of larval morphotypes

with that of pupae and reared adults from different collections as reported

in the Ecology section.

Table 2. Relative abundance of *Hellichiella* Type 1 and YY based on chromosome analysis of larvae from the Renådalen and Åsmyrtjørna* bogs during June and July 1979 and 1980.

		June							July					Total	%	Ås	Ren	Total
		9	14	18	24	25	26	28	1	2	6	11	12					
1979																		
Type 1 rendalense	♂				2		2	32	8	6		8		58				
	♀				5		8	47	14	22		3		99				
														157	96.9			
YY nr. dogieli	♂				2		0	0	0	0		0		2				
	♀				1		0	2	0	0		0		3				
														5	3.1			
1980																		
Type 1 rendalense	♂	3*	0			17			2	0*	4		0			3	23	26
	♀	3	0			7			2	0	6		0			3	15	18
																16.7	58.5	43.6
YY nr. dogieli	♂	10	2			5			0	2	0		0			12	7	19
	♀	15	0			19			0	3	0		1			18	20	38
																83.3	41.5	56.4
																30	27	57

54

Table 3. Frequency distribution of cephalic fan ray numbers in larval carcases of _Hellichiella_ Type 1 and YY after chromosome analysis.

		Number of rays									
		59	60-62	63-65	66-68	69-71	72-74	75-77	78-80	81-83	84-86
Type 1	1979	0	4	14	8	1	0	0	0	0	0
H. rendalense	1980	1	2	4	6	7	3	0	0	0	0
	Total	1	6	18	14	8	3	0	0	0	0
YY	1979	0	0	0	0	0	0	0	0	0	0
H. nr. dogieli	1980	0	0	0	3	6	16	13	6	1	0
	Total	0	0	0	3	6	16	13	6	1	0

Fig. 5a. Frequency distribution of the number of rays in the primary
head-fan of mature larvae of H. rendalense after chromosome
analysis. (Derived from Table 3). These larval carcasses have
the second antennal segment subdivided into 5-6 annuli.

Fig. 5b. Frequency distribution of the number of rays in the primary
head-fan of mature larvae of H. near dogieli after chromosome
analysis. (Derived from Table 4). These larval carcasses have
the second antennal segment subdivided into 4 annuli.

Fig. 5a

Hellichiella rendalense

Fig. 5b

Hellichiella
nr. dogieli

Number of larvae
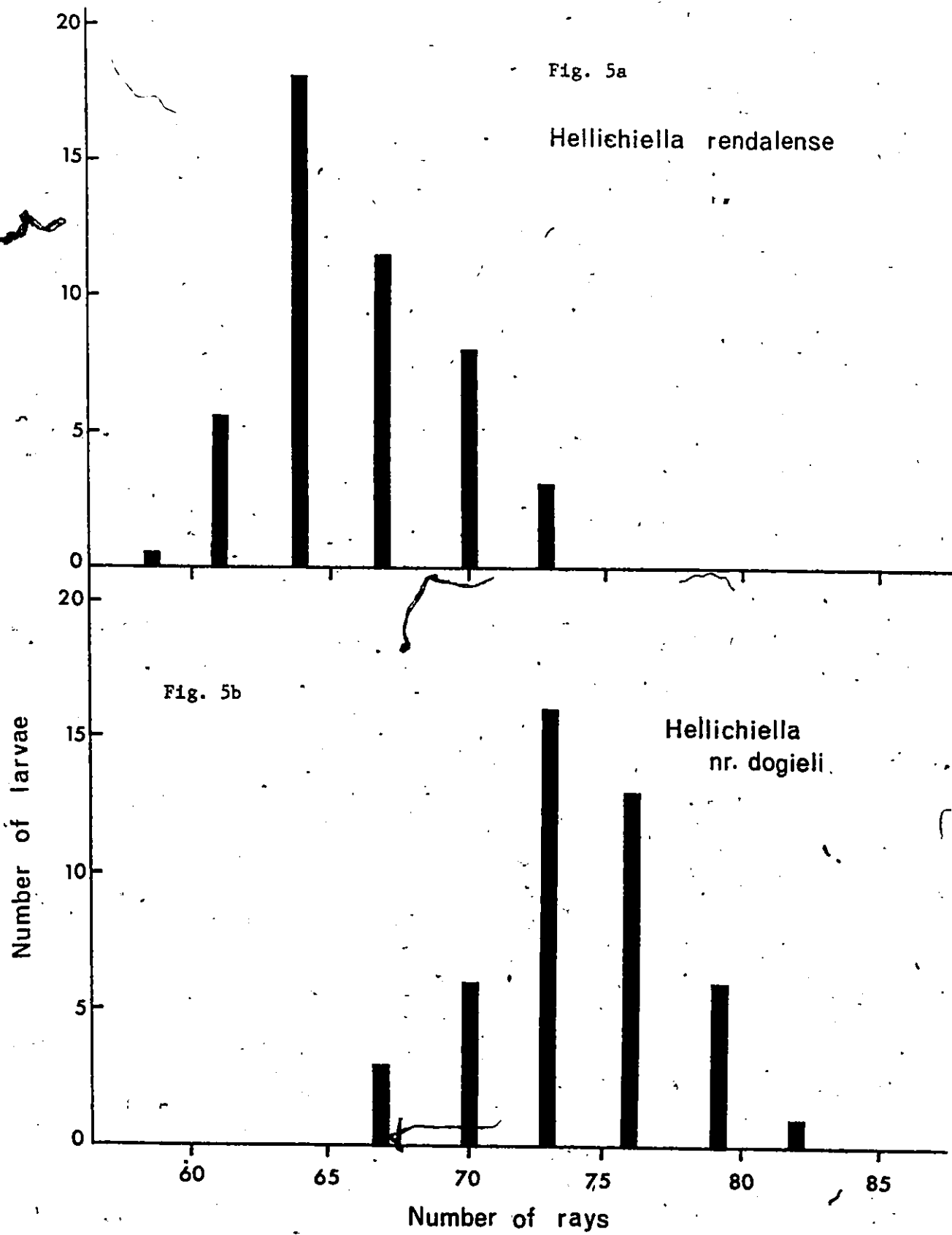
Number of rays

Table 4.   Frequency distribution of cephalic fan ray numbers in last instar larvae identified only
morphologically as <u>Hellichiella</u> Type 1 and YY from Rendalen 1979 and 1980.
*

					Number of rays					
	59	60-62	63-65	66-68	69-71	72-74	75-77	78-80	81-83	83-86
Type 1 - H. rendalense 1979	1	24	82	77	26	10	2	0	0	0
1980	0	3	6	9	12	6	1	0	0	0
Total	1	27	88	86	38	16	3	0	0	0
YY 1979	0	2	3	7	4	1	1	1	0	0
H. nr. dogieli 1980	0	0	3	18	31	67	40	16	5	2
Total	0	2	6	25	35	68	41	17	5	2

* Larvae separated into <u>H. rendalense</u> and <u>H.</u> near <u>dogieli</u> first by the differnt
number of annuli on the second antennal segment.

Fig. 6a. Frequency distribution of the number of rays in the primary
head-fan of mature larvae of H. rendalense from ethanol
collections, separated first by the 5-6 annuli on the second
antennal segment.

Fig. 6b. Frequency distribution of the number of rays in the primary
head-fan of mature larvae of H. near dogieli from ethanol
collections, separated first by the 4 annuli on the second
antennal segment.

Fig. 6a

Hellichiella rendalense

Fig. 6b

Hellichiella
nr. dogieli

Number of larvae
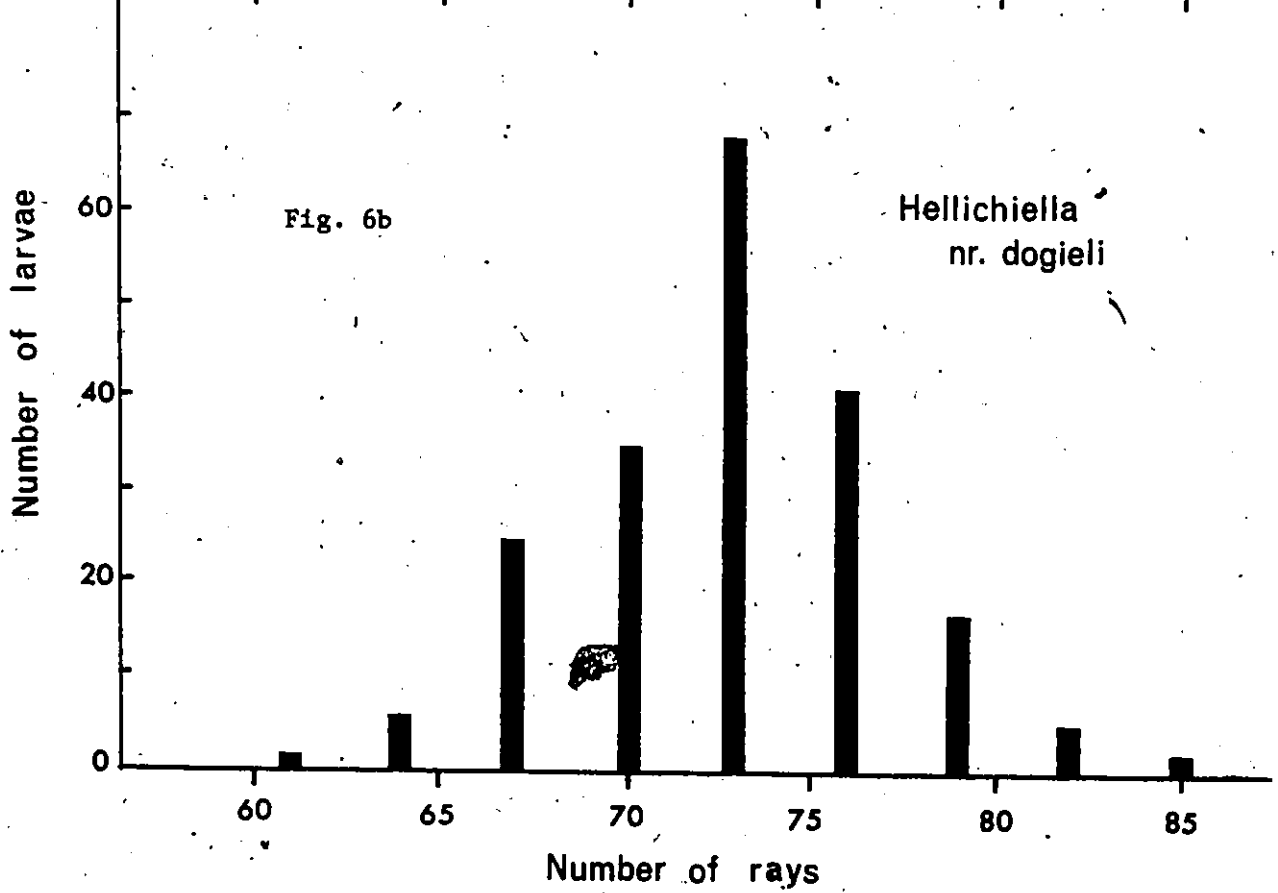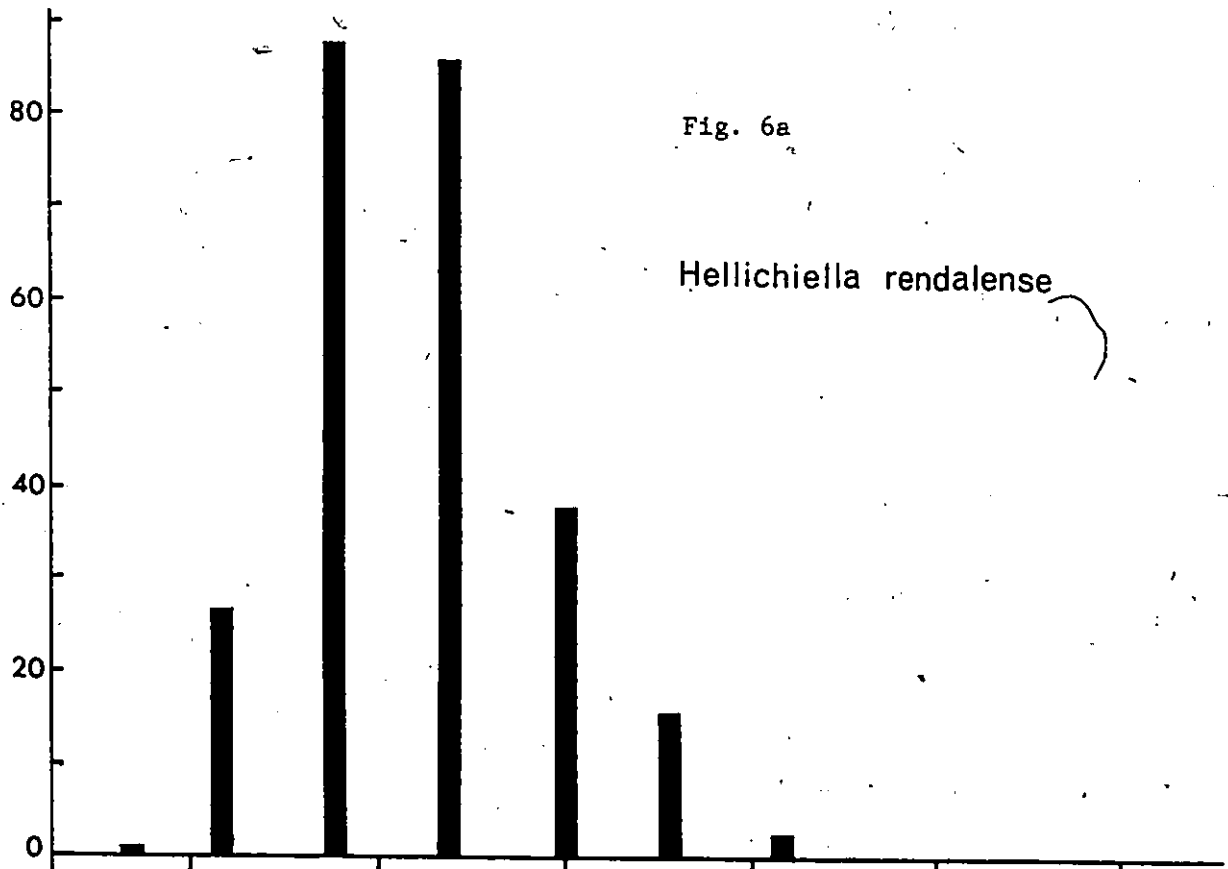
Number of rays

Table 5. Number of rows and frequency distribution of hooks/row in posterior adhesive circlet of mature larvae of H. rendalense and H. nr. dogieli.*

Larva #	Number rows	Number hooks	Frequency of rows									Total rows
			5	6	7	8	9	10	11	12	13	
near dogieli												
1	57			1	1	2	2	6	7	3		22
2	61					1	5	10	4			20
3	60		1	1	2	6	17	3	1			30
4	61				1	1	10	9	1			22
5	62		1	1	3	4	10	2				20
6	62				4	16	3					23
7	62						5	12	12	2	2	33
8	61				2	3	10	7				22
9	61				1	4	9	7	2			23
10	62			1	1	3	4	7	4	3		23
11	58				1	1	3	6	8			19
12	61				2	7	7	3	2			21
13	61				1	2	3	11	7	1		25
mean	61±2		2	4	19	50	88	83	48	9	2	303
rendalense												
1	63				3	15	14					32
2	62			1	2	7	9	2				21
3	62					4	12	4	3			23
4	60				2	4	10	3				19
5	57				2	7	7	4				20
6	62				2	10	9	8				29
7	57					3	10	7	1			21
8	61					6	10	2				18
9	61				1	9	12	5	1			28
10	64				1	2	7	16	2			28
11	60						4	8	3			17
12	61			2	5	9	4	2				22
13	58				1	1	2	7	14	5		30
14	63				1	3	7	5	3			19
15	62				1	3	6	11	4			25
mean	61±2			3	21	83	123	84	31	7		352

* All specimens were larval carcasses after chromosome analysis

Table 6. Morphometrics of _Hellichiella_ larval carcases after treatment for chromosome analysis, Rendalen 1979 & 1980.

Cytotypes		annuli on 2nd segment	Antenna segment lengt 1st	2nd	3rd	Cephalic fan rays no.	stem length	Head capsule width post.	ant.	gena leng.	Postgenal cleft leng.	width	Mandible leng.	wid.	Submentum leng.	wid.	Histo. filam. no.	Posterior circlet rows	hooks/ row
Type 1	mean.	5	0.22	0.22	0.21	65	0.44	0.48	0.62	0.48	0.07	0.08	0.39	0.17	0.16	0.07	12	61	9
rendalense	min.	5	0.20	0.20	0.20	58	0.42	0.45	0.56	0.45	0.04	0.06	0.36	0.14	0.14	0.06	12	57	5
	max.	7	0.28	0.25	0.25	74	0.45	0.50	0.67	0.50	0.08	0.11	0.42	0.17	0.17	0.08	12	64	12
	N	104	104			51	104	85			103		104		100		23	15	352
YY	mean	4	0.21	0.20	0.21	75	0.43	0.46	0.62	0.48	0.06	0.07	0.38	0.17	0.15	0.07	12	61	9
near dogieli	min.	4	0.18	0.17	0.20	67	0.42	0.42	0.56	0.45	0.06	0.06	0.36	0.14	0.14	0.06	12	57	5
	max.	4	0.25	0.22	0.22	82	0.45	0.50	0.67	0.50	0.08	0.08	0.39	0.17	0.17	0.08	12	62	12
	N	51	51			46	48	45			48		51		50		15	13	303

Table 7. Morphometrics of _Hellichiella_ larvae preserved in 95% ethanol, Rendalen 1979 & 1980

Species		annuli on 2nd segment	Antenna segment length 1st	2nd	3rd	Cephalic fan rays no.	stem length	Head capsule width post.	ant.	gena leng.	Postgenal cleft leng.	width	Mandible leng.	wid.	Submentum leng.	wid.	Histoblast gap wid.	filam. no.	Body leng.
Type 1 rendalense	mean	5	0.22	0.22	0.21	66	0.45	0.48	0.64	0.48	0.06	0.09	0.38	0.17	0.14	0.07	0.44	12	5.6
	min.	5	0.17	0.17	0.17	59	0.42	0.42	0.56	0.42	0.04	0.06	0.34	0.14	0.13	0.06	0.34	11	4.2
	max.	7	0.28	0.28	0.28	76	0.48	0.56	0.70	0.53	0.10	0.11	0.42	0.17	0.15	0.07	0.56	12	6.0
	N	262	222	222	222	259	62	96			87		87		62		111	46	105
YY near dogieli	mean	4	0.20	0.18	0.21	73	0.44	0.45	0.60	0.45	0.06	0.09	0.37	0.16	0.14	0.07	0.34	12	5.3
	min.	4	0.17	0.17	0.17	60	0.42	0.36	0.56	0.39	0.04	0.08	0.31	0.14	0.11	0.06	0.31	11	4.2
	max.	4	0.22	0.22	0.25	85	0.48	0.53	0.67	0.50	0.10	0.11	0.39	0.17	0.14	0.07	0.48	12	6.0
	N	255	78	78	78	202	71	108			42		59		58		98	34	108
dogieli Ussova *	mean	4	0.19	0.19	0.22	63		leng.> width 1/3 of head capsule leng.					0.19					12	
	min.		0.17			61		capsule leng.	0.35	0.16	0.13	0.04							
	max.		0.25			71			0.49	0.20	0.18	0.06							

Dimensions in mm; * from Ussova 1961, pp. 79-80

Description of Species of _Hellichiella_ from Rendalen

Hellichiella _rendalense_ Golini (Figs. 7A-E,
8A-C, 9A-G).
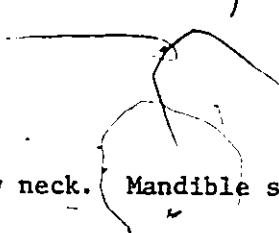
Eusimulium _rendalense_ Golini, 1975 Ent. scand. 6: 229-239. (Female)

FEMALE. General body colour blackish-brown, covered with silvery to pale yellow pubescence. Length: body 2.4 - 3.5 mm; wing 2.5 - 2.8 mm.

Head dark-brown, about 2/3 the width of thorax at humeral angles. Frons moderately broad, narrowest point equal to width of antenna, subparallel and expanding gradually toward the vertex to about 140 μ, frontal angle 76° - 80°, moderately covered with silvery hairs, a medial sulcus extends from apex of clypeus to about 1/3 the length of frons. Clypeus swollen, almost square, blackish brown with silvery hairs. Posterior surface of head and occiput densely covered with long erect silvery hairs.

Antenna 11-segmented, uniformly blackish-brown, covered with silvery pubescence, pedicel and first flagellomere each about 1.5 longer than second flagellomere.

Mouthparts. Labrum, labella and maxillary palps blackish-brown, covered with pale yellow to coppery hairs; segment III twice as long as wide, moderately swollen dorsally, about as long as segment IV; segment V slightly less than twice the length of segment III. Sensory vesicle oval to boot-shaped, 1/4 to 1/3 the length of its segment, opening from a

shallow neck. Mandible strongly serrated along inner edge, outer edge smooth or jagged. Maxilla with acute retrose teeth. Cibarium smooth.

Thorax black to dark-brown. Scutum blackish-brown uniformly covered with silvery pubescence with some yellowish tinge, hairs slightly longer on posterior margin. Scutellum blackish-brown covered with long silvery hairs. Postscutellum, pleuron and katepisternum blackish-brown, grey pollinose, subshining, bare. Pleural membrane dark-brown to dark-red, bare. Pleural tuft and hairs on pronotum and proepisternum silvery. Basisternum connected to proepisternum by a thin precoxal bridge. Internal arms of furcasternum of metasternum lacking subbasal tubercles.

Wings. Veins pale to light-brown. Base of costa with silvery hairs, remainder with black to coppery hairs and black spicules. Base of subcosta with a row of about 15 black to coppery hairs ventrally, distal 1/3 bare. Radius with black to coppery hairs dorsally, length about 1/3 of distance from base of R_s to wing tip. R_1 with black hairs dorsally interspersed on distal 1/2 with about 12 black spicules. R_s simple, ventrally proximal 1/3 with single row of 6-7 blackish hairs, distal 2/3 with double row of similar hairs, dorsally distal 1/3 with single row of hairs, proximal 2/3 bare. Hair tuft on stem vein mostly coppery with few silvery hairs distally. Fringe of calypter and hairs on anal lobe silvery. Second basal cell complete. Halteres white to pale yellow.

Legs. Coxa dark-brown to black as pleuron, with moderately long silvery hairs. Trochanter, femur, tibia and tarsi uniformly dark-brown with silvery pubescence, coppery hairs on tarsi. Fore basitarsus cylindrical, moderately widened apically. Hind basitarsus with small calcipala 1/4 to 1/3 the width of segment at distal end; anteroventral

margin moderately arcuate medially and parallel with posterodorsal margin. Second hind tarsus bearing a shallow pedisulcus with transverse wrinkles. Claw blackish-brown, slender, moderately curved with a large subbasal tooth about 1/2 the length of the claw.

Abdomen dark-brown to black covered with silvery pubescence, hairs on tergites less dense than on sterna and pleura, basal fringe silvery. Sternites VII and VIII sclerotized. Gonapophyses bluntly rounded apically, medial margin narrowly sclerotized, slightly curved to straight. Paraproct triangular; cercus trapezoidal to triangular, long, tapering to a narrow distal margin; both combined length: width about 1.4: 1. Genital/fork with long thin stem heavily sclerotized and tip generally straight or slightly dilated; arms arcuate, uniformly broad, expanding into short rectangular plates broadly joining to IX tergite, inner margin of arms uniformly concave with a minute notch distally. Spermatheca oval, dark-brown to black with hexagonal reticulate pattern.

MALE. General body colour dark-brown to black with concolorous hairs. Length: body 2.5 - 2.8 mm; wing 2.0 - 2.4 mm.

Head as wide as thorax at humeral angles. Clypeus and posterior surface of head blackish, sparsely covered with concolorous hairs. Antenna 11-segmented, uniformly blackish-brown with recumbent silvery pubescence on flagellomeres, scape and pedicel with dark-brown hairs, pedicel and first flagellomere each about 1.5 longer than other flagellomeres. Palps uniformly blackish-brown with short concolorous hairs; sensory vesicle small, flask-shaped, 1/3 to 1/4 length of segment. Labrum and labella blackish-brown.

Thorax black to dark-brown with some grey pollinosity. Scutum velvety black with silvery pubescence and some pale yellow sheen. Pronotum and scutellum dark-brown, the latter with erect long concolorous hairs. Pleuron, postscutellum and katepisternum greyish pollinose, subshining, bare; pleural tuft and hairs on pronotum and proepisternum dark-brown. Wings as those of female, except black hairs at base of costa and on stem vein.

Legs uniformly blackish-brown, covered with dark-brown to black hairs. Hind basitarsus flattened with parallel margins, anteroventral margin slightly arcuate medially; calcipala minute about 1/4 as wide as segment at distal end; pedisculcus shallow with few transverse ridges.

Abdomen generally black with blackish hairs. Tergites velvety black with dark-brown erect hairs among dark-brown pubescence. Sternites and pleural membranes greyish pollinose with dark-brown, long erect hairs on sternites. Basal fringe coppery to black. Basistyle and dististyle uniformly blackish-brown with concolorous hairs; basistyle nearly square, dististyle moderately curved, tapering uniformly with a stout short apical spine. Ventral plate triangular, tapering distally, with blackish hairs, lip curved ventrally; basal arms rather long, slightly curved inwardly. Paramere with 4 long and 4 short slender, weakly sclerotized teeth. Median sclerite transparent, with a small forked tip.

LARVA. Length of last instar 4.2 to 6.0 mm, average 5.6 mm; general body colour pale yellow to light-brown; histoblast 12-filamented.

Head capsule generally pale-yellow. Cephalic apotome with marked positive head spots, almost with no background pigment except some near the posterior margin; 6 - 8 anteromedian spots, 2 contiguous or fused

double anterolateral spots, 12 - 16 contiguous posteromedian spots, 5 - 7 posterolateral spots with some marginal infuscation. Labrum dorsal surface light-yellow with minute microtrichia. Antenna weakly pigmented, first segment darker than other two; relative length of the three segments ratio 1: 1: 1, first and second segments combined as long as stem of cephalic fan; second segment subdivided into 5 to 7 (usually 5) annuli separated by rings of unpigmented membrane, basal annulus may be resubdivided once or twice; third segment slender, with a minute apical sensory spicule. Postgenal cleft small, rectangular usually with uneven anterior margin, slightly wider than long, width: length 3: 2, distance from anterior margin to apex of hypostomium about 4 times the length of the cleft. Subesophageal ganglion outline subrectangular. Hypostomium with 9 heavily sclerotized apical teeth, lateral teeth strongly developed and slightly elevated above intermediate ones, central tooth longer than mediolateral teeth, 2 to 3 lateral serrations adjacent to corner tooth usually strongly developed. Hypostomial setae 3 in a row, nearly equidistant from each other, posterior seta microtrichia-like farther from the second, anterior seta longest with relative length of the three setae 10: 5: 1.

Cephalic fan with 59 to 76 pale yellow rays (average 66), penultimate instar with about 10 fewer rays; setae on primary rays short and nearly touching, their length about half the thickness of the ray, longer setae alternating between groups of 6 to 8 short setae; marginal 3 or 4 rays adjacent to secondary fan with short setae only. Mandible ratio of length: width 2.2: 1, outer and apical teeth heavily sclerotized, 3 subapical and 3 to 4 shorter inner teeth, mandibular serrations with a long anterior tooth and 3 to 5 smaller posterior teeth

varying in number and size between the two mandibles of the same larva and among different specimens. Maxillary palp slender, about 5 times longer than its basal width.

Thorax: dorsal gap between bases of mature histoblasts (interhistoblast gap) relatively wide, almost as wide as post occipital width of the head capsule; histoblast normally with 12 filaments. abdomen·with dark yellow pigments, cuticle apparently smooth; last abdominal segment with two large conical ventral papillae; rectal "gills" compound, three major branches each resubdivided into smaller papillae. Anal sclerite X-shaped with shorter and contiguous anterior arms, posterior arms extending to 9th or 10th rows of hooks, cuticle between anterior and posterior arms with minute microtrichia. Posterior adhesive circlet with about 61 rows of 8 to 10 hooks.

PUPA. Respiratory gills light to dark yellow, average length 2.8 mm (1.5 to 3.4 mm) consisting of 12 filaments/side arising from two main trunks of equal length the latter diverging about 45° dorsoventrally; each trunk dividing horizontally into two branches, each branch resubdivided into two plus one filaments, hence producing branching pattern (3+3) + (3+3). Filaments straight and pointing horizontally forward. Integument and cocoon light to dark yellow, thoracic setae 5/side; tergite I with a simple setaform spine/side, II with 4 simple spines/side, III and IV each with 4 compound (double pronged) hooks/side, rest of tergites each with a row of comb spines - all pointing forward. Sternites, IV with one fine setaform spine/side, VI with 2 spines/side, VII and VII with one simple spine/side, last segment with two stout tail hooks. Cocoon slipper-shaped, finely woven, about 1.5 the length of filaments, with one long, slightly thicker anteromedial projection almost as long as

filaments; about 1/3 of basal portion of projection less tightly woven medially than rest.

HOLOTYPE. Female, type No. 13913 in the Canadian National Collection (C.N.C.), Ottawa.

TYPE LOCALITY. Östvollen Renåa River, Ytre Rendal, Hedmark, Norway. Attracted to CO_2-baited trap at water level, July 16, 1968, V.I. Golini. Larva, pupa, reared male and female from Sphagnum-bog in Rendalen, in June 1979. V.I. Golini.

RECORDS. Known from Rendalen; reported also from Murmansk U.S.S.R. (Rubtsov 1971). Material examined: 54 females from Östvollen, Ytre Rendal, July 16, 1968, 304 larvae, 506 pupae, 493 reared males and females from Östvollen, June - July 1980, V.I. Golini.

REMARKS. This species belongs chromosomally and morphologically to the congareenarum-group A of Dunbar (1967). Its closest relatives are H. near dogieli and H. fallisi as diagnosed in Golini (1975) and in text Discussion section.

BIOLOGICAL NOTES. This species was discovered initially as females feeding on blood of domestic ducks (Anas boschas) and attracted to CO_2-baited traps at water level on the Renåa River from early June to late July. Host-seeking females are restricted to within 10 m from shore and 1 m above water level (Golini 1975), and are vectors of Leucocytozoon simondi in ducks (Eide and Fallis 1972). Larvae develop on decaying vegetation in shallow seepages of sedge-Sphagnum bogs, preferentially at the periphery, in water current of 1-30 cm/sec and temperature $12°-16°C$, from early to mid May. The first pupae occur around mid May and adult

emergence from 2nd-3rd week of May to mid July. It overwinters in the egg stage. Reared adults have little stored nutrient and require a blood meal to develop eggs. Mating and oviposition habits are unknown.

Hellichiella near dogieli (Figs. 10 A-3, 11 A-C, 12 A-G)

Eusimulium near dogieli; Golini 1975, Ent. scand. 6: 229-239 (Female)

FEMALE.   General body colour dark brown to blackish, covered with silvery to pale yellow pubescence. Length: body 2.5 - 3.8 mm; wing 2.3 - 2.5 mm.

Head dark-brown about 2/3 to 3/4 width of thorax at humeral angles. Frons moderately broad, narrowest point as wide as antenna, subparallel and expanding gradually toward the vertex to about 140 µ, frontal angle about 75°, moderately covered with silvery hairs, a medial sulcus extends from apex of clypeus to about 1/3 the length of frons. Clypeus swollen, almost square, blackish-brown with silvery hairs. Posterior surface of head and occiput densely covered with long erect, silvery hairs.

Antenna 11-segmented, uniformly blackish-brown, covered with silvery pubescence, pedicel and first flagellomere about 1.5 the length of the second.

Mouthparts:labrum, labella and maxillary palps pale to dark yellow covered with coppery hairs, palp segment III darker than the others with an oval sensory vescicle; lengths of palp segments I+II (fused) 84 µ, III 112 µ, IV 112 µ and V 196 µ, all combined as long as hind basitarsus. Mandible serrated along inner edge, maxilla with retrorse teeth, cibarium smooth.

Thorax dark-brown to blackish, grey pollinose. Scutum uniformly

black to dark-brown, covered with silvery pubescence with some pale-
yellow tinge. Scutellum pale to dark yellow covered with long silvery
hairs. Postscutellum, katepisternum and pleuron dark-brown to black,
grey pollinose, subshining, bare. Pleural membrane dark-brown to dark-red,
bare. Pleural tuft and hairs on pronotum and proepisternum silvery.
Pronotum pale to dark-yellow. Basisternum connected to proepisternum
by a weak precoxal bridge. Internal arms of furcasternum of metasternum
lacking subbasal tubercles.

Wings. Veins pale to light-brown. Base of costa with silvery
hairs, remainder with coppery to black hairs and black spinules. Base
of subcosta with a row of about 15 black hairs ventrally, distal 1/3
bare. Radius with black hairs dorsally; hair tuft on stem vein mostly
silvery, some light yellow. R_1 with dark hairs dorsally interpsersed
on distal 1/2 with about 8 black spinules. R_s simple, ventrally proximal
1/3 with single row of 6 - 7 black hairs, distal 2/3 with double row of
similar hairs, dorsally proximal 2/3 bare, distal 1/3 with single row
of hairs. Fringe of calypter and hairs on anal lobe silvery. Second
basal cell complete. Halteres white to pale yellow.

Legs covered with silvery to pale yellow hairs. Fore and mid
coxa dark-brown, hind coxa pale yellow medially and dark-brown laterally.
Trochanter mostly pale yellow with some dark brown marginally. Femora
mostly pale yellow, distal 1/8 dark-brown. Tibiae pale yellow medially,
proximal and distal 1/4 dark-brown. Tarsi of fore and mid legs dark-
brown; tarsi of hind legs generally pale yellow, basitarsus with some
dark brown on proximal end, calcipala minute, about 1/4 to 1/3 width of
segment at distal end, anteroventral margin compressed, slightly arcuate
medially, posterodorsal margin round and straight; pedisulcus shallow

with transverse wrinkles. Claw black to dark-brown with a large subbasal tooth about 1/2 the length of claw.

Abdomen dark-brown with silvery pubescence; basal fringe silyery. Tergites dark-brown to black, moderately covered with short silvery hairs. Sternite VIII sclerotized, VII not sclerotized. Gonapophyses bluntly rounded apically with nearly straight inner margins. Paraproct and cercus combined length: width about 1.2: 1, cercus trapezoidal with sloping anterior edge, truncated to bluntly rounded apically. Genital fork with long thin stem, tip broadly dilated; arms arcuate, uniformly broad, expanding to rectangular plates joining broadly to IX tergite, inner margin uniformly concave with a minute notch distally. Spermatheca oval, dark brown with hexagonal reticulate pattern.

MALE. General body colour black to dark-brown with concolorous hairs. Length: body 2.4 - 2.7 mm; wing 2.0 - 2.2 mm.

Head as wide as thorax at humeral angles. Clypeus and posterior surface of head dark-brown to black covered with erect black hairs. Antenna 11-segmented, uniformly blackish-brown with recumbent silvery pubescence on flagellomeres; scape and pedicel with dark-brown hairs, pedicel and first flagellomere each about 1.5 longer than other flagellomeres. Palps pale yellow, segment III darker brown with small sensory vesicle about 1/5 the length of segment; labrum and labella pale-yellow.

Thorax black to dark-brown with some grey pollinosity. Scutum velvety black with silvery pubescence and some bronzy to yellowish sheen. Postnotum pale to dark yellow. Scutellum pale yellow with long black hairs. Pleuron, postscutellum and katepisternum grey pollinose, dark-brown, subshining bare; pleural tuft and hairs on pronotum and proepisternum dark-brown. Wing as that of female, with black hairs at base of costa

and on stem vein. Legs covered with dark-brown to black hairs. Fore coxa and mid coxa dark-brown, hind coxa pale yellow medially and dark-brown laterally. Trochanters mainly pale yellow with some dark-brown marginally. Femora mostly pale yellow, distal 1/8 dark-brown. Tibiae pale yellow medially, proximal and distal 1/4 dark-brown, hind tibia with long black hairs; tarsi of fore and mid legs dark-brown, tarsi of hind legs mostly pale yellow with some dark-brown on proximal end of basitarsus, the latter with parallel margins and slightly arcuate medially on anteroventral margin; calcipala minute 1/4 to 1/3 width of segment at distal end, pedisulcus shallow with some transverse wrinkles.

Abdomen. Tergites velvety black with dark brown, long, erect hairs and dark-brown pubescence. Sternites and pleural membranes greyish pollinose and dark-brown, long, erect hairs on sternites. Basal fringe black to coppery. Basistyle almost square, mostly pale yellow except for a narrow band of dark-brown at proximal and distal ends; dististyle uniformly dark-brown with concolorous hairs, long spines mainly on lateral surface, tapering uniformly with a stout short apical spine. Ventral plate triangular, tapering distally, covered with blackish brown hairs, lip slightly curved ventrally; paramere with four long and four short slender, weakly sclerotized teeth; median sclerite with a small forked tip.

LARVA. Length of last instar 4.2 to 6.0 mm (average 5.5 mm); general body colour pale yellow to light brown; histoblast 12-filamented.

Head capsule generally yellow. Cephalic apotome with marked positive head spots, almost with no background pigment except some near the posterior margin; 6 to 8 anteromedian spots, one or two contiguous double anterolateral spots, 10 to 16 contiguous posteromedian spots, 5

to 7 posterolateral spots with some marginal infuscation. Labrum dorsal
surface light yellow with few minute microtrichia. Antenna weakly
pigmented, first segment usually darker than other two; relative length
of the three segments 10: 9: 10.5, first and second segments combined
slightly shorter than stem of cephalic fan; second segment subdivided
into 4 secondary annuli separated by rings of unpigmented membrane; third
segment slender, longest with a minute sensory apical spicule. Postgenal
cleft small, rectangular, usually with uneven anterior margin, slightly
wider than long, width: length 3: 2; distance from anterior margin to
apex of hypostomium about 4 times the length of the cleft. Suboesophageal
ganglion outline triangular. Hypostomium heavily sclerotized, with 9
teeth, lateral ones strongly developed and slightly elevated above
intermediate teeth; central tooth longer than mediolateral teeth, 2 main
lateral serrations adjacent to corner tooth usually strongly developed.
Hypostomial setae 3 in a row nearly equidistant from each other, posterior
seta microtichia-like slightly farther from the second, anterior seta
longest, their relative length 10: 5: 1. Mandible relative length: width
2.3: 1; outer and apical teeth heavily sclerotized, 3 subapical teeth
and 3 to 4 shorter inner teeth, mandibular serrations with a long
anterior tooth and 2 to 5 smaller posterior teeth varying in size and
number even between mandibles of same specimen. Maxillary palp slender,
about 5 times longer than its basal width.

Cephalic fan with 60 to 85 pale yellow rays (mean 74; penultimate
instar with about 10 fewer rays); primary ray with 7 to 9 short setae
between two longer setae per segment length equal to ray thickness,
marginal 3 or 4 rays adjacent to secondary fan with short setae only;
stem with 5 to 8 microtrichia dorsally. Thorax, dorsal gap between bases

of mature histoblasts (intrahistoblast gap) narrower than postoccipital width of head capsule; histoblast normally with 12 filaments. Abdomen with dark yellow pigments, cuticle apparently smooth; last abdominal segment with two large conical rectal papillae; rectal "gills" compound, three major branches each resubdivided into smaller papillae. Anal sclerite ⋊-shaped with shorter and more contiguous anterior arms, posterior arms extending to 7th or 8th rows of hooks, cuticle between anterior and posterior arms with minute microtrichia. Posterior adhesive circlet with 61 rows of 8 to 11 hooks.

PUPA. Respiratory gills light to dark yellow, average length 2.0 mm (1.5 to 2.5 mm) consisting of 12 filaments arising from two main trunks of equal length which diverge about $60°$ dorsoventrally; each trunk dividing horizontally into two branches, each branch resubdivided into two plus one side-branches producing branching pattern (3+3) + (3+3). Filaments flared, diverging within $180°$ in different directions in front of the pupa, occasionally recurving backward. Integument and cocoon light to dark yellow, thoracic setae five per side; tergite I with a simple spine/side, II with 4 simple spines/side, III and IV each with 4 double spines/side, rest of tergites each with a row of simple comb spines - like others pointing forward. Sternites, IV with one fine setaform spine/side, VI with 2 spines/side, VII and VIII with one simple spine/ side, last segment with two stout tail hooks. Cocoon-slipper-shaped, finely woven, light to dark yellow, about 1.8 the length of filaments, with on slightly thicker, long, anterior projection slightly shorter than filaments, about 1/3 of basal length of projection less tightly woven medially than the rest.

RECORDS. Known from Rendalen, Norway, Material examined: 30 females from Östvollen, Renåa River, July 16, 1968, June-July 1979 and 1980; 84 larvae, 54 pupae and 54 reared adults; Fuglåsen, Ytre Rendal, June-July 1980, 203 larvae, 62 pupal and 62 reared adults, V.I. Golini.

REMARKS. This species was separated chromosomally from H. rendalense (see Chapter 1), and morphologically it resembles H. dogieli (Rubtsov sensu Usova) as diagnosed in this Chapter. Character differences between this and H. dogieli sensu Rubtsov (1956) and Usova (1959) indicate it is a new species (see diagnosis in Discussion section).

BIOLOGICAL NOTES. The biology of this species as larvae, pupae and adult females is similar to that of H. rendalense. Females are attracted to CO_2-baited traps and engorge on duck blood and are vectors of L. simondi to ducks (Golini 1975; Eide and Fallis 1972). Immature stages develop in bog seepages as H. rendalense except that larvae occur preferentially in mid rather than peripheral seepages in water current 1-30 cm/sec and temperature 12°-16°C from early to late May.

<u>Hellichiella</u> <u>fallisi</u> Golini (Figs. 13 A-J)

<u>Eusimulium fallisi</u> Golini, 1975. Ent. scand. <u>6</u>: 229-239 (Female).

FEMALE. General body colour blackish-brown, covered with silvery to pale yellow pubescence. Length: body 2.7 - 3.0 mm; wing 2.5 - 2.6 mm. Very similar to <u>rendalense</u>. Head dark-brown, about 2/3 the width of thorax at humeral angles. Frons moderately broad, narrowest point nearly equal to width of antenna, subparallel and expanding toward the vertex, moderately covered with silvery hairs, frontal angle 76° - 80°. Clypeus swollen, blackish brown with silvery hairs. Posterior surface of head and occiput densely covered with long erect silvery hairs.

Antenna 11-segmented, uniformly blackish-brown, covered with silvery pubescence, pedicel and first flagellomere each about 1.5 the length of the second segment.

Mouthparts. Labrum, labella and maxillary palps blackish-brown, covered with pale yellow to coppery hairs; segment III twice as long as wide, moderately swollen dorsally, about as long as segment IV, segment V slightly less than twice the length of segment III. Sensory vesicle about ¼ the length of the segment. Mandible strongly serrated along inner edge, outer edge with few apical teeth. Maxilla with acute retrorse teeth. Cibarium unarmed.

Thorax dark-brown to black. Scutum blackish-brown uniformly covered with silvery pubescence with some yellowish sheen, hairs slightly longer on posterior margin. Scutellum blackish-brown covered with long silvery hairs. Postscutellum, pleuron and katepisternum blackish-brown, subshining, bare. Pleural tuft and hairs on pronotum and proepisternum silvery.

Basisternum connected to proepisternum by a thin precoxal bridge.
Furcasternum of metasternum lacking subbasal tubercles.

Wings. Veins pale to light brown. Base of costa with silvery hairs,
remainder with black hairs and spinules. Base of subcosta with a row of
about 15 black to coppery hairs ventrally, distal 1/3 bare. Radius with
black to coppery hairs dorsally, length about 1/3 of distance from base of
R_S to wing tip. R_1 with black hairs dorsally; R_s simple, ventrally proxi-
mal 1/3 with single row of blackish hairs, distal 2/3 with double row of
similar hairs, dorsally distal 1/3 with single row of hairs, proximal 2/3
bare. Hair tuft on stem vein coppery with few silvery hairs distally.
Fringe of calypter and hairs on anal lobe silvery. Second basal cell
complete. Halteres white to pale yellow.

Legs. Coxa dark-brown to black, with moderately long silvery hairs.
Trochanter, femur, tibia and tarsi uniformly dark-brown with silvery pube-
scence, coppery hairs on tarsi. Fore basitarsus cylindrical, moderately
widening distally. Hind basitarsus with a small calcipala 1/4 to 1/3
the width of segment at distal end; second hind tarsus with a shallow
pedisulcus with transverse wrinkles. Claw blackish-brown, slender, with
a large sub-basal tooth about ½ the length of the claw.

Abdomen dark-brown covered with silvery pubescence, basal fringe
silvery. Sternites VII and VIII sclerotized. Gonapophyses bluntly —
rounded apically, medial margin narrowly sclerotized, slightly concave.
Cercus short, subrectangular truncated to gently rounded apically; para-
proct and cercus combined lateral view ratio length: width about 1:1,
paraproct triangular. Genital fork with long thin stem, darkly sclerotized

but less so on anterior tip which is markedly dilated; arms arcuate, uniformly broad, usually expanding into short rectangular plates broadly joining to tergite IX; inner margins of arms concave, with a minute mid notch apically. Spermatheca oval, dark brown to black with hexagonal reticulate pattern.

PUPA. Respiratory gills light to dark yellow, length about 2.0 mm (1.5 to 2.5 mm) consisting of 12 filaments arising from two main trunks of equal length which diverge about 60° dorsoventrally; each trunk dividing horizontally into two branches, each of which resubdivides into two plus one side-branch resulting in a branching pattern (3+3)+(3+3). Filaments flared, diverging in different directions. Exuvia and cocoon light to dark yellow, thoracic setae five per side; tergite I with a simple spine/side, II with 4 simples spines/side, III and IV each with 4 double spines/side, rest of tergites each with a row of spine combs- like others pointing forward. Sternites, IV with one setae form spine/side, VI with 2 spines/side, VII and VIII with one simple spine/side, last segment with two stout tail hooks. Cocoon slipper-shaped, finely woven, light to dark yellow, about 1.8 the length of filaments, with one long, anteromedial projection slightly shorter than filaments, about 1/3 basal length of projection less tightly woven medially than the rest.

MALE similar to that of _rendalense_.

LARVA unknown.

HOLOTYPE. Female, type No. 13914 in the Canadian National Collection (C.N.C.), Ottawa.

TYPE LOCALITY. Östvollen Renåa River, Ytre Rendal, Hedmark, Norway. Attracted to CO_2 trap at water level, July 16, 1968, V.I. Golini. Pupa, reared female and male collected from Sphagnum bog on Fuglåsen, Ytre Rendal, in June 1980, V.I. Golini.

RECORDS. Known only from Rendalen. Material examined: 22 females from Ostvollen, July 16, 1968; 32 pupae and reared females and males from Ostvollen and Fuglåsen June-July 1980, V.I. Golini.

REMARKS. This species has not been distinguished chromosomally; larvae and adult males are morphologically indistinguishable from those of H. rendalense. Differences between these species are diagnosed in the Discussion section.

BIOLOGICAL NOTES. This species was discovered initially as females feeding on blood of domestic ducks (Anas boschas L.) and attracted to CO_2-baited traps at water level on the Renåa River, from early to late July. Host-seeking females are restricted to within 10 m from shore and 1 m above water level (Golini 1975), and are vectors of L. simondi in ducks (Eide and Fallis 1972). Immature stages develop in sedge-Sphagnum bogs, preferentially in mid bog, in shllow seepages with water current of 1-30 cm/sec and temperature of $12^{\circ}-16^{\circ}C$, from early to late May. Pupae occur from mid to end of May and adults in late May-early July. Reared females have little stored nutrients and require a blood meal for the first ovarian cycle. Mating and oviposition habits are unknown.

Stegopterna dogieli Usova

(Usova, 1956, Proceedings of the Leningrad Society of

Naturalists). (as quoted in Rubtsov, 1956)

Isolated Species. (see also Fig. 4a, this thesis)

Male

Only prepared genitalia are present from the pupae. The gonocoxites (basistyles) are elongated; their length exceeds their breadth. The gonostyles (dististyles) are long, conically pointed towards the end, weakly and gradually bent, with a small groove on the external side; at the end of the gonostyles is a single small spinule. The gonosternum (ventral plate) laminated, the hooks (parameral teeth) are short and fine; the body of the gonosternum is blunt and conically pointed to the back; the width of its body exceeds the length by almost twofold.

Female

The length of the body is 2.3-2.5 mm, of the wings 2.7 mm. The frons is narrow, its height is twice as high as the width; pubescence of frons is general light-colored golden hairs. The antennae, according to Usova, are 10-segmented, completely black. The maxillary palps are relatively short; the 4th segment is shorter than the second and third put together; the 2nd segment is almost twice as thick as the 4th. The Lauterborn organ (sensory vesicle) is small. The scutum is grayish-black with dense golden hairs. The scutellum is dark-brown with long sparse dark-golden hairs. The halteres are light yellow. The legs are completely yellowish with long hairs. Dark in colour: the coxae, the distal ends of the femora, the top quarter of the tibiae, the tarsi of

the fore and mid legs. The first segment of the fore-tarsus is slightly flattened and broadened towards the tip; its length is 7 times greater than the width. The first segment of the hind tarsus is slightly broadened in the middle, is equal to the tibia in width, and is 3/4 of its length; its length is 5 times greater than its width. The calcipala on the 1st segment of the hind tarsi is well developed, the pedisulcus is lacking on the 2nd segment. The anal plates are small, semi-circular, the cerci are elongated.

Larva. Length of the body 5.0-5.6 mm. The coloration of the body is light grayish. The cephalic apotome with an obvious positive pattern. Three lateral spots on each side; they are separate and the lower one is larger than the middle and upper one, the middle spots in the middle of the frons are almost joined to each other. The antenna is 4-segmented, the 1st segment is equal in length to the 2nd and twice as thick, the third segment is the longest. In the primary head fan there are 48 rays. The apical tooth of the mandible is large, the anterior preapical tooth is significantly larger than the middle one; there are many marginal teeth, more than 6, of these the first is larger than the others. The submentum is as in the species of Stegoptera, i.e. it seems to consist of three groups of teeth whereby the lateral ones are significantly larger than the median. There are two thick setae along each side of the submentum. The ventral incision in the head capsule is shallow, unevenly triangular, with uneven edges. The rectal "gills" are simple. On the ventral side at the end of the abdomen are two conical growths (ventral papillae). In the adhesive organ are 74-76 rows of hooks with 9 hooks in each row. The posterior branches of the anal sclerite reach the 12th row of hooks.

Pupa. The length of the body is approximately 3.0 mm. The cocoon, with a long horn-like growth, covers completely the body of the pupa. The lateral edges of the horn-like growth (anterior projection) are thickened. The pupal gills have respiratory filaments on each side. At the base of the organism is a long stem separating into two; on each stem there are six filaments; their branching is uneven and separate filaments depart in varying distance from the base, while several of them in the upper third go the whole length of the organ. The aggregate of the filaments is close to one vertical plane and their tips are located approximately on a single level. The coloration of the filaments is black and towards the tip the filaments are lighter. The posterior segment of the body of the pupa bears two thin long bristles.

Biology. The larvae and pupae are attached on stones in small cold swampy streams where there is an average current of approximately 0.3-0.5 m/sec., at a water temperature of $10-12^{\circ}C$. Pupation in June. Emergeance at the beginning of July.

Distribution. Karelia, Pryazhinsky District, stream by Vilga; Belozersky District, stream behind village of Vedlozero; Belomorsky District, environs of the town of Belomorsk; Kensky District, stream by the Eligozero Station (Usova).

The presence of a well developed cocoon with a horn-like growth, the fine and elongated gonostyles with a single spinule at the end, the claws in the female with a large tooth, sharply differentiate this species from all other species of the Stegoptera. The enumerated aggregate of characteristics appears as the basis for separating the species into a special (separate) species.

Figs. 7-9   H. rendalense line drawings of morphological characters of
             adults male and female, larva and pupa.   (Dimensions in mm)

Figs. 7   H. rendalense female.
A-E   A. Hypopygium showing shape of genital fork, paraproct and
             long tapering cercus, sclerotized VII and VIII sternites.
             B. 1st, 2nd, 3rd legs showing uniformly dark pigmentation,
             small calcipala and shallow pedisulcus on hind (3rd) leg.
             C. Tarsal claw showing large subbasal tooth.   D. Frons,
             shape and size.   E. Antenna with the normal number of
             11-segments, pedicel and first flagellomere are each longer
             than subsequent segment.

Figs. 8   H. rendalense male.
A-C   A. Basistyle and dististyle.   B. 1-4 Ventral plate (gonosternum)
             in different orientations: 1 horizontal, 2 oblique to vertical,
             top view, 3 vertical, ventral view, 4 lateral view-note large
             angle of lip curvature.   C. Paramere, showing shape and number
             of spines-four long and four short spines. (Length of bars
             0.05 mm)

Figs. 9   H. rendalense larva A-E, pupa F-G
A-G   Larva.   A. Head capsule, ventral view showing postgenal cleft,
             subrectangular shaped subesophageal ganglion, hypostomium with
             position and relative size of three setae/side.   B. Hypostomium
             apex showing nine inner teeth and lateral serrations, the
             corner teeth are largest and lightly raised above level of
             intermediate teeth.   C. Cephalic apotome showing pattern of
             positive head spots on relatively unpigmented background.
             D. Antenna, showing the second segment subdivided by the normal
             five annuli.
             E. Mandibles, left and right of the same larva showing large
             apical teeth, 3+4 subapical + inner teeth, and mandibular
             serrations whose size and number of distal teeth is highly
             variable.

Figs. 9   H. rendalense   pupa F-G

F-G   Pupa.   F. Gill, showing branching pattern of respiratory
         filaments, upper trunk 3+3, lower 3+3 branches.   Note
         filaments pointing straight forward in the same direction.
         G. Cocoon with prominent anteromedial projection.
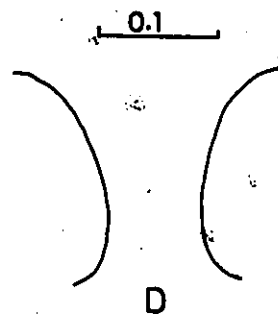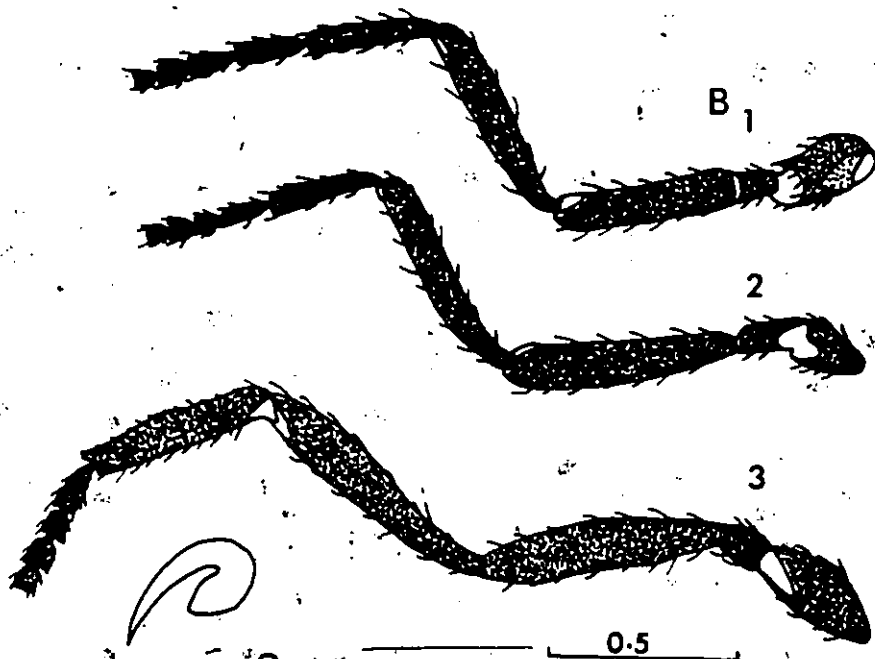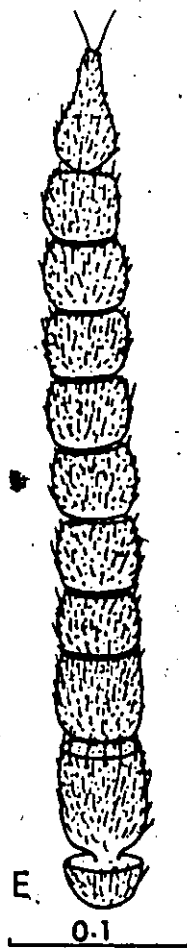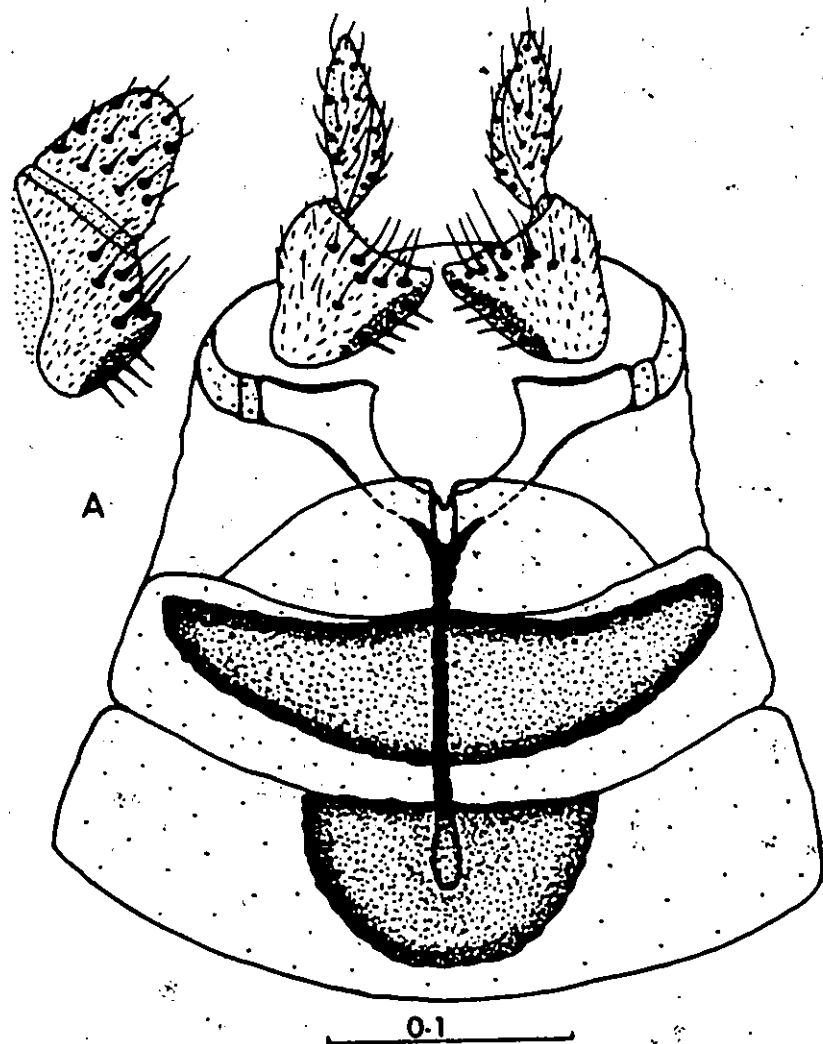
Figs. 7A-E
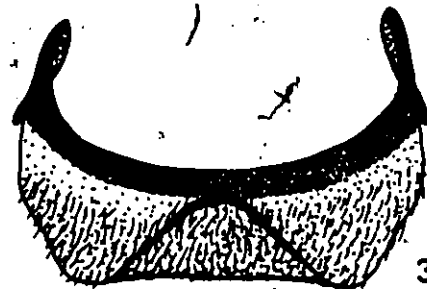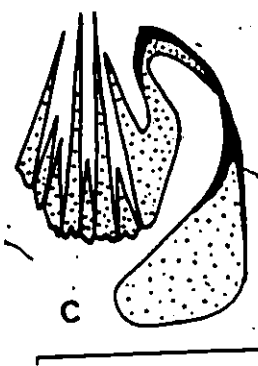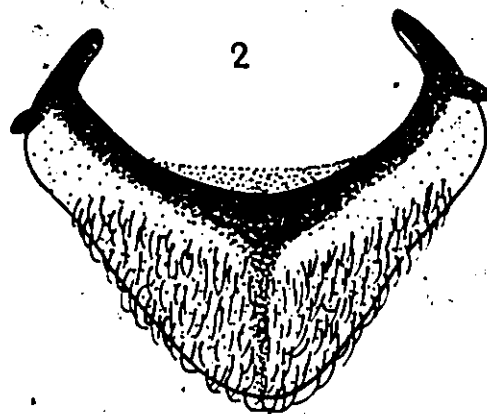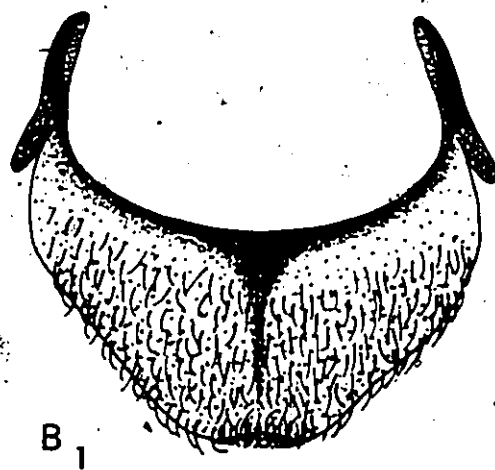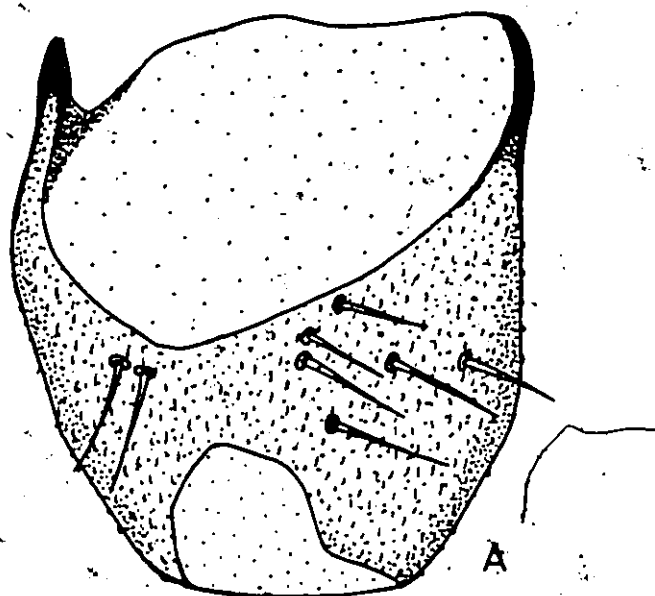
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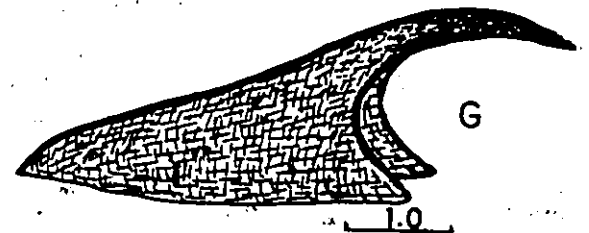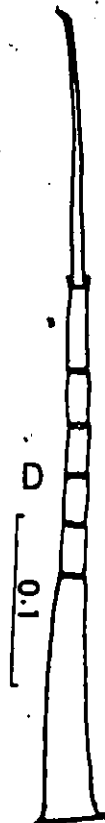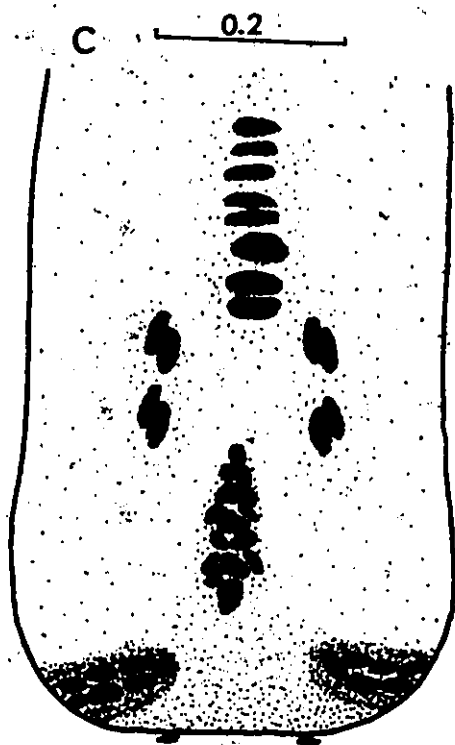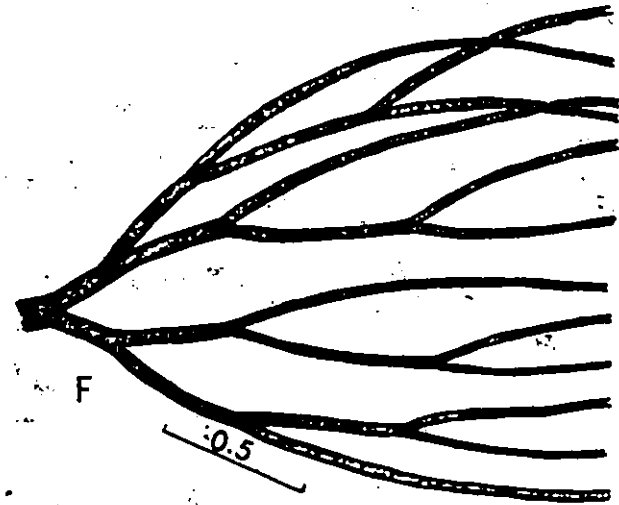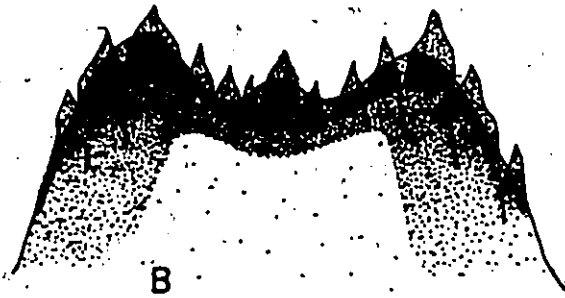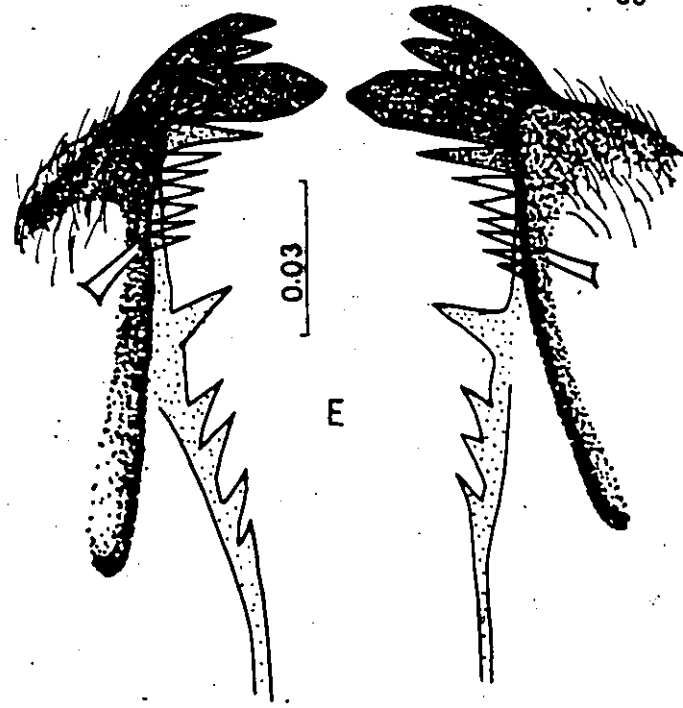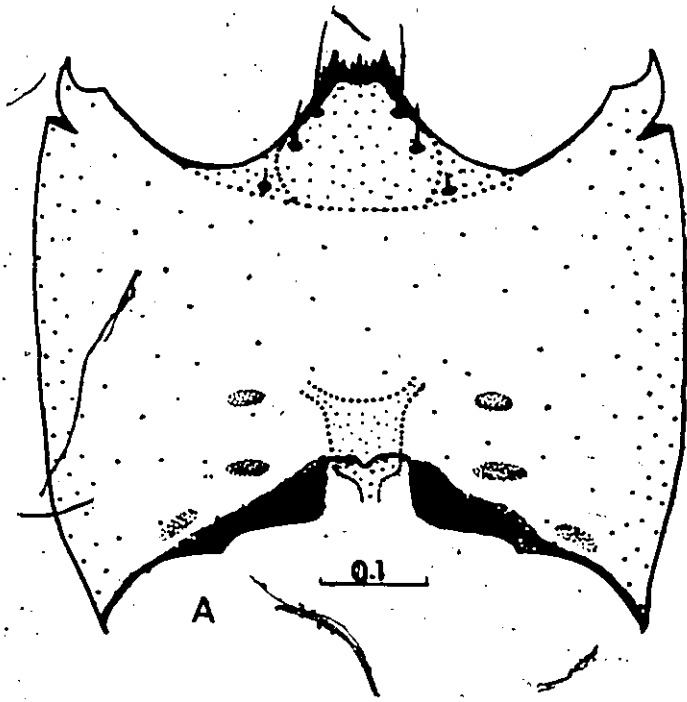
Figs. 9A-G

Figs. 10–12   H. near <u>dogieli</u> line drawings of morphological characters of
adults male and female, larva and pupa. (Dimensions in mm)

Figs. 10   H. nr. <u>dogieli</u> female.
A–E   A. Hypopygium showing shape of genital fork, note dilated
anterior tip; paraproct and medium length subtruncated cercus;
sclerotized VIII tergite. B. 1st, 2nd, 3rd legs showing
pattern of dark and light pigmentation, small calcipala and
shallow pedisulcus on hind (3rd) leg. C. Tarsal claw showing
large subbasal tooth. D. Frons, note narrower shape.
E. Antenna with the normal number of 11-segments, pedicel
and first flagellomere are each longer than subsequent segment.

Figs. 11   H. nr. <u>dogieli</u> male.
A–C   A. Basistyle and dististyle, note darker pigmentation on
proximal and distal margin of basistyle and on entire
dististyle. B. 1–4 Ventral plate in different orientations;
1 horizontal, 2 vertical, top view, 3 vertical ventral view,
4 lateral view–note small curvature, thus nearly straight lip.
C. Paramere, showing shape and number of spines–four long and
four short–and widely diverging arm. (Length of bars 0.05 mm)

Figs. 12   H. near <u>dogieli</u> larva A–E, pupa F–G
A–E   Larva. A. Head capsule, ventral view showing postgenal cleft,
subtriangular shaped subesophageal ganaglion, hypostomium with
position and relative size of three setae/side. B. Hypostomium
apex showing nine inner teeth and lateral serrations, the
corner teeth are largest and slightly raised above level of
intermediate teeth. C. Cephalic apotome showing pattern of
positive head spots on relatively unpigmented background.
D. Antenna, showing the second segment subdivided by the
normal four annuli, distal annulus slightly longer than basal
ones. E. Mandibles, left and right of the same larva showing
large apical teeth, 3 + 4 subapical + inner teeth, and mandibular
serrations whose size and number of distal teeth is highly variable.

Figs. 12   H. near dogieli pupa F-G
F-G   Pupa. Gill showing, showing branching pattern of respiratory
          filaments, upper trunk 3 + 3, lower 3 + 3 branches. Note
          flaring filaments pointing in various directions. G. Cocoon
          with prominent anteromedial projection.

A

0.1

B

1

2

3

C

0.5

D

0.1

E

0.1

Figs. 10A-E

A

B 1

C

2

4

3

Figs. 11A-C

A

B

C

D

E

F

G
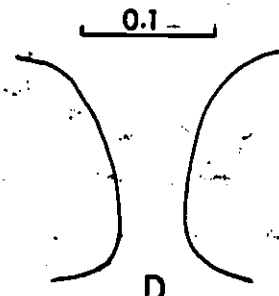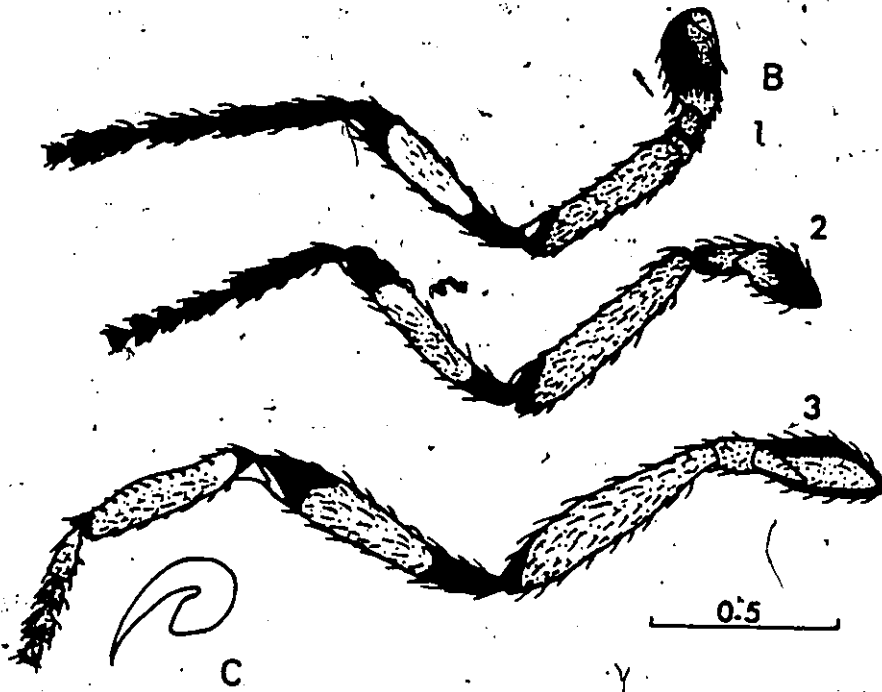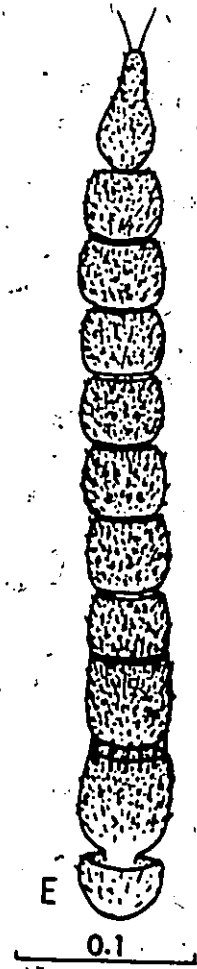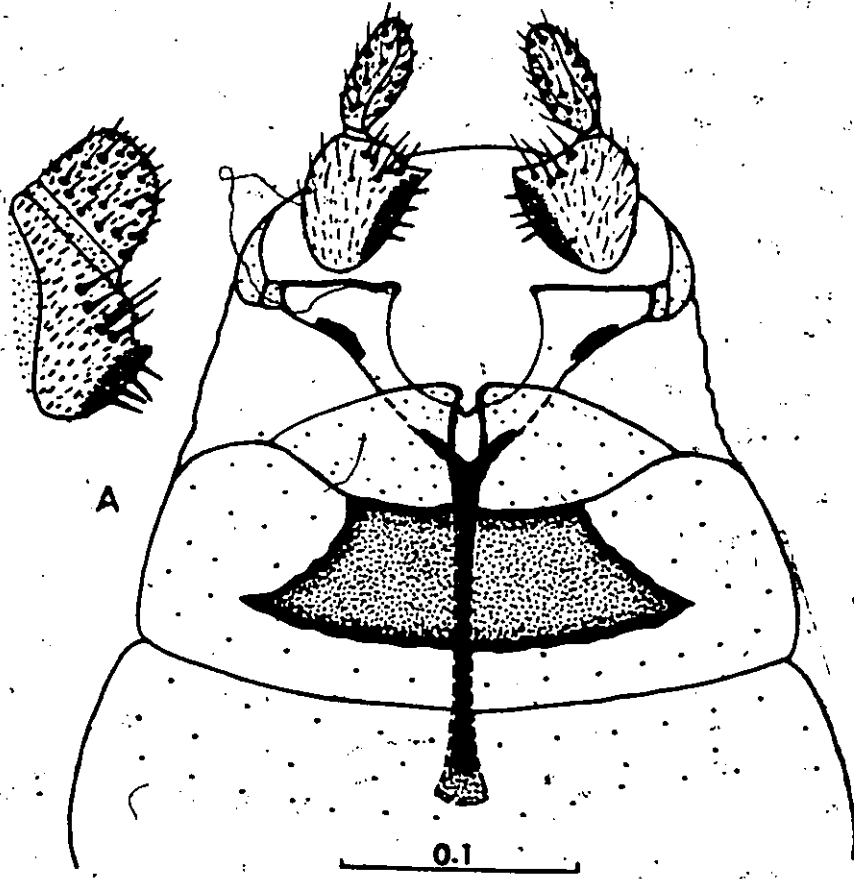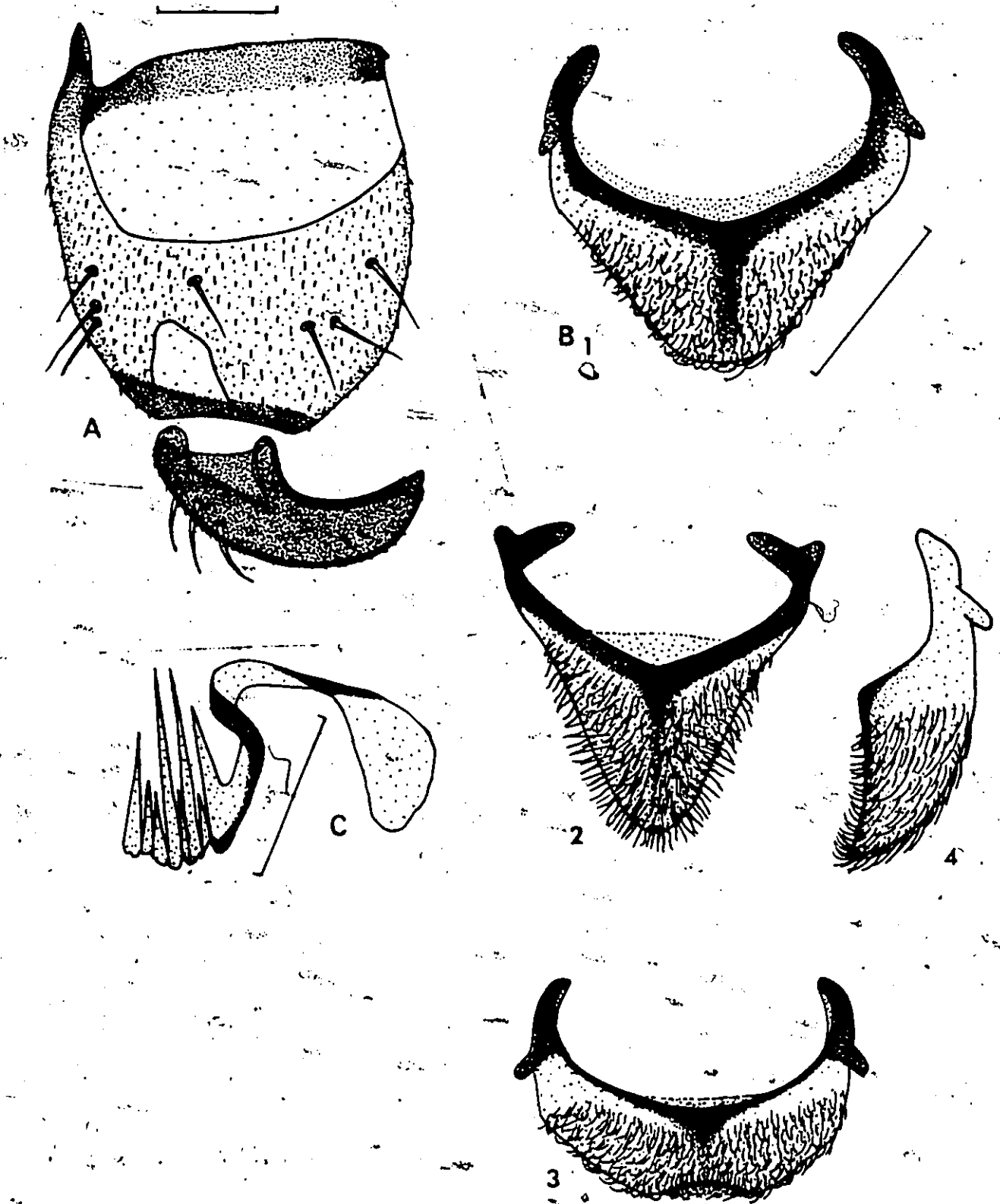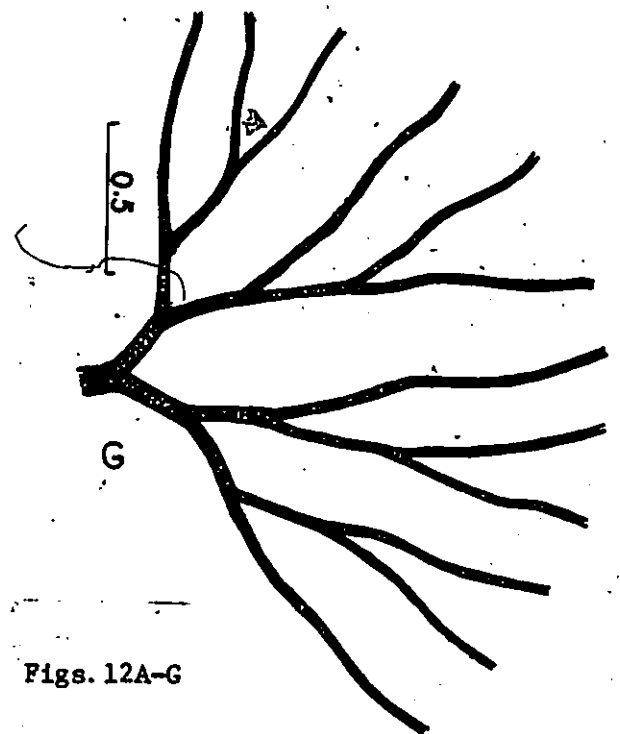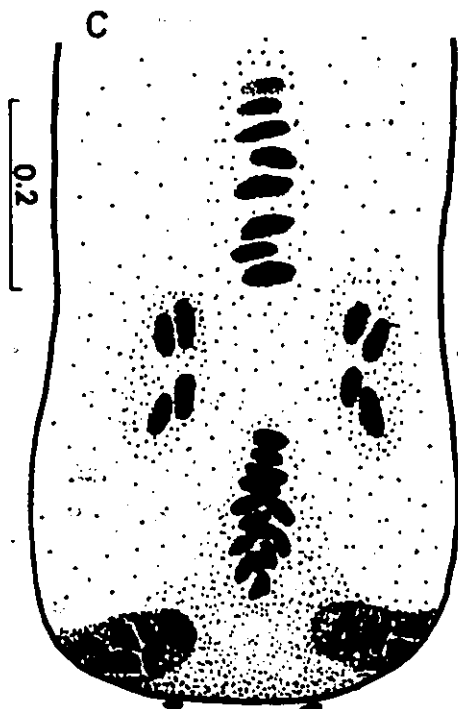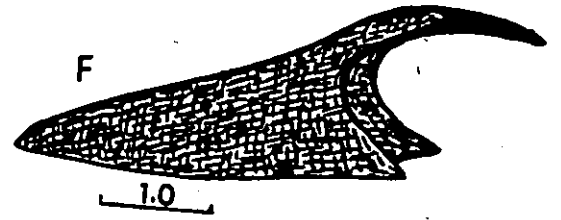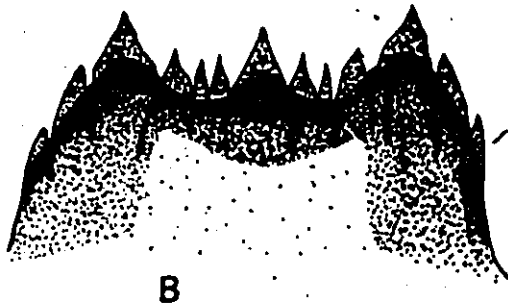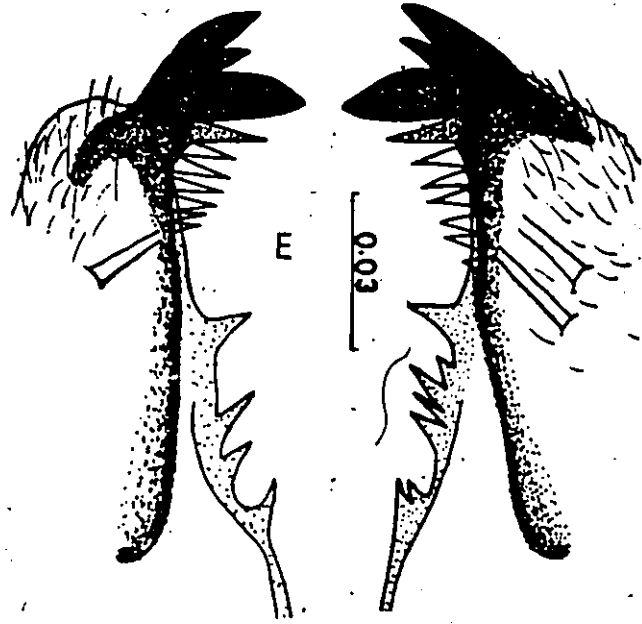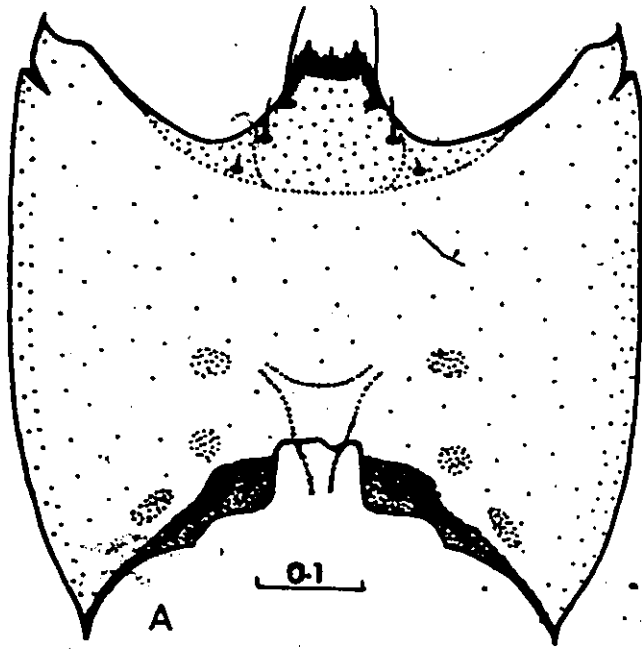
Figs. 12A-G

Figs. 13   H. fallisi line drawings of adult female (A-H) and pupa (I-J).
A-J   (A-F redrawn from Golini 1975; dimensions in mm)

Figs. 13   H. fallisi female.
A-H
              A. Maxillary palp.   B. Apex of mandible.   C. Tarsal claw.
              D. Hypopygium showing genital fork, portion of hypophysis
              and sternum VII and VIII both sclerotized, spermatheca.
              E. Paraprocts and cerci, ventral and side view, note low
              circus truncated distally.   F. Paraproct and cercus, side
              view, showing variation in shape.   G. Antenna with the normal
              number of 11-segments, pedicel and first flagellomere each
              longer than subsequent segment.   H. 1st, 2nd, 3rd legs, showing
              uniformly dark pigmentation on all segments, small calcipala
              and shallow pedisulcus on hind (3rd) leg.

Figs. 13   H. fallisi pupa.
I-J
              I. Cocoon with prominent anterior projection.   J. Gill showing
              branching pattern of respiratory filaments, upper trunk 3 + 3,
              lower 3 + 3 branches.   Note filaments flaring out, pointing
              in different directions.
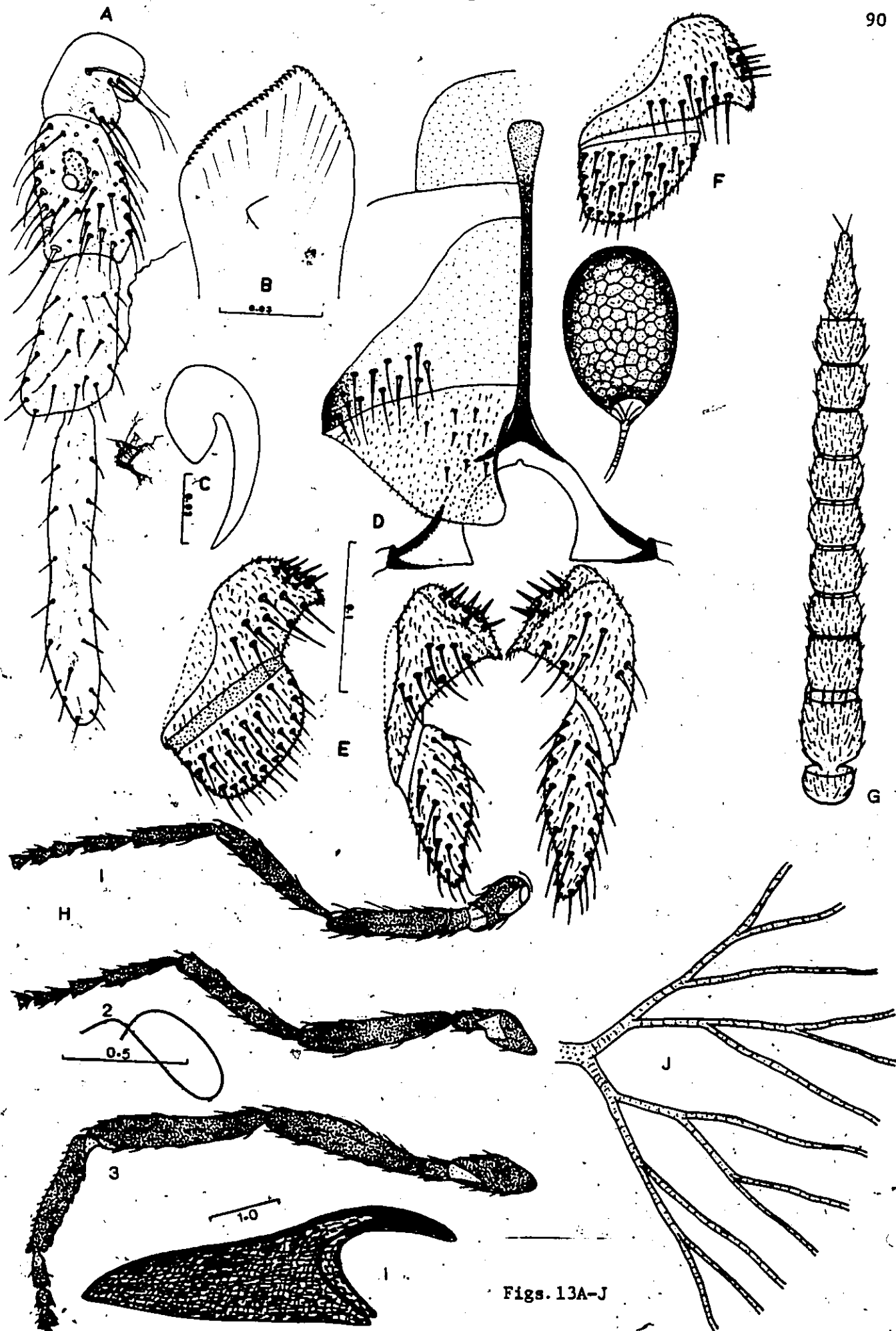
Figs. 13A-J

DIAGNOSIS AND DISCUSSION

H. rendalense and H. near dogieli

The adults of these two species differ essentially in degree of pigmentation of the legs and other body parts. Both male and female of H. rendalense are uniformly dark-brown to black, while adults of H. near dogieli have dark-brown and pale yellow pigmented legs and other body parts. This differential pigmentation is a stable character and not the result of incomplete hardening of the cuticle of teneral specimens. This character occurred consistently in reared specimens kept alive for as long as five days after emergence, and also in wild females caught while biting ducks (Golini 1975). This differential pigmentation is detectable most readily in ethanol-preserved specimens, while in dry-pinned specimens the contrast is less obvious. In both males and females of H. rendalense these body parts are all uniformly blackish-brown. However, the integument colour of adults may vary from generally black, in dry-pinned specimens, to dark-brown, in ethanol-preserved specimens; this colour range given in the description applies to these conditions of preservation.

The female of H. near dogieli is distinguished also by the sclerotization on the VIII sternite and its absence on the VII; H. rendalense has both the VII and VIII sternites sclerotized. In H. near dogieli the frons is slightly narrower and the cerci are generally semitruncated distally with a gently sloping ventral margin; in H. rendalense the

frons is generally broader and the cerci are typically long and taper posteriorly to a narrow distal margin.

The male of H. rendalense has the lip of the ventral plate markedly recurved ventrally and the parameral arm recurves contiguously beside the parameral teeth; in H. near dogieli the lip of the ventral plate is almost straight, and the parameral arm has a wide curvature. The basistyles of the two siblings have characteristic contours in the openings on the inner surface. The shape of the ventral plate when viewed in different orientations appears in different shapes, as shown in the text drawings. Hence, when analysing this character the orientation should be standardized or specified.

Although the antennae of adults have normally 11 segments (scape, pedicel and 9 flagellomeres), the number of flagellomeres is variable. In about 5% of reared adults of both species the number of flagellomeres varied from 6 to 8 (8 being common) due to fusion of one or two distal segments. Segment fusion is sometimes difficult to detect, and the antennae may appear to have 10 normal segments.

The pupae of these two species are distinguished by the orientation of the respiratory filaments. In H. rendalense the filaments are parallel and point directly forward in front of the pupa; whereas, in H. near dogieli they flare out, pointing in all directions within a 180° angle in front of the pupa.

It should be noted that of the reared pupae of Hellichiella from Rendalen, comprising 249 from 1979 and 831 specimens from 1980 (see Ecology section), almost all had the normal number of 12 respiratory filaments/side. In about 10% of these pupae, primarily of the 1979 collection, the third lateral filament in each upper two trunks

occurred as a short branch near the tip of its parent filament. In an equally low proportion one of these side filaments was completely missing, producing a branching pattern (2+3) + (3+3). In 53 pupae of the 1980 collection, primarily from Åsmyrtjörna, the two upper lateral filaments were missing entirely, resulting in pupae with 10 normal filaments/side and a branching pattern (2+2) upper + (3+3) lower. This loss of one or two filaments occurred invariably in the upper branches and in reared pupae of both _H. rendalense_ and _H._ near _dogieli_. This indicates that reduction to 10 respiratory filaments is not species specific in _Hellichiella_ from Rendalen. However, cytological evidence is still required to show that the 10-filamented form is not another species, since each of the 38 larval carcasses of both species whose histoblasts were analysed had 12 filaments.

The cocoon of about 3% of specimens, mainly _H._ near _dogieli_, derived from open bog seepages was less tightly woven, and the anteromedial projection was incompletely formed, being less than half its normal length.

The larvae of _H. rendalense_ and _H._ near _dogieli_ are distinguished morphologically as last instars by the following characters:

1) The second antennal segment in _H. rendalense_ has five annuli, and that of _H._ near _dogieli_ has four annuli; the length of the first and second antennal segments of _H._ near _dogieli_ is slightly shorter than the stalk of its head-fan; in _H. rendalense_ they are as long as the stalk of its head fan. The differential number of annuli is the main character that distinguishes the mature larvae of these two siblings. These two species cannot be separated with certainty as immature larvae

because the number of annuli varies from 2 to 4 in second to penultimate instars.

2) The suboesophageal ganglion is subrectangular in H. rendalense and subtriangular in H. near dogieli. This character difference is evident also in most younger instars.

3) The thoracic gap between the bases of mature histoblasts in H. rendalense is wide, usually as wide as the length of its cephalic fan stalk; in H. near dogieli this interhistoblast gap is narrow, the width being smaller than the length of its cephalic fan stalk.

4) The mature larva of H. rendalense has generally a slightly larger head capsule and an average of eight fewer rays in the primary cephalic fan than H. near dogieli. However, although these numerical differences help to distinguish the two populations, they may not always distinguish individual larvae. No differences are evident among the other measured characters reported in Tables 5 and 6. The shape and number of mandibular serrations are variable in both species; differences of two or three teeth are common, even between the left and right mandibles of the same larva. The number of hypostomial setae is normally 3 per side, and the smallest posterior seta resembles a microtrichia which in some specimens may be missing, broken off or difficult to detect; however, hair sockets are present where setae are broken off. A summary of the differences between these two species is given in Table 8.

H. rendalense, H. fallisi and H. near dogieli

The first two of these species were initially described from females and distinguished by characters outlined in Golini (1975). In the present study H. fallisi was not distinguished from the other

two species by chromosomal analysis of the larvae. The larvae that were distinguished from those of H. near dogieli were considered to belong to H. rendalense on evidence primarily of larval head capsules in association with exuviae and reared adults whose females corresponded to this species (present study). However, among the reared adults of H. rendalense, 30 specimens were distinguished by the 12 filamented pupae whose respiratory filaments flared outward, contrasting with the straight parallel filaments of this species. Fourteen of these reared adults were females which were identified as H. fallisi, based on the low truncated cercus; in H. rendalense the cercus is distinctly long and tapering apically. The other sixteen were males not distinguishable by external morphology from those of H. rendalense. The hypopygia dissected from two of these males were not significantly different from those of H. rendalense. Hence, H. fallisi is distinguishable from H. rendalense only in the female and pupa. Further analysis is needed of the remaining fourteen males in this group of adults to ascertain their relationship to the male of H. rendalense.

The pupae of H. fallisi and H. near dogieli have identical branching pattern of respiratory filaments, and thus cannot be distinguished by this character. However, the adults of H. fallisi have uniformly dark legs, and in females the cercus is low and truncated; adults of H. near dogieli have differentially pigmented legs and the cercus, although generally truncated apically, is longer and sloping ventrally.

It should be noted that the low proportion of pupae and reared adults of H. fallisi was probably associated with a correspondingly low proportion of larvae of this species, thus precluding their sampling for chromosome analysis. In addition, the large quantity of larvae

fixed in relatively small volumes of Carnoy and kept unrefrigerated in the field, reduced the quality of chromosome preparations below optimal, especially of the 1980 collection. Further cytological analysis of better fixed larvae may increase the probability of detecting chromosomal differences between H. fallisi and the other two species.

It is pertinent to note here that the close similarity of these species invalidates the placement by Raastad (1979) of H. dogieli and H. rendalense in Cnephia (Greniera),and H. fallisi in synonymy with E. meigeni in Eusimulium (Hellichiella). E. meigeni sensu Rubtsov (1971) is a misidentified entity (see this Chapter and Crosskey pers. comm.), and thus has no relationship with H. fallisi.

H. dogieli and H. near dogieli

There was no opportunity in this study to analyse certified specimens of H. dogieli. The apparent scarcity of this species has contributed to the difficulty of obtaining on loan specimens for study (Rubtsov 1969 in litt.). The first description of the species, in the genus Stegopterna, was reported by Rubtsov in 1956 who attributed species authorship to Usova. Rubtsov's (1956) reference to Usova (1956) in a journal not yet published at that time indicates Usova's intention to publish her description in 1956; but her formal publication of the species, in the genus Hellichia was delayed until 1959 (see below). This created the condition which, according to the International Code of Zoological Nomenclature, 1960, relating to priority of first date of publication, gives Rubtsov and not Usova authorship for the species description. Hence, references to Usova as author of H. dogieli should be amended, supported by R.W. Crosskey (in litt. 1982), as shown below.

Hellichiella dogieli (Rubtsov, 1956)

Stegopterna dogieli Rubtsov, 1956, Fauna SSSR 6 (6) : 841-843.

> (In Russian: specific name attributed to Usova with citation
> of non-existent reference.)

Hellichia dogieli (Rubtsov, 1956): Usova, 1959, Trudy karel. Fil. Akad.
> Nauk SSSR 14 : 110-113. (In Russian: species purportedly
> new, Rubtsov 1956 not cited.)

Eusimulium dogieli (Rubtsov, 1956): Usova, 1961 Blackflies of Karelia
> and Murmansk region : 80-84. (In Russian: species attributed
> in error to Usova 1958 (sic.).)

Eusimulium dogieli (Rubstov, 1956): Rubtsov, 1962, Fliegen paläarkt.
> Reg. 14 : 281-282. (In German: name incorrectly attributed
> to Usova with incorrect 1957 (sic) reference "Arb. Karel.
> Fil. Ak. Wiss. USSR. 13 :" uncompleted and different from that
> of Rubtsov 1956 : 841).

Greniera dogieli (Rubtsov, 1956): Rubtsov, 1963, Fliegen paläarkt.
> Reg. 14 : 591. (In German: species name incorrectly attributed
> to Usova without date. Indication published that same species
> was formerly assigned to either Stegopterna or Eusimulium.)

Eusimulium dogieli (Rubtsov, 1956): Usova, 1964, Blackflies of Karelia
> and Murmansk region : 77-83. (In English: IPST translation
> of Usova, 1961, from the Russian. Species attributed in
> error to Usova 1958 (sic).)

There is no mention of a holotype of H. dogieli by either
Rubtsov (1956) or Usova (1959, in 1961). Rubtsov (1956) gives only a

verbal description of the species, and it is different from that of
Usova (1959/1961). The larva by Rubtsov has the primary head fan with
48 rays and simple rectal gills; Usova reports 60 rays and compound
"gills". The branching pattern of the 12 pupal filaments shown by
Usova (1961) is wide and flaring, similar to that of H. near dogieli,
while that of Rubtsov (1956; 1962) is parallel, with filaments pointing
forward in one direction, as that of H. rendalense. The descriptions
of this species as reported by these two authors are compared in text
Figs. 4a and 4b.

The variation in number of flagellomeres in adults of H. near
dogieli and H. rendalense, as noted in this section, may also occur in
H. dogieli. Usova (1961) shows the antenna of H. dogieli with 10 segments,
and Rubtsov (1956 and 1959-64), referring to Usova, reports H. dogieli
also with 10 antennal segments. This variation may have led him to
transfer this species from Eusimulium to Greniera (Rubtsov 1959-64, pp. 281
and 591). The only obvious similarity between H. rendalense and H. dogieli
reported by Rubtsov (1956; 1962) is in the branching pattern of the pupal
filaments. The differences between H. near dogieli and the more similar
entity reported by Usova (1961) are summarized in Table 8.

This evidence indicates that H. dogieli (Usova) is a different
entity and thus a junior homonym of H. dogieli (Rubtsov). This would
give H. near dogieli new species status on morphological evidence alone.
However, further study would be desirable by comparing specimens from
the present study with the original specimens from which H. dogieli was
described, and by collecting additional material for cytological and
morphological analysis over a wide area of Scandinavia and U.S.S.R.

H. dogieli was intially described from material collected
in Murmansk, U.S.S.R. It has been reported also from polar Urals and
middle Ob River basin (Patrusheva 1962, 1976)*, from northern Finland
(Kuusela 1971) based on only one exuvia and from Norway (Raastad and
Davies 1977) based on one exuvia from Rendalen and two exuviae from
Tynset. Chubareva and Petrova (1979) reported only the karyotype of
H. dogieli (placed in Greniera) from U.S.S.R., without giving details
on the chromosome banding pattern nor on its distribution. However,
the uncertain identity of this species and the similarity of most stages
within this species complex sheds doubt on the correct identifications
of these records. Raastad (1979) placement of H. rendalense in probable
synonymy with H. dogieli is mere speculation since he did not analyse
any specimens of either species. According to the present study, H.
near dogieli is morphologically the species closer to H. dogieli (as
defined by Usova, 1959) not H. rendalense.

H. latipes and H. yerburyi.

Edwards (1920) described H. yerburyi from a single female
and associated exuvia with 8 filaments, branching (2+2) + (2+2). This
female had three lines of brownish hairs on the scutum, contrasting
with the yellowish hairs on the general scutum surface. Although he
distinguished this speices from H. latipes (his S. subexcisum) by the
above characters, Edwards (1920, 1939) continued to doubt the distinctive-
ness of H. yerburyi. In addition, Grenier (1953) questioned the validity
of H. yerburyi based on pupae, with 7, 8 and 9 filaments from a temporary
stream in France. He considered these to be variants of pupae of
H. latipes (his subexcisum). L. Davies (1966) re-examined the type

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* not seen in the original

material of H. yerburyi at the British Museum (N. H.), and his observations
(pp. 453-454) agree with mine of August 1980 on the same material; the
holotype female and associated pupal skin have features as described
by Edwards (1920) and suggest that H. yerburyi deserves species status.

However, according to L. Davies (1966) and R.W. Crosskey
(pers. comm.), the status of H. yerburyi in Britain remains doubtful,
mainly because it lacks a male with recognizable differences from that
of H. latipes and also because they have been unable to find any
specimens in Britain with the scutal hair pattern of the yerburyi
holotype. In 1962-63 L. Davies and R.W. Dunbar collected 132 Hellichiella
pupae from the type locality stream of H. yerburyi at Knebworth Woods,
Herts.; 95 adults reared from these pupae were all typical H. latipes
(L. Davies 1966). Subsequently, R.W. Crosskey made a series of
collections between March and April 1977 from south-east England, in
and around the type locality of H. yerburyi (pers. comm.). The
Hellichiella pupae and exuviae of this collection included 42 specimens
with 6 filaments/side with the typical branching pattern 2 + (2+2) of
H. latipes, and 102 with variable branching patterns in several combinations
of the 6 and 8 and 10 filamented forms. I have re-analysed this material
and found, as did Crosskey (in litt. 1980), that the variable branching
of pupal gills include the following patterns: 2 + (2+3), 2 + (3+3),
(2+2) + (2+3), (2+1) + (3+3), (2+2) + (3+3) and (2+2) + (2+2); often different
branching on either side of the pupa. I have analysed also 10 to 15
pinned reared adults associated with these collections; the scutum is
uniformly covered with silvery to yellowish pubescence. I tend to agree
with Crosskey's conclusion that they are essentially H. latipes. Based

on the variable number of filaments from this collection it would be
reasonable to conclude that H. yerburyi represents a variation of
H. latipes with supranumerary filaments. All the extra branches in
these specimens originated from the distal half or very close to the
tip of the main filament, and thus would be considered adventitious or
supranumerary filaments of the basic type 2 + (2+2). The Carnoy-
preserved larva, from the Dorset sample, determined to be close to
H. yerburyi, and whose chromosome banding pattern was found indistinguishable
from that of H. latipes (see Chapter 1), also had this basic type of
branching. The mature histoblasts in this larva had two short filaments
very near the tip of the main upper two filaments, and thus could be
considered a variant of H. latipes.

The above evidence, based essentially on number and branching
pattern of pupal filaments, tends to disprove the status of H. yerburyi
as a valid species. However, there are no reports of detailed studies
of hypopygia of adults of this species from the type locality. Rubtsov
(1956; 1959-64, p. 280-1, Fig. 153) gives a description of the male of
H. yerburyi and associated 8-filamented pupa from the Kola Peninsula,
U.S.S.R. Also, Patrusheva (1971) reports this species from South Yamal,
U.S.S.R.; she describes the male and female reared from three pupae
collected together with 19 exuviae from a second order stream, 28-VII-1968.
Although the female hypopygium is typical of Hellichiella, she does not
mention the distinguishing features of the scutal hair colour nor does
she compare the species with H. latipes. The branching pattern of these
pupae from U.S.S.R. is identical with that of the yerburyi holotype;
the upper and lower four filaments bifurcate in pairs from a secondary

trunk which is 2-3 times the length of the basal primary trunk. Thus each pair of filaments bifurcates from a well-defined secondary trunk; in pupae with adventitious filaments this trunk is not distinguished from the primary filament. The significant character of this male is its rectangular-shaped ventral plate which is three times longer than wide. This type of ventral plate is apparently different from the narrower and tapering ventral plate of H. latipes shown by Rubtsov (1959-64, Fig. 152). However, L. Davies (1966) shows the ventral plate of H. latipes (his subexcisum) to be broadly subrectangular, more like that of H. yerburyi shown by Rubtsov. These differences should be interpreted by understanding that the apparent shape of the ventral plate may change depending on its orientation, as shown in the present study. Davies (1966) also states that the second segment of the larval antenna of H. latipes has 4 annuli, while Rubtsov (1959-64) shows 6 annuli which corresponds with Edward's (1920) report, and my own observations of 5-6 annuli in mature larvae of this species from southern England. Additional larvae with histoblast filaments like those of H. yerburyi from Britain should be analysed cytologically, or electrophoretically, to determine definitely the relationship of this species with H. latipes.

H. latipes and H. saccai

In his description of saccai, Rivosecchi (1967) recognized the close relationship of this species with H. latipes (his subexcisum) and delineated the morphological differences distinguishing them. His diagnosis of these two species generally agree with my comparison of the morphological characters of larvae, before and after chromosome

analysis, pupae and adults of these two species. The differences

separating them are summarized in Table 10. According to L. Davies

(1966) the second segment of the larval antenna of H. latipes has

four annuli, but in mature larvae of this species I have counted 5

to 6 (18 larvae analysed) which agrees with the nine-segmented antenna

reported by Edwards (1920). H. saccai also has 6, occasionally 7,

annuli on the larval antenna (38 larvae analysed) which, however,

differs from that of H. latipes by the slightly longer segment I

relative to segment III. The number of rays of the primary cephalic

fan in the two species have a different modal distribution, with a mean

of 52 rays (47-56; 5 mature larvae) in H. latipes and 60 rays (58-65; 5

mature larvae) in H. saccai.

A previously unreported character in H. latipes consists

of its primary rays having uniformly short setae along their length, as

observed in larvae from Knebworth, Herts.; in contrast, those of H. saccai

have groups of 10-12 short setae alternating with a longer seta, as

shown by Rivosecchi (1967). This character in H. saccai has been

redrawn incorrectly in Rivosecchi, 1978 (Fig. D11, #11), i.e. the short

setae between the widely-spaced long ones, have been left out. However,

the larvae of both species have simple three-lobed anal "gills" and both

probably overwinter as larvae. Mature larvae of both species occur

in March, and Crosskey (pers. comm.) has found H. latipes larvae even

in December. These contrast with H. rendalense and H. near dogieli larvae,

both of which have compound anal "gills" and overwinter as eggs.

Also previously unreported in the pupa of H. latipes is a

longitudinal medial line of more thickly woven silk extending from the

base to the tip of the anterior projection of the cocoon. This mid line

stands in contrast with the loosely woven surface of the projection, and is visible in most clean pupae from southern England. The anterior projection is also 1/3 to 1/4 shorter than the dorsal filaments. In H. saccai the anterior projection is loosely woven (analysed 6 exuviae, from Lazio, Italy, collected III-1967 by L. Rivosecchi), being thicker only along the edges, as in latipes, its tip is usually forked and its length is equal to that of the dorsal filaments. The cocoons of these two species also have a discrete difference in surface texture which is more clearly discernable when they are placed beside each other. In H. latipes the silk threads of the cocoon extend generally longitudinally and are plainly interwoven with oblique threads; in H. saccai the general surface texture of the cocoon has a more definite and compact chain-link or honey comb-like pattern, with fewer oblique threads.

In males, the ventral plate of H. latipes is generally broader (analysed 4 reared males from Dorset, England, collected by J.A. Bass III-1982); in H. saccai it has a more tapering and recurved margin (analysed 1 reared male from Lazio, Italy, collected by L. Rivosecchi III-1967). The median sclerite also has a different shape in the two species, as shown by L. Davies (1966) and Rivosecchi (1967, 1978). In females, the scutum of H. latipes has uniformly silvery to yellowish pubescence; in H. saccai the scutum has three longitudinal stripes of silvery hairs over a darker background. The adults of H. latipes have uniformly dark-brown legs; those of H. saccai are variegated dark-brown and yellow colour.

Rivosecchi (1967) was aware of the similarity of the scutal pattern of H. saccai with that of H. yerburyi, but he distinguished them by referring to L. Davies (1966) who reported three brown stripes

on a light background on the scutum of <u>H. yerburyi</u>, while in <u>H. saccai</u>

this colour pattern is reversed. Rivosecchi (1967) also referred to

the broad ventral plate of <u>H. yerburyi</u> shown by Rubtsov (1959-64),

being 1/3 as long as it is wide, compared to the ratio 2/3 for that of

<u>H. saccai</u>. Furthermore, the branching pattern (2+2) + (3+3) of the 10

pupal filaments of <u>H. saccai</u> is considered by Rivosecchi (1967) to be

a distinguishing character for this species. He considered, in reference

to Grenier (1953), that the variability in the number of filaments

in <u>H. latipes</u> from 6 to 9 does not apply to <u>H. saccai</u> whose original

43 pupae had all the same number and branching pattern of filaments.

It is notable that among the 102 <u>H. latipes</u> pupae with

supranumerary filaments collected from southern England by Crosskey

(see section above), 5 had the branching pattern of <u>H. saccai</u>. The

surface of these cocoons was not analysed closely because of the fine

clay particles covering them, but some surface areas on the 10-filamented

forms showed a texture similar to that of <u>H. saccai</u>-as described above.

This indicates that the population from England generally recognized

as <u>H. latipes</u> may include <u>H. saccai</u> in small proportion, less than 5%

according to Crosskey's collection. Indeed, the fringe of distribution

of <u>H. saccai</u>, thus far known only from its type locality (Lazio province,

Italy), may extend to north-central Europe where it might occur

sympatrically with <u>H. latipes</u>. In the region of overlap, these two

species may partially hybridize and produce intermediate forms recognizable

from pupae with number of filaments varying between 6 and 10. Thus,

<u>H. yerburyi</u> may be an unstable hybrid occurring in low frequency where

the two parent species hybridize. Other closely related species of

simuliids are known to hybridize and produce viable and fertile F_1 progeny

in regions where their ranges overlap (Rothfels and Nambiar 1982).
More extensive collecting in bog habitats in Europe should clarify
this problem by determining the distribution of these species and the
frequency of probable intermediate forms in overlapping regions.

H. congareenarum and H. anatinum

These two species were initially treated as one entity under
the name congareenarum, although it was considered a complex (Davies
et al. 1962). One member of this complex was described under the name
anatinum (Wood 1963). The differences between these two entities were
appreciated by both Wood (1963a; b) and Dunbar (1962, 1967) who worked
in collaboration, one on morphological features and the other on the
distinction in chromosome banding pattern between them. This is one of
the first cases in taxonomoy of simuliids in which the two disciplines
of cytology and morphology were employed simultaneously and successfully
to distinguish two sibling species. The morphological differences
distinguishing these two species are now compared and summarized in
Table 11.

The larvae are distinguished by the number of annuli on the
second segment of the antenna, being four in H. congareenarum and five
to seven (usually six) in H. anatinum (Wood et al. 1963; present study).
The length of first and second antennal segments, combined, compared to
the stalk of the cephalic fan, is equal or slightly longer in H. anatinum
and shorter in H. congareenarum. The fainter head spot pattern in
H. congareenarum from Ontario reported by Wood et al. (1963) is not like
the darker pattern of larvae from Delaware (based on 12 last instar
larvae, collected by R.W. Lake, 1982) and Georgia (10 mature larvae,

collected by P.E. Catts, 1979) which have a similar dark pattern as in

H. anatinum. Another distinguishing larval character that has not

been reported before is the shape of the anal "gills". In H. congareenarum

from New York (Jamnback and Stone 1957), Delaware, Georgia (present

study) and presumably all southeastern states, the "gills" are simple

three finger-like lobes; in H. anatinum from Churchill, Manitoba (3 larvae,

collected by R.W. Dunbar 1959), Quebec (8 larvae from James Bay, collected

by D.M. Wood 1977) and southern Ontario (11 larvae, author's collection

1980), the "gills" are compound, i.e. the three major lobes are each

subdivided into 10-12 smaller lobes. This character holds true also for

young and last instars. Another unreported character, which, however,

does not distinguish these two species, is the number of primary cephalic

fan rays. Mature larvae of H. congareenarum from Delaware have 52-62

rays (average 56, n=8); mature larvae of H. anatinum from southern Ontario

and Quebec have 48-59 rays (average 55, n=11). The setae on the primary

rays in both species consist of series of 10-12 short setae alternating

with one longer seta.

The pupae of these two species were not distinguished until

the difference in their branching pattern was detected in the present

study. In H. congareenarum (N.Y., Jamnback and Stone 1957, and South

Carolina) the twelve filaments are straight and parallel pointing in

one direction in front of the pupa (analysed 9 reared adults from South

Carolina, collected III-1960 by D.M. Wood). Each of the upper and

lower major petioles is about 2-3 times the length of the basal common

trunk from which they bifurcate at about $50°-60°$ angle. Each of these

two petioles bifurcates again at about $30°-40°$ angle, producing four

secondary petioles each of which give rise to three filaments, resulting

in the branching pattern (3+3) + (3+3). In <u>H. anatinum</u> the twelve
filaments flare out, pointing generally in all directions within a 180°
angle in front of the pupa, with some filaments recurving back over the
pupa (analysed 3 reared specimens from Algonquin Park, Ontario and 25
exuviae and larvae from Sakami, James Bay, Quebec, D.M. Wood collection
3-VI-1977). In this species the primary basal two petioles are missing,
and the four secondary petioles (primary for this species) diverge
directly from the common basal stalk into two upper and two lower branches.
These four petioles, bifurcate at nearly similar 60°-70° angles, each
giving rise to three filaments, resulting in the branching pattern (3+3) +
(3+3).

The adults are distinguished by leg pigmentation. In
<u>H. congareenarum</u> from the Bruce Peninsula, Ontario, as in those from South
Carolina, the legs are variegated in colour, i.e. the coxae of fore legs
are light yellow, the others slightly darker; the other leg segments are
light yellow except at the joints of distal end of femora, distal and
proximal ends of tibiae and tarsi which are dark-brown. In <u>H. anatinum</u>
the legs are uniformly dark-brown. Females have distinctive frons; in
<u>H. congareenarum</u> it is wider and the sides are almost parallel, the
narrowest point at the base is twice the width of the antennal pedicel;
in <u>H. anatinum</u> it is narrow and the sides taper downward, the narrowest
point at the base is as wide as the antennal pedicel. Considering reared
females of both species, the clypeus of <u>H. congareenarum</u> has a much
denser white pollinosity and silvery hairs; in <u>H. anatinum</u> the white
pollinosity is nearly absent and the sparser silvery hairs have a coppery
tinge over a darker grey clypeus surface. The tarsal claw in females
of <u>H. congareenarum</u> is smaller, being about 1/3-1/2 the length of last

tarsal segment, and has a relatively small subbasal tooth which is 1/2 or slightly shorter than the claw. In _anatinum_ the tarsal claw is larger, being 1/2 or slightly longer than the last tarsal segment, and has a large subbasal tooth which is 1/2 or slightly longer than the claw. The hair tuft on base of the radius in females of _H. congareenarum_ is usually silvery, about 80% frequency (n=10), in some specimens being coppery with some silvery hairs; in _H. anatinum_ it is usually coppery, about 80% frequency (n=10), in some specimens being silvery. In both species the VII and VIII sternites of females are sclerotized, and the cerci are long and tapering.

In the male of _H. congareenarum_ the lip of the ventral plate is significantly recurved, projecting at 90° angle with the vertical axis of the plate in side view; this gives the plate a broad, rectangular shape when viewed horizontally, its width: length being 3:1 (as shown by Jamnback and Stone 1957 and Stone 1964). In _H. anatinum_ the lip of the ventral plate is almost straight, forming a nearly 30° angle with the vertical axis, hence the plate acquires a triangular shape when viewed horizontally (as shown by Wood 1963).

It should be noted that _H. congareenarum_ from the eastern U.S.A. (see Zoogeography section) includes the population from the type of locality of South Carolina. This species was originally described only from females derived from Congaree, S.C. (Dyar and Shannon 1927), and the other stages were not described until thirty years later (Jamnback and Stone 1957). On chromosomal evidence, Dunbar (1962, 1967) distinguished the standard _H. congareenarum_ from South Carolina from the _H. congareenarum_ 'b' from the Bruce Peninsula, Ontario. However, new evidence (see Part 1) indicates that 'b' is a variant occuring at

the extremes of the same population. Nonetheless, the description
of H. congareenarum from Ontario was derived from the Bruce Peninsula
collection (Davies et al. 1962, Wood et al. 1963); hence, it applies
to the Ontario population distinguished by Dunbar (1967). One obvious
morphological difference between the southeastern and Ontario populations
is that the pupae from the Bruce (analysed 42 exuviae with reared adults,
coll. 18-VI-1959) have the branching pattern identical with that of
H. anatinum; therefore, they are distinguished from those of the south-
eastern population but not from those of H. anatinum. The ventral plate
of the male of H. congareenarum from Ontario has a significantly shorter
recurved lip, in side view, projecting from the vertical axis by about
two times the thickness of the arms. Hence, horizontally the plate
has a trapezoidal shape, tapering distally, its width:length being 3:2.
The parameral teeth consist of 3 long and 4 short spines. In H. congareenarum
from New York and Connecticut (Jamnback and Stone 1957; Stone 1964) the
lip of the ventral plate has a longer curvature, in side view projecting
from the vertical axis by about four times the thickness of the arms.
Hence, horizontally the plate has a rectangular shape, its width:length
being 3:1. The parameral teeth consist of 3 long and 8 short spines.
        Also it is notable that H. congareenarum from the southeastern
states overwinters as larvae (Jamnback and Stone 1957) which have simple
rectal "gills" (a correlation found also with H. latipes and H. saccai).
The females of this species from Alabama and other southern states are
known to feed on turkeys (Stone and Snoddy 1969). In New York, Long
Island, its larvae were found in a sluggish stream draining a pond with
ducks (Jamnback and Stone 1957), and these birds were most likely hosts
of the adult flies. In Ontario the adults of this species may also feed

on ducks, as do females of its closest relative H. anatinum (Bennett 1960; Fallis and Bennett 1960). Thus the southern and northern form of H. congareenarum may be adapted to seek and bite different hosts. If H. congareenarum from Ontario is found to overwinter in the egg stage and to have larvae with compound anal gills, as in H. anatinum, this would provide additional evidence indicating that the IIIL-6,7 form of Dunbar is taxonomically different from the southeastern H. congareenarum.

H. congareenarum, H. innocens and H. saccai

H. congareenarum and H. innocens are almost indistinguishable in the larval stage, except for the difference in number of respiratory filaments detectable only in mature histoblasts. Mature larvae of H. innocens have four annuli on the second antennae segment, occasionally only three annuli are discernible. In both species the length of the first and second larval antennal segments are shorter than the head fan stalk. The number of rays in the primary head fan of H. innocens is about 56 (43-60), as counted in 13 mature larvae from Huntsville and Dundas, Ontario and Michigan (the latter collection by I.B. Tarshis, V-1969), and 44 (42-46), as counted in 5 mature paratype larvae from Bell's Corners, Ontario (Shewell's 1950 collection, BRI). These numbers are not significantly different from those of H. congareenarum (see above).

Most of the 43 examined larvae of H. innocens had the normal square, shallow, postgenal cleft with a straight anterior margin; only 8 larvae had a small notch on the anterior margin, as shown in Wood et al. (1963). Hence this character may not always distinguish this species from H. congareenarum. Also both these species have simple three-lobed rectal "gills", a character previously unreported for H. innocens.

The pupa of H. innocens has 10 respiratory filaments, branching (2+2) + (3+3) as described by Shewell (1952), and is thus distinguished from the 12-filamented pupa of H. congareenarum.

The adults of H. innocens are uniformly black or dark-brown, and the frons in females is parallel and narrower than the basal width of the antenna. The adults of H. congareenarum have differentially variegated dark-brown and yellowish legs, and the frons in females is wider and expanding toward the vertex.

The larvae of H. innocens and H. saccai differ by the number of annuli on the second antennal segment and number of rays of the primary head fan (see above). The larvae of both species have simple three-lobed rectal "gills" which are wider apically in H. saccai. The pupae have the same number of 10 respiratory filaments, and similar branching (2+2) + (3+3) in both species; however, in H. saccai the dorsal primary petiole diverges from the two lower ones by a wide angle of 90° to 100° (analysed in 6 exuviae from Lazio, Italy), whereas in H. innocens this angle is smaller, being about 50° to 60° (analysed in 35 exuviae with reared adults from Kaladar, Ontario, collected 22-V-1961 by D.M. Davies and D.M. Wood).

The adults of H. saccai have differentially variegated dark-brown and yellowish legs, and are thus distinguished from those of H. innocens which have uniformly dark-brown legs. In females of both species the genital-fork is indistinguishable, but the cerci of H. saccai are shorter and sloping ventrally, compared to the longer and tapering cerci of H. innocens.

H. minus Dyar & Shannon

This species is known to occur in western North America (see Zoogeography section) and has apparently a variable number of pupal filaments. In 1981 I analysed three female paratypes of this species at the Biosystematic Research Institute, Ottawa, where they were on loan from the USNM. The external characters of these three females are similar to those of adults reared from Hellichiella pupae collected by G.C. & D.M. Wood in May 1964 from Kaslo, British Columbia. This collection of more than 40 reared specimens from B.C. contains two forms of pupae; a 6-filamented pupa with branching pattern 2 + (2+2) (similar to H. latipes) and and 8-filamented pupa with branching pattern not quite like that of H. yerburyi. The branching pattern of the 8-filamented form consists of three equally short primary petioles which branch at about 30° from each other in a vertical plane a short distance from the common trunk. The upper and lower petioles each bifurcates in a horizontal plane into two equally long filaments; the middle petiole bifurcates in a horizontal plane into two equally long secondary petioles, each of which bifurcates horizontally into two equally long filaments. The resulting branching pattern is 2 + (2+2) + 2; based on 5 reared male with exuviae from Butterfly Lake outlet, Utah VII-1963, 9 reared males from Rabbit East Pass, Colorado, 30-VI-63, and one reared male from Kamloops, B.C., 13-16-V-1963, all collected by G.C. & D.M. Wood and deposited at the BRI, Ottawa. The adults reared from these two forms of pupae have similar external characters and are distinct from H. excisum whose pupa is also 6-filamented, but the female has a significantly wider frons than that of H. minus. However, these adults appear to be closer to H. innocens Shewell and H. anatinum Wood, both of which have been reported from

British Columbia (see Distribution section). Furthermore, it is not known which of these two forms of pupae belongs to the true H. minus, since the species was initially described only from females, and there are no pupae, exuviae or males associated with the original collection from Yosemite, California, the type locality of the species (Dyar and Shannon 1927).

This species has been reported from British Columbia by Hearle (1932) who reared series of males of both sexes from pupae collected in a shallow, sluggish stream flowing from a beaver dam, at Lone Butt, Cariboo district. The pupae had 8 filaments, but with branching pattern apparently unlike that of Wood's collection. However, identification of Hearle's material as H. minus remains in doubt until specimens of his collections are reanalysed. Also, Stone (1952) reports H. minus from College, Alaska, based on males and females collected in considerable number from an emergence trap; no adults were reared from pupae, nor did he find pupae corresponding to Hearle's (1932) description. Stone's collection should also be reanalysed.

This problem of H. minus is apparently similar to that of H. latipes in relation to H. yerburyi and H. saccai (see above). Comparative studies of chromosomes banding pattern of western North America Hellichiella species associated with morphological studies may help to resolve the identity of H. minus.

Conclusion

Evidence presented in this section shows that species of Hellichiella from both Europe and North American are very similar morphologically. Reliable identifaction is best made by considering all

stages of a given species and their collection locality. _H. rivuli_ and
H. excisum are two sister species which have not been treated in this
study in detail. The larvae are almost indistinguishable from each
other, except as mature last instars whose histoblast show four filaments/
side in _rivuli_ and six in _excisum_. Larvae of both species lack annuli
on the second antennal segment, thus they are distinguished from those
of the other species. Furthermore, other species from Eurasia, such
as _E. acutum_ Patrusheva, 1971 and _E. barabensis_ Rubtsov, 1973 and the
autogenous species _E. crassum_ Rubtsov and _E. baffinense_ Twinn are
tentatively placed in _Hellichiella_, but their affinity to species of
this taxon and those of _Parahellichiella_ gen. n. remains to be determined.
A summary of species differences and similarities based on pupal
respiratory filaments is given in Table 12.

Table 8. Morphological differences between H. rendalense and
H. near dogieli.

	rendalense	near dogieli
Larva		
antenna		
number of annuli	5	4
1st + 2nd segments	equal to stalk of head fan	shorter than stalk of head fan
number of rays on cephalic fan	66 (60–75)	74 (60–85)
subesophageal ganglion	subrectangular	subtriangular
infrahistoblast gap	wide	narrow
Pupa		
filaments	pointing forward, parallel	flaring out
Adults		
legs	uniformly dark-brown	differentially pigmented light yellow and dark-brown
scutellum	dark-brown	light to dark yellow
♂ basistyle	dark-brown	light yellow medially, dark-brown edges
ventral plate	lip recurved	lip straight
♀ sternite VII	sclerotized	not sclerotized
VIII	sclerotized	sclerotized
genital fork stem	uniformly thin	expanded distal tip
cerci	long, tapering	truncated, sloping ventrally

Table 9. Morphological differences between H. dogieli (Ussova 1961, pp. 77-80) and H. near dogieli (present study).

	dogieli	near dogieli
Larva		
number of rays cephalic fan	63 (61-71)	74 (60-85)
postgenal cleft	rectangular longer than wide	almost square wider than long
Pupa		
filaments	flared (Usova 1961), straight (Rubtsov 1959-64)	flared
anteromedial projection	1/3-1/4 densly woven	2/3 densly woven
Adults		
scutum	golden pubescence	silvery pubescence
scutellum	dark-brown golden hairs	pale to dark yellow silvery hairs
hind metatarsus	arcuate	parallel
♀ genital fork stem	uniformly thin	expanded distal tip
sternite VII	?.	not sclerotized
VIII	?	sclerotized
♂ parameral teeth	3 long + 3 short	4 long + 4 short
basistyle	? uniform colour	pale yellow medially, dark-brown edges

Table 10. Morphological differences between H. latipes and H. saccai

	latipes	saccai
Larva		
antenna		
segment I length	equal to III	longer than III
hypostomial setae	bifid tip	simple tip
rays of cephalic fan	52 (47–56) with uniformly short setae	60 (58–65) with series of short & alternating long setae
cephalic apotome anterolateral spots	2	3
posterolateral spots	2	1
posterior margin	clear	infuscated
mandibular serrations teeth	4–6	8–9
Pupa		
filaments	6	10
branching	2 + (2+2)	(2+2) + (3+3)
cocoon woven pattern	longitudinal & diagonal, loose	chain-links, compact
anterior projection	ca. 1/4 shorter than upper filaments; with a long mid line of thicker woven silk	not longer than upper filaments; simple, often with bifid tip
Adults		
legs	uniformly dark-brown	segments paler medially than at extremities
♀ scutum	uniformly covered with silvery to yellowish hairs	3 stripes of silvery hairs over a darker background
♂ ventral plate	rectangular to triangular and straight lip	triangular with tapering and recurved lip
median sclerite		

Table 11. Morphological differences between H. congareenarum D. & S.
          and H. anatinum.

	congareenarum	anatinum
Larva		
antenna		
number of annuli	4	5-6
1st + 2nd segments	shorter than stalk of head fan	longer than stalk of head fan
rectal "gills"	simple three lobed	compound multilobed
Pupa		
filaments	parallel, pointing forward	flaring out
Adults		
legs	differentially variegated yellow and dark-brown	uniformly dark-brown
♀ frons	wide and parallel	narrow at base
tarsal claws	1/3 - 1/2 the length of tarsal segment	1/2 or longer than tarsal segment
hair tuft at base of wing	usually silvery	usually coppery
♂ ventral plate	broad; lip recurved at about 90°	narrower; lip almost straight

Table 12. Comparison of number and branching pattern of pupal respiratory filaments of _Hellichiella_ species.

Number of filaments/side	Branching pattern		Species	Distribution
	dorsal	ventral		
4	2	2	rivuli	Eastern North America
6	2	2+2	latipes	Western Europe (Britain, France)
			minus excisum	North America
8	2+2	2+2	yerburyi	Western Europe (Britain, France)
			minus	Western North America
10	2+2	3+3	innocens	North America
			rendalense near dogieli	Scandinavia (Norway)
			saccai	Southern Europe (Italy)
12	3+3	3+3	anatinum congareenarum *Opinaga	North America
			dogieli near dogieli fallisi rendalense	Northern Europe

* The pupa of this cytospecies is unknown,
but it is presumed to be similar to this group of species with 12 filaments.

Chapter 3

ECOLOGY

Ecology and Geographical Distribution of <u>Hellichiella</u> Species

GENERALITIES

Aquatic stages of simuliids develop in almost all types of freshwater streams ranging from first-order brooks to large multiple order rivers. Within this broad range of lotic habitats simuliid species exhibit various degrees of preference associated with stream size, current speed, volume output, temperature, type of substrate and possibly water quality (Twinn 1936; Grenier 1953; Usova 1961; Carlsson 1962; Rubtsov 1959-64; Davies et al. 1962; Rivosecchi 1978; Glatthaar 1980; Grunewald 1981). Most species of Eusimuliini are known to breed in first and second order streams, while species of Hellichiella have been found invariably in first order, eurythermal streams which tend to desiccate during late spring and summer. However, larvae and pupae of Hellichiella have always been difficult to find in significant numbers compared to the relatively larger population of adult females captured during the host-seeking phase of their life cycle. Specifically, adult females of H. anatinum and H. rendalense have been much easier to capture while biting ducks along certain lakeshores and rivers than to find them in streams as larvae and pupae (Bennett 1960; Fallis and Smith 1964; Fallis and Bennett 1966, Golini 1975). Consequently, some species, such as H. congareenarum, H. minus, H. rendalense (s.l.), became known initially as adult females while their larvae, pupae and males remained undescribed until their breeding habitats were found (Jamnback and Stone 1957; Golini, present study).

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Initially, when <u>H. rendalense</u> and <u>H. fallisi</u> were first described, Golini (1975) proposed a hypothesis predicting the time of adult emergence and the type of habitat where the larvae and pupae were likely to develop. Based on the transmission of <u>Leucocytozoon simondi</u> by females of these flies (Eide and Fallis 1972), the hypothesis predicted that the adults emerged, and females searched for the first blood meal during the second half of June in Rendalen; accordingly, the developmental period of larvae and pupae would occur in the first half of June, assuming the species to be anautogenous for the first ovarian cycle. Furthermore, the aquatic stages were expected to develop in semipermanent streams less than 50 cm wide, with slow water current and much emergent vegetation. These predictions were tested when I returned to Rendalen in June of 1979 and 1980. I made additional observations of the breeding habitats of species from Ontario and examined available collection records from Europe and North America, all of which led to some general conclusions about the ecology and distribution of <u>Hellichiella</u> species.

METHODS AND OBSERVATIONS

Collecting Season of 1979

Beginning in the first week of June 1979, an extensive
search was made in Rendalen (about 61 40'N, 11 20'E) for larvae and
pupae of simuliids from small streams less than 1 m wide, with
emphasis on those with water current of 1 to 100 cm/sec and relatively
warm water temperatures of 8° to 15° C. Simuliids were collected
initially from four areas, including Renådalen (Östvollen), Osadalen,
Flenadalen, and Fuglåsen plateau, covering an area of about 80 km^2
(Figs. 1,16). The larvae of each collection were preserved usually in
Carnoy solution (95% ethanol:glacial acetic acid 3:1) or alternatively
in 95% ethanol. The pupae were kept alive for individual rearing, and
emerged adults and their exuviae preserved individually in microvials
or pinned (Golini 1981). The larvae and pupae were analysed intially
in a field cabin usually within two or three days after collection to
determine whether species of Eusimuliini and Cnephiini were present, with
particular attention being placed on larvae with annulated second
antennal segment and on pupae with 4 to 20 respiratory filaments.

Following the discovery of Greniera sp. and subsequently
Stegopterna sp. and Hellichiella sp. during the second week of June, the
search was restricted the Renådalen area (Figs. 1,17), particularly to
three small contiguous streams where these species were found. These
streams (Figs. 2,18,19,23) are referred here to as #12, #13 and #14
following a series of brooks draining the eastern side of Renådalen

and flowing into the Renåa R. (Fig. 2). Although the discovery of
Hellichiella larvae and pupae at this site was in itself significant,
the number of specimens occurring in these three streams was too small
relative to the large population of adult females captured from ducks
eleven years earlier, 2 km downstream. The problem was further
compounded by the sudden swarming in mid June of large number of
female simuliids resembling H. fallisi which occurred all over Renådalen;
for a period of nearly a month these flies were attracted to humans and
entered buildings and vehicles. This phenomenon led to the hypothesis
that these adults had emerged from these three small streams and others
like them, but that the immature stages had been missed as collections
were begun too late in the 1979 season. The problem, however, remained
that small streams like these, with relatively few immatures of Hellichiella,
could not possibly give rise to the present large population of these
fallisi-like females nor to those of rendalense of the past. Yet, these
were the most typical streams expected and found to produce Hellichiella
larvae and pupae with 12 respiratory filaments. If there was an
answer to this mystery of numerical discrepancy between immature and
adult stages, this was the place to find it. Faced with this enigma and
determined to extend the initial findings to a more significant level,
I proceeded to explore in more detail the nature of these streams.

These three brooks are situated about 50 to 75 m apart, and
their obvious common features include water temperature in mid June of
about 13°C, nearly 6°C higher than the other forest or mountain streams
sampled in this area; mean width about 50 cm and water depth about 10 cm,
except stream 13 with a mean depth of about 50 cm; mean water current
about 30 cm/sec ranging from 0 to 50 cm/sec. The bottom of both

stream 12 and 14 consisted of relatively firm sandy substrate, interspersed with few small stones and some decaying and emergent vegetation; the bottom of stream 13 consisted essentially of humic matter and was densely overgrown with emergent vegetation (Fig. 22,23). Bushes of Salix, Betula and Alnus are the dominant plants along the margin of these brooks. Both streams 12 and 14 originate 2 and 5 m respectively east of Renådalen road from small pools of water springing imperceptibly from thick soggy mats of Sphagnum and sedges. Stream 12 dissipates 5 to 7 m from the edge of the Renåa R. into marshy ground, while streams 13 and 14 drain directly into the Renåa about 30 to 50 m from their origin. Stream 13, being the longest, originates further up along the edge of a treeless bog that was filled completely with thick mats of Sphagnum and sedges saturated with water.

-This bog has an area of about 2 hectares and few scattered dwarf pine trees; and it slopes gently from its centre to its periphery (Fig. 21). It is surrounded by slightly higher forest ground covered mainly with lichen, Cladonia rangiferina, and mature stand of Pinus sylvestris which dominated the entire valley (Fig. 17). The vegetation in the bog is dominated by Sphagnum spp. which blankets the entire surface, and low sedges, such as Scirpus spp. and Carex spp.; Betula nana is ubiquitous but occurs more profusely on the periphery of the bog together with Alnus sp. and Salix spp. The sedge-Sphagnum surface complex of this bog contains in the upper region low palsa mounds about 20 to 50 cm high, and in the lower region numerous miniature hummocks 5 to 20 cm wide and similarly as deep, both interlaced by a network of standing to slow-moving surface water. This water merges at the lower edge of the bog into more defined rills flowing from 1 to 30 cm/sec. One of these

rills, cascading about 30 cm down the edge of the bog into a 1 m deep pool (Fig. 20), gives rise to the upper fork of stream 13; five other major rills drain further along the edge of the bog into a 15 m long drainage brook about 30 cm wide and as deep (Fig. 22) which forms the lateral branch of stream 13.

This bog is thus the source of all three streams 12,13 and 14. This delicate biotope is reminiscent of the breeding habitat of anopheline mosquitoes, and the last insects expected to breed here were simuliids. The submerged vegetation, however, revealed an awe-inspiring number of simuliid larvae and pupae loosely attached to decaying stems and leaves of mainly Scirpus and Carex floating in the miniature rills over the bog surface. Larvae and pupae became more numerous near the lower periphery of the bog and decreased significantly in the collector brook immediately below the bog's edge. The simuliids from this bog, when discovered on July 27, consisted primarily of mature larvae and pupae of Hellichiella with 12 respiratory filaments, the rest were mainly larvae and pupae of the subgenus Nevermannia (vernum-group).

To determine the relative abundance of Hellichiella from this biotope, larvae and pupae were collected two or three times per week at various sites in the bog and from the three streams originating from it. An emergence cage was also placed on the drainage stream at the edge of the bog (Fig. 25) to monitor the emergence period of the adults. The cage consisted of white dacron screening (12 mesh per cm), sewn in the form of a cube (54 cm x 54 cm square bottom and 50 cm high),with only the bottom left open; the upper side had a collapsible sleeve sewn to it in order to gain access to the cage by inserting one arm and aspirator into the cage to collect insects. This foldable cage was erected on the

stream by planting four sticks into the stream bottom and inserting
the four inside corners of the cage over them so that the sides
remained taut and the open bottom rested about 3 to 5 cm above water
surface. The emerged simuliids were collected daily with an aspirator
in mid afternoon and preserved in 75% ethanol in individual vials for
subsequent identification and enumeration. Collections were terminated
on July 11 when pupae of Hellichiella were no longer found and a new
larval population of other simuliid species was developing.

Collecting Season of 1980

A more quantitative assessment of the relative density of
simuliids from the bog and the issuing streams was made in the following
1980 season. To measure larval density rubber strips 26 cm long and 1.2 cm
wide, cut from the rubber inner tube of a bicycle tire, were floated in
each of stream 13 and 14 at about 10 m intervals from each other and
from the stream origin so that the strip farthest downstream was about
30 m from the edge of the bog. The objective was to measure the number
of larvae that colonized each strip at different sites during a certain
time period common for all strips. The strips were placed at sites in
the stream containing a noticeable number of larvae on vegetation,
where the water current was about 15 to 20 cm/sec. Six other similar
strips were placed in different rills at the edge of the bog, each
strip floating in water currents ranging from 0 to 5 cm/sec, 5 to 10 cm/sec,
and 20 to 30 cm/sec, with replicates where larvae were numerous; another
strip was placed in the drainage stream where cascading water reached a
speed of 50 to 60 cm/sec, as measured by the speed of a leaf of Betula
nana floating on the water surface. The first collection of larvae from
these strips was made in the second week of June, four days following -

their initial deployment in the water. However, the significantly
fewer larvae found on the strips than expected from the larger number
on floating vegetation led to a slight modification of these strips.
To simulate more closely the natural substrate of submerged black,
decaying, thin stems of sedges on which numerous larvae were attached,
each strip was cut longitudinally into four 3 mm wide strands which
remained joined together apically by a 1 cm piece of uncut rubber
(Fig. 26). These fringed strips were refloated at their original sites
for periods usually of 4 to 8 days. At the end of each exposure period
the strips were removed from the water, and the larvae attached to each
strip were picked off with forceps and preserved in 95% ethanol in
individual vials for subsequent identification and enumeration. Analysis
of these collections involved determining species composition and
relative density of larval simuliids at the bog and issuing streams,
in relation to distance from the bog and to water current.

An attempt was made in June 1980 to determine the rate of
larval drift from the bog into stream 13. A 30 cm diameter sieve, with
nylon screening of 14 mesh/cm stretched on a brass ring with sides 8 cm
high (see Fig. 20), was placed vertically across the drainage brook at
a site where the water current reached about 50 cm/sec. The sieve was
kept in the water for periods of 12 to 24 hrs; the larvae trapped in
the screen were preserved in 95% ethanol for subsequent analysis.

The emergence period of simuliids from Renådalen bog was
monitored again during the 1980 season. Six emergence cages, similar
to that used in 1979, were deployed; three cages were placed on seepages
at the edge of the bog, and one on each of streams 12,13 and 14 (Figs. 18,
22,23,24,25). Emerged simuliids trapped in each cage were collected

with an aspirator daily in mid afternoon and preserved in 75% ethanol
in individual vials for subsequent identification. A second small 1/2
hectare sedge-Sphagnum bog sloping directly into the Renåa R. was
located in 1980 about 1/2 km down the road from the first Renådalen
bog. This bog is fed primarily by cold water of $8^{\circ}-9^{\circ}C$ from a forest
stream (stream #9 of the Renådalen series) which dissipates at the
upper edge of the bog. Because of scarcity of larvae only one collection
was made at this site on June 15. .

Åsmyrtjörna Bog

The third site studied in 1980 was an extensive sedge-Sphagnum
bog located on Fuglåsen plateau on the western ridge of Storjøen, on the
other side of a deep valley about 20 km west of Renådalen bog (Figs. 1,27).
This bog is nearly 2.5 km long and 1/4 to 1/2 km wide (Fig. 3) and
represents the climax stage of natural eutrophication of an apparent
ancient lake which is now reduced to a small lakelet, Åsmyrtjörna, on
the upper reaches of this bog. The bog surface slopes gently in a
southeasterly direction from this lakelet toward a small stream about 1m
wide and 0.5 m deep which, farther down, doubles in width to form
Sagbekken stream.

A collection of larvae made in June 1979 from the upper reaches
of Sagbekken, near the edge of the bog, revealed, when analysed six
months later, few larvae with annulated second antennal segment. This
evidence, suggesting another breeding habitat of Hellichiella, prompted
in 1980 a more intensive exploration of the area around upper Sagbekken
which led to the discovery of the extensive Åsmyrtjörna bog. Because
of its enormous area, difficult terrain, and lack of time, only the

lower reaches of this bog were investigated for presence of simuliids.

The first collection from Åsmyrtjörna was made June 9, 1980, at two sites in the bog, one at the lower-most edge from two seepages draining part of this area (Fig. 28) and the other about 1/2 km further up from a small seepage in mid bog (Fig. 29). Subsequent collections were made from the same two sites at about weekly intervals, depending on weather conditions and the availability of a borrowed Panther motorcycle or VW pick-up truck which alleviated considerably the 20 km tortuous hike from Renådalen base station to Åsmyrtjörna.

To characterize this palustrine biotope, a collection of plants was made in July and August from both Renådalen and Åsmyrtjörna bogs; each of these plant samples was glued and pressed between the sheets of a 28 cm by 22 cm field notebook. Some plants were identified in the field using Ursing (1966). Others were subsequently identified with help from the Royal Botanical Gardens, Hamilton and Biosystematic Research Institute, Ottawa and the use of Gleason and Cronquist (1963). One liter of water samples were also taken periodically, using precleaned 1 liter plastic bottles: Renådalen bog on June 4,8, July 11 and August 8; stream 12 on June 12; streams 13 and 14 on June 8 and August 8; stream 15 on June 4; Renåa river on August 8; Åsmyrtjörna bog edge on June 9 and 23 and mid bog on June 9, 23 and July 18. For each liter sample, two additional 20 ml water samples were taken - one was fixed with 3 drops of chloroform for nitrate-nitrite and ammonia analyses, the other was fixed with 3 drops of concentrated hydrochloric acid used for phosphate, silicate and sulphate analyses. These water samples were kept refrigerated at near $0^{\circ}C$ until chemically analysed three to four months later in Canada. Analyses of some parameters were made at McMaster University

for chlorides, acidity and alkalinity by manual titration, and for

concentrations of nitrate and nitrite, ammonia, dissolved phosphates and silica

using the Auto Analyser II system, manufactured by Technicon Corporation.

The other cation parameters were determined by the Water Quality

Laboratory, Ontario Ministry of the Environment, Toronto, following

standard methods in "Handbook of Analytical Methods for Environmental

Samples". At McMaster University concentration of suspended solids was

determined for each sample by filtering a volume of water, usually 500 ml,

through a millipore filter using 0.45 µ pore BA85 paper; the filtrate

was weighed with a microbalance.

Water pH and conductivity was measured in the field with a

portable pH meter, type PHM296 No 157428 Danimark Radiometer A/S,

loaned by the Zoological Museum, Oslo. Air and water temperatures,

of Renådalen bog were taken daily with two maximum-minimum mercury

thermometers kept in the shade; the air thermometer was placed on a

tree trunk, about 2 m above ground. Rainfall was also monitored at

the base camp by measuring the depth of water accumulated, after each

rain period, in a 40 cm diameter and 12 cm deep plastic basin kept

exposed 1 m above ground and about 100 m from Renådalen bog.

To compare the breeding habitat of _Hellichiella_ from Norway

with those of other _Hellichiella_ species elsewhere, a study was also

made of several bog-like sites in Ontario expected to contain _Hellichiella_

during late April and early May 1980 and 1981. Larval and pupal

simuliids were collected and later identified; also water and plant

samples were collected and analysed following the same methods for

samples from Norway. On my way back from Norway to Canada in August 1980,

I had an opportunity to stop over in England to meet with Dr. R.W. Crosskey.

at the British Museum (National History), London, who kindly accompanied
me to a few breeding sites of H. latipes in Herts.   Although no
simuliids were found this late in the season, a few plant samples from
a site at Knebworth Wood, Herts. (Fig. 32) were taken and identified at
the BMNH to characterise the habitat for this species (Table 22).

Fig. 1 Topographic map of part of Rendalen showing the location of Rendalen and Asmyrtjorna bogs where Hellichiella spp. were found. Note, potential breeding sites of these simuliids can be predicted from the location of bog areas (cross hatched) on the map.

133
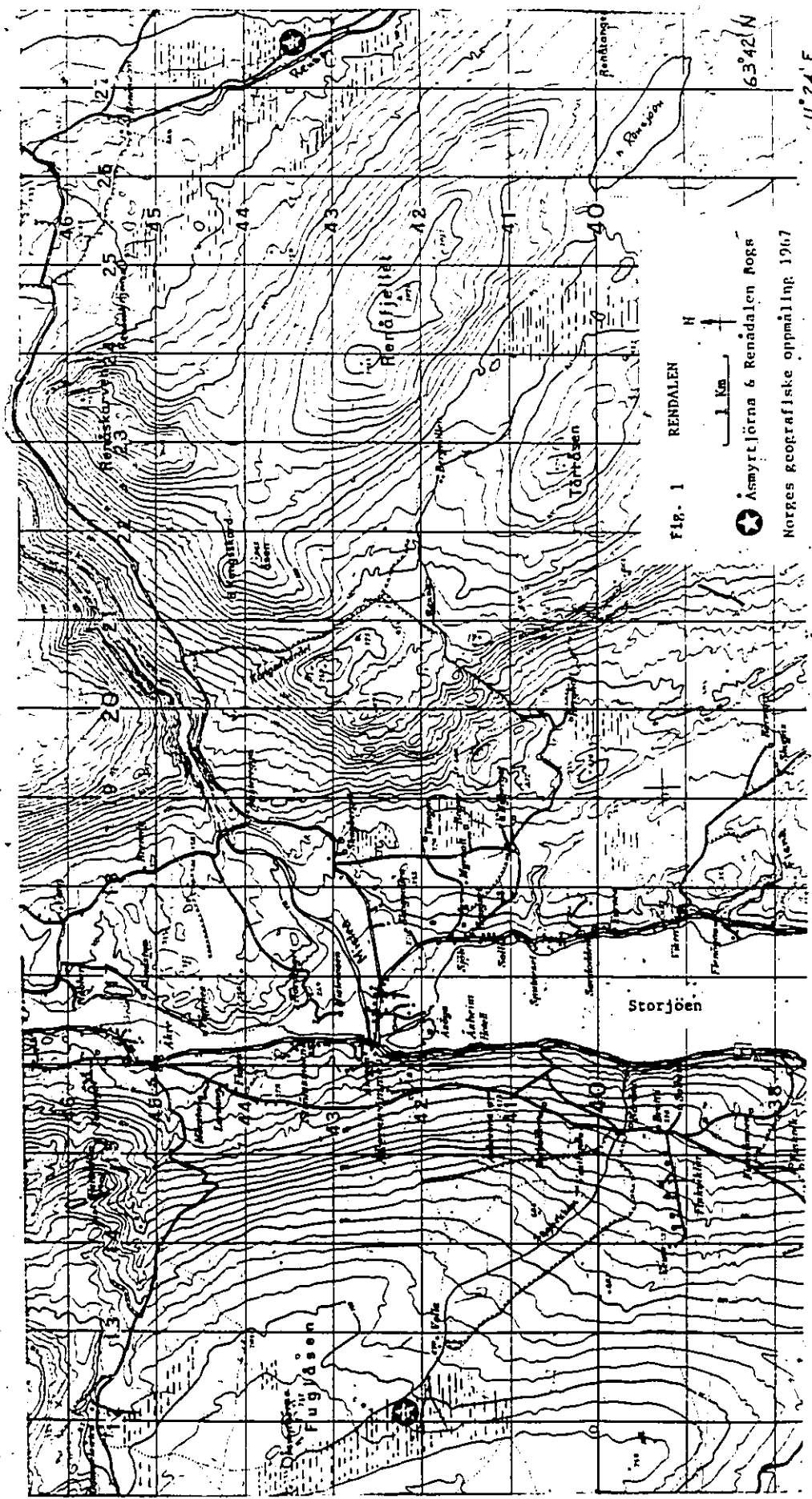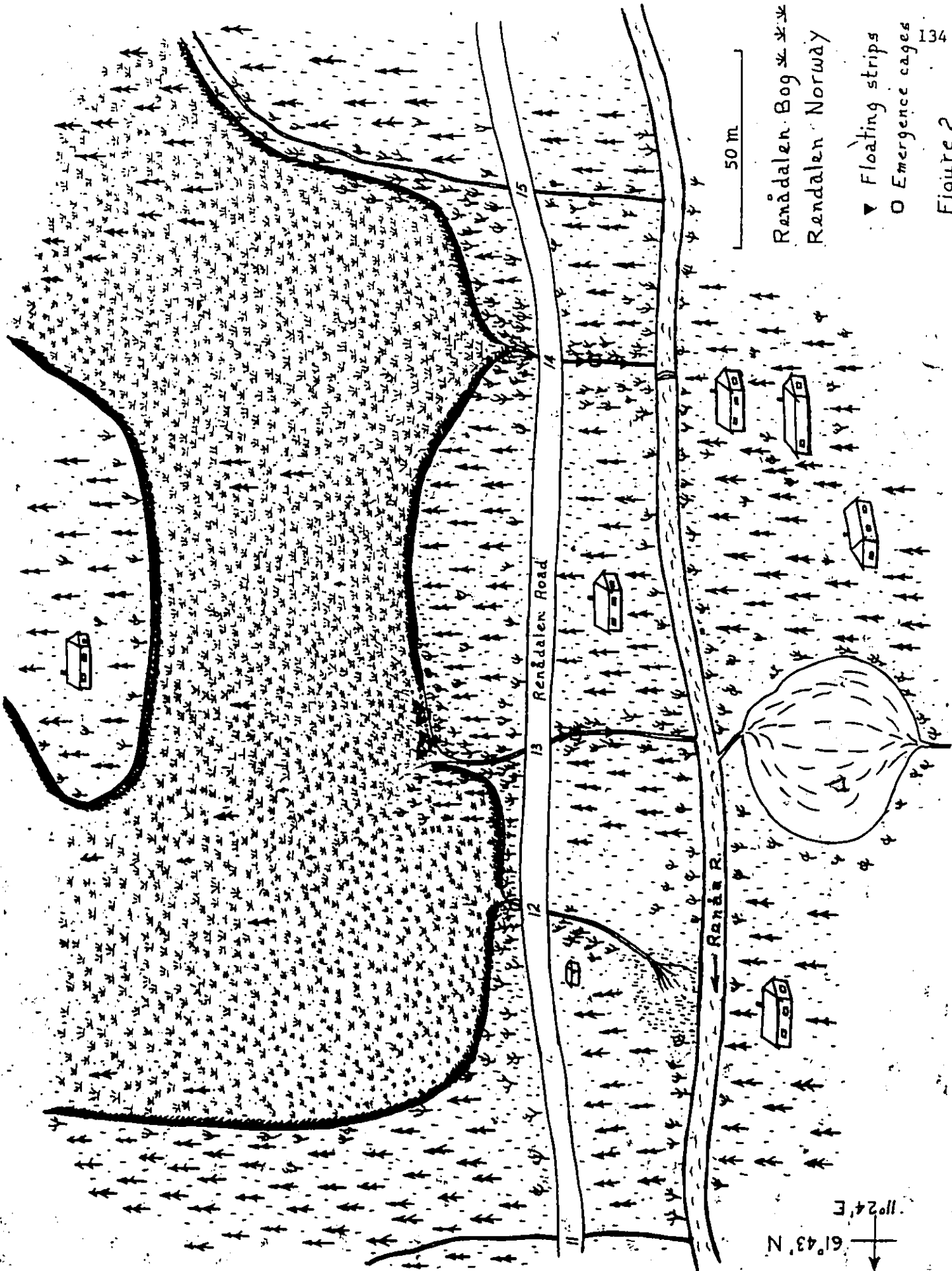
Renådalen Bog
Rendalen Norway

▼ Floating strips
○ Emergence cages

Figure 2

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Renådalen Road

Renåa R.

61°43'N
11°24'E

50 m
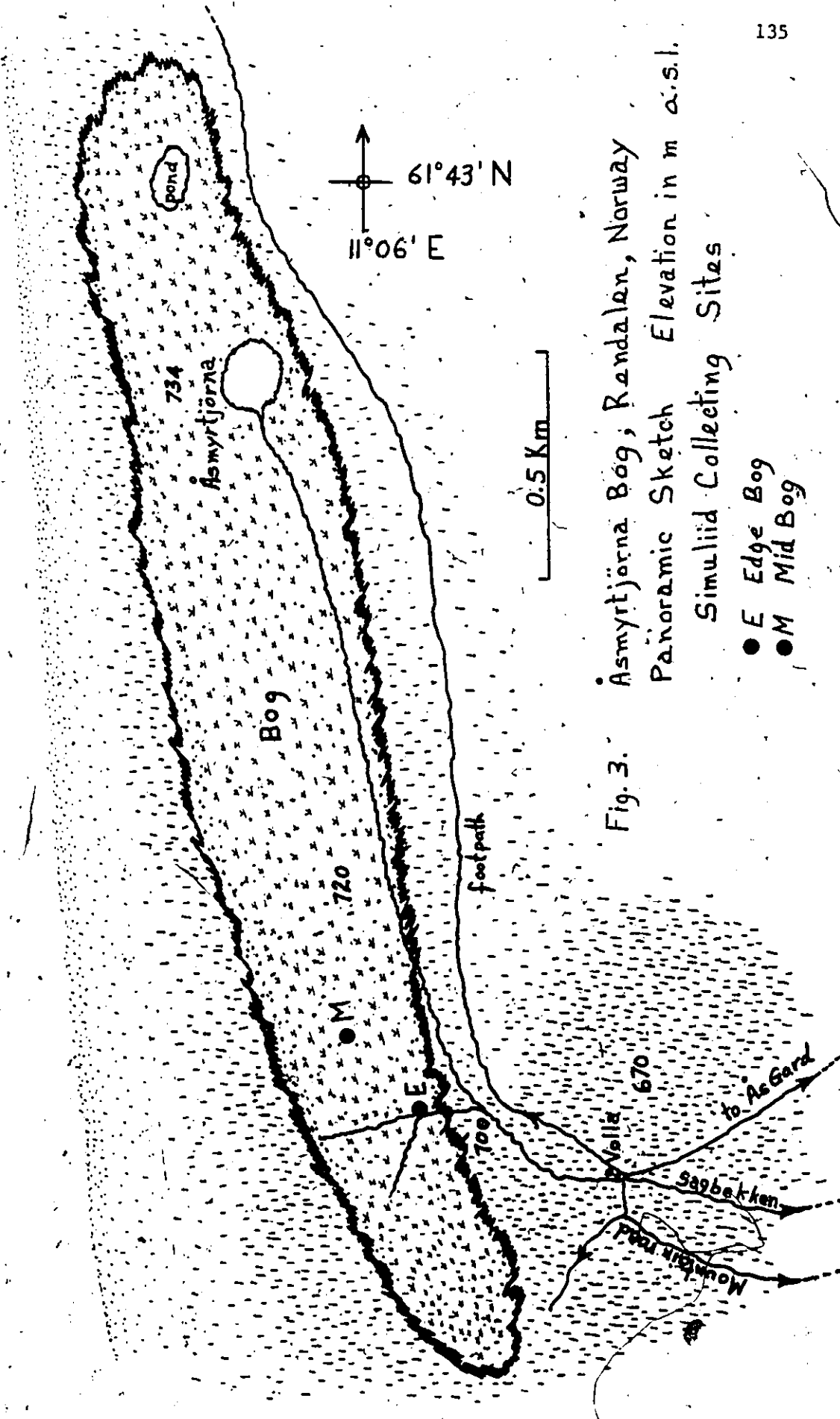
Fig. 3. Åsmyrtjørna Bog, Rendalen, Norway
Panoramic Sketch Elevation in m a.s.l.
Simuliid Collecting Sites

● E Edge Bog
● M Mid Bog

61°43' N
11°06' E

0.5 Km

Fig. 4   Daily air and water temperatures recorded at Renådalen
         bog during the summer of 1980. Note, the relatively
         uniform bog water temperature corresponds to the mean
         air temperature.

Fig. 4

Renådalen 1980

Air max.

min.

Bog Water max.

min.

TEMPERATURE °C.

JUNE 5 15 25 JULY 5 15 25 AUG. 5

136
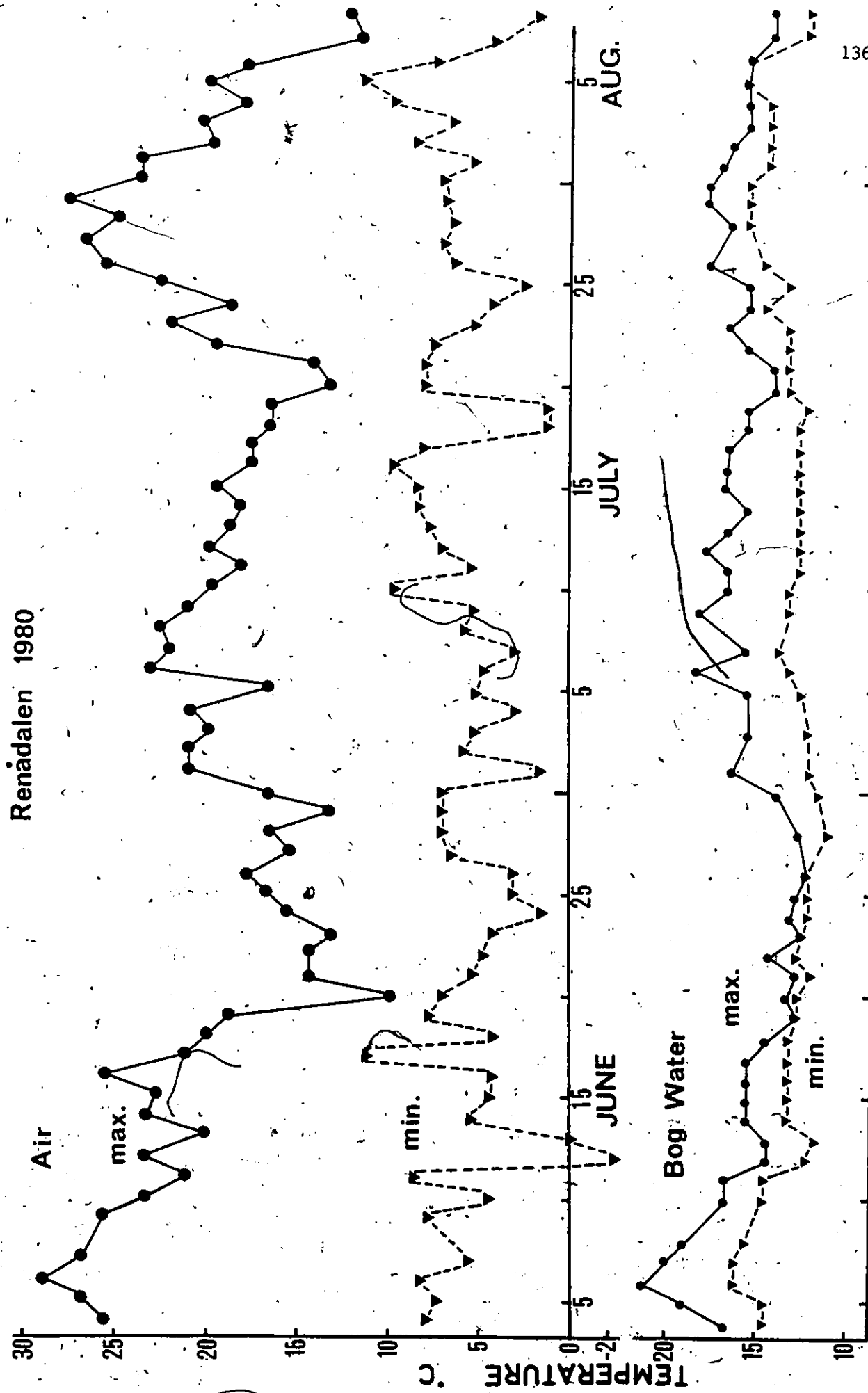
Fig. 5 Accumulated rainfall and pH values of bog and rain
water recorded at Renådalen during the summer of
1980. Note: 1) The low pH of bog water relative
to the slightly lower pH of rain water. 2) Rainfall
is the only source of water that maintains surface
water flowing in the bog during the simuliid
breeding season.

Fig. 5

Renådalen 1980

Bog Water

Rain

pH

RAINFALL mm

JUNE JULY AUG.
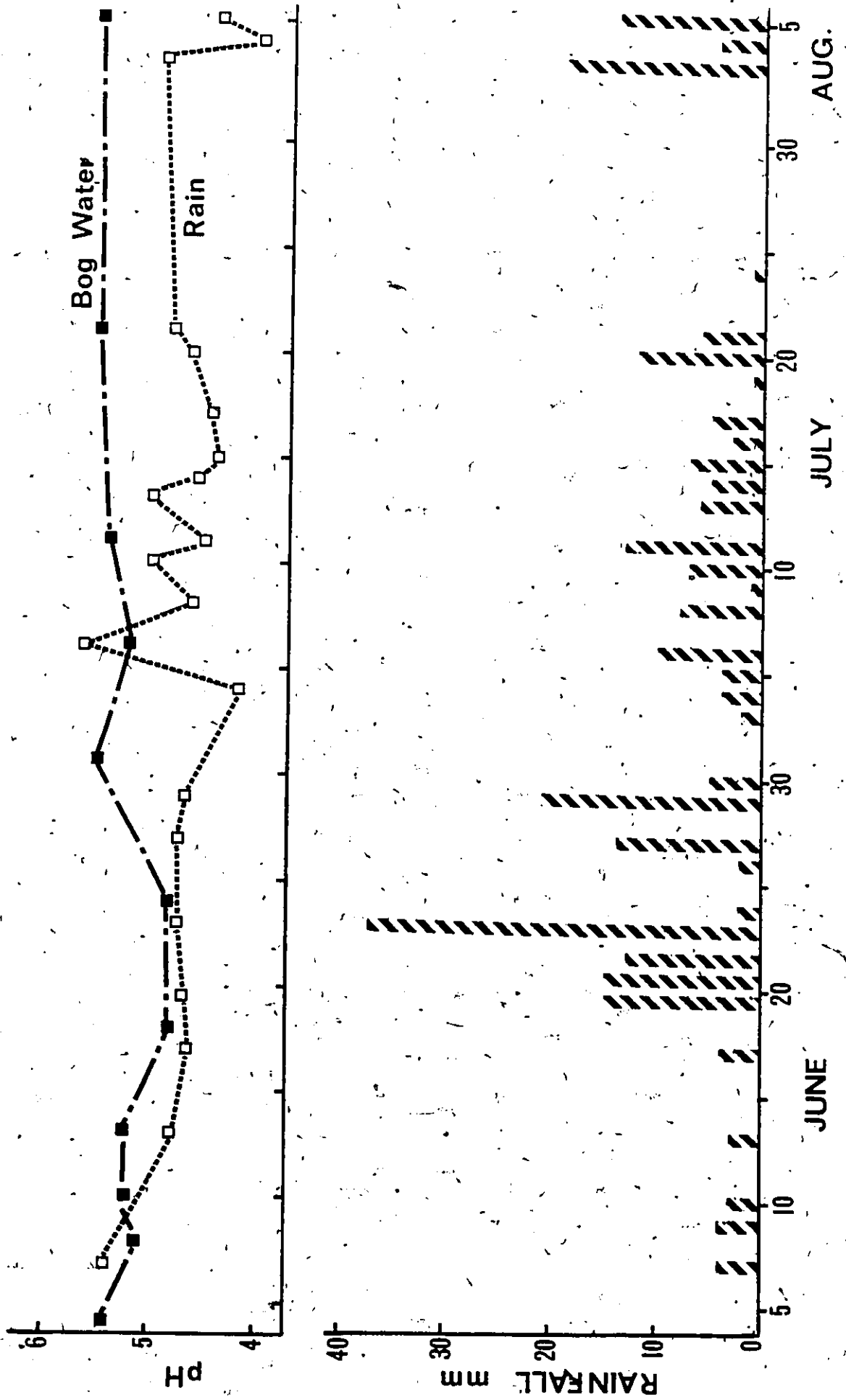
Fig. 6 Precipitation as accumulated monthly rainfall in
        Åkreströmmen, Rendalen, for 1979 and 1980 compared
        to 10 years mean values. Note, the highest
        precipitation occurs during early summer, coinciding
        with the development of aquatic stages of bog simuliids.

Fig. 6

Åkreströmmen
RENDALEN

1979
1980
mean
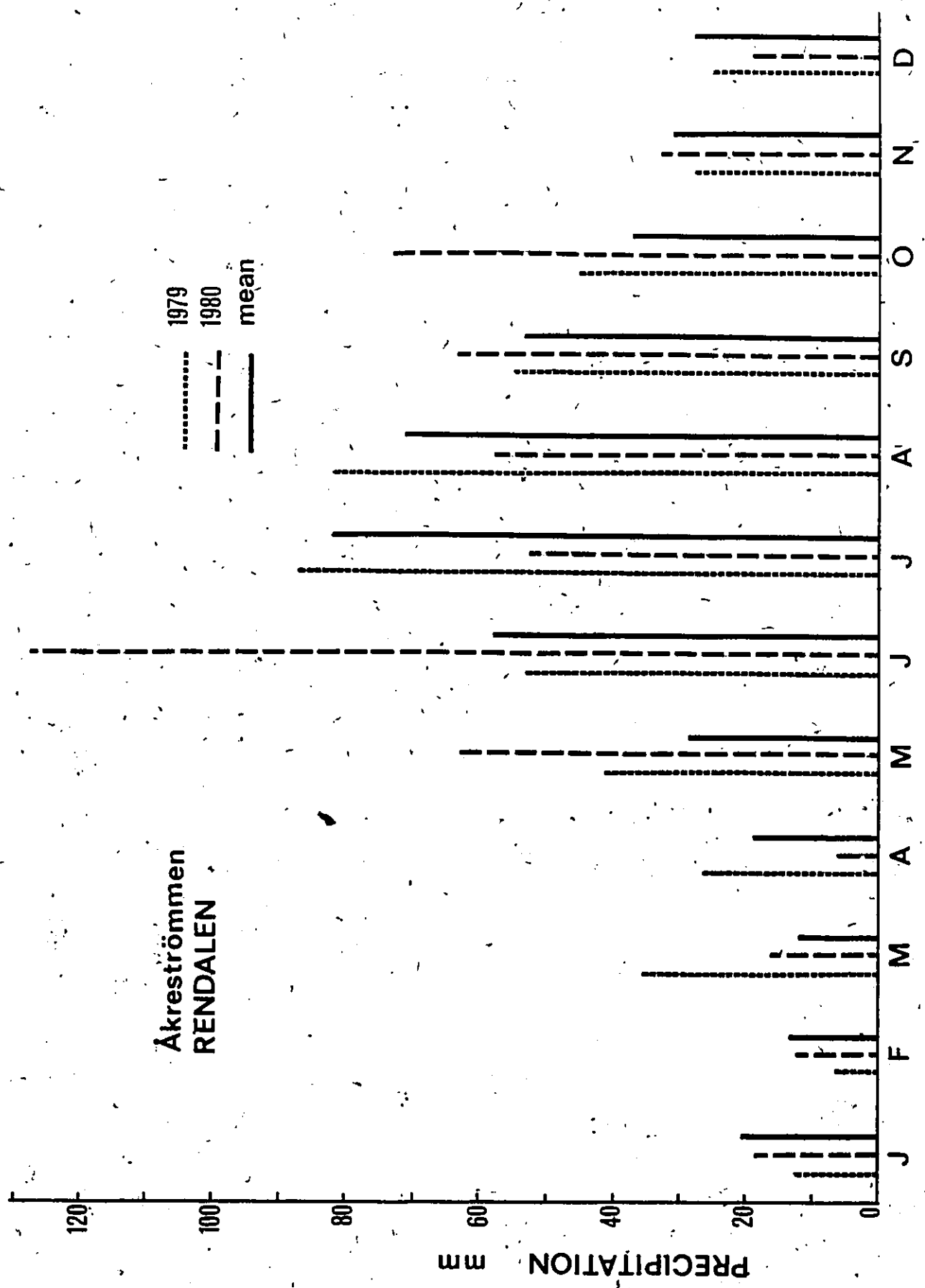
RESULTS AND DISCUSSION

The Palustrine Biotope

Characterization of Renådalen and Åsmyrtjörna bogs in terms
of vegetation and water quality is summarized in Tables 1 and 2. Except
for size, both bogs have several characteristics in common, the most
obvious being an open, treeless, and gently sloping surface exposed to
direct sunlight from which water drains via numerous interconnecting
seepages into a common collector stream at the lower edge of the bog.
The entire bog surface is covered with Sphagnum spp. and overgrown with
sedges, particularly Carex spp., Eriophorum sp., Molina sp., Schoemus
sp., Scirpus spp. and several other common and occasional plants (Table 1).
The relative abundance of these plants was determined semiquantitatively
by visual inspection. The vascular plants listed at the end of Table 1
occur primarily on the periphery of the bogs and along the streams
draining them. This vegetation is associated with a water-saturated
and partially decomposed substrate about 1.0 m thick, estimated by
pushing a pointed 2 cm diameter pole vertically through various points
on the bog surface. Similar sloping bogs with characteristic vegetation
are common in Norway and other Scandinavian countries (Osvald 1954; Sjörs 1961)
In Åsmyrtjörna bog, flatter areas are often flooded with surface pools
of standing water 10 to 50 m wide, particularly after 15 to 20 mm of
continuous rainfall in June and July. These areas have a particularly
soft and fragile surface which could be made to quake or vibrate by

bouncing over the periphery, and are impassable without risk of sinking into the mire. These localized mires, occur invariably on slightly more elevated areas of the bog, and are focal reservoirs of water which drain through the substrate into surface seepages flowing from 0 to about 30 cm/sec. These seepages (Figs. 20, 28, 29), ranging in size from 5 to 30 cm deep and as wide, are the foci containing numerous simuliid larvae and pupae attached loosely to decaying sedges. In deeper seepages simuliids were found also on bottom humus, mainly of decaying Sphagnum which occurs as irregular-mounds resembling miniature coral reefs, with attached larvae and pupae waving like tiny polyps in the sluggish water current. Detection of simuliids in these seepages was facilitated in reduced glare, by wearing polaroid sun glasses, during overcast skies and in early morning or late afternoon when the angle of sunlight reflected from the water surface is low; even then, simuliids were difficult to detect unless they were viewed closely, about 10 cm from the water surface. Consequently, collecting larvae and pupae with the conventional forceps method in this type of habitat proved relatively difficult, not only because of the required low, back-breaking posture over the water-logged substrate, but also because the fragile, decaying vegetation on which larvae and pupae were attached invariably disintegrated as it was lifted out of the water. Thus, simuliids became covered in black, slimy humus from which they were extremely difficult to separate.

Analysis of the water sampled from Renådalen and Åsmyrtjörna bogs and streams is shown in Table 2. The most obvious characteristic of this water was its brown colour, typical of dystrophic conditions. A comparison of the parameters analysed shows that water quality from Renådalen bog is relatively similar to that of streams 12, 13 and 14

originating from the bog, the main difference being in higher conductivity of water from stream 12, higher concentration of phosphates from the bog and lower suspended solids from 13. Water quality from Åsmyrtjörna bog is also relatively uniform, with lower concentrations of suspended solids and sulphates, phosphates, potassium and iron, and higher concentration of calcium occurring at the lower edge of the bog. One main difference between the two bogs is the higher conductivity and dissolved organic carbon (DOC) of water from Åsmyrtjörna. Although only one water sample was taken from each of stream 15 and the Renåa river, neither of which originated from bogs, they differ from bog water essentially in being neutral as shown by their near 7 pH values. By contrast, both bogs and ensuing streams have pH values of about 5.0 to 5.5 which are 0.2 to 0.5 pH units higher than rain water during the summer (Fig. 5). All the water samples tested show relatively low concentration of bicarbonate ions, indicating that both bogs and streams in Renådalen have relatively soft water and are thus highly susceptible to acidic precipitation.

Water temperatures remained relatively high during the summer; records from Renådalen bog water showed an average daily maximum temperature of about 15°C, of 2° to 3°C lower than the maximum daily air temperatures (Fig. 4), and 6° to 8°C higher than those of other mountain or forest streams. Depletion of surface water through drainage from these bogs is apparently enhanced by relatively high rate of evaporation through direct solar radiation. During the first two relatively dry weeks of June 1980 when maximum air temperatures soared to about 25°C, the water level in Renådalen bog decreased from an initial discharge of about 200 l/min (from all three streams combined) to about 60 l/min. This drought

caused significant reduction in seepage flow from the bog, resulting in a reduction of water volume in deeper sections of streams to less than half their full capacity (Fig. 25). A total of about 15 mm of intermittent rain that fell during nights in these first two weeks of June had little effect in maintaining water flow from the bog.

By contrast, a cold weather front passing through Renådalen during the third week of June 1980, as shown by the change in air temperature (Fig. 4), brought a total of 85 mm of rain from June 18 to 24, exceeding by 15 mm the average precipitation for the whole month of June in this region (Fig. 6). During these seven days of continuous rain, Renådalen bog became completely flooded, and water from the three issuing streams reached a maximum outflow of about 1000 l/min. The amount of rainfall during July remained below average for this region, but it was sufficient to maintain surface water flowing through the bogs and streams. In early August 1980 only the lower periphery of Renådalen and Åsmytjörna bogs had some flowing water, as in the drought period of early June. This indicates that rainfall is the main source of water input into these sloping, open bogs at high elevation, as occurs in similar habitats in Scandinavia (Osvald 1954). This factor may explain the low mineral content in the water, as is typical of similar ombrotrophic bogs (Sjörs 1952; Jeglum et al 1974). The implication of water runoff from these bogs on population density of simuliids will be discussed in subsequent results.

It is significant to indicate that the seasonal development of plant and animal life on Fuglåsen plateau where Åsmyrtjörna is situated, is advanced in the spring normally by about one week relative to Renådalen. This observation is supported by naturalist land owners

of this region, e.g. Herr Ajas Kiaer, and by personal observations.

This plateau receives more direct solar radiation for a longer period

of the day than the Renådalen watershed which is surrounded by forested

terrain and is overshadowed to some extent by the western mountain

ridge of Renåfjellet and Renåskarven. Hence, in the first and second

week of June when deciduous trees, e.g. _Betula_ and _Salix_, are at the

early budding stage in Renådalen (Fig. 19), in Fuglåsen these same

trees had already developed a full complement of leaves. This initial

vegetative period was associated with the spring reproductive period

of birds and development of larvae and emergence of _Hellichiella_ spp.

and other ornithophilic simuliids in Renådalen. This time differential

in local climate affected the developmental period of simuliids from

Renådalen and Åsmyrtjörna, as will be indicated subsequently.

Table 1.   Vegetation ocurring in Renadalen and Asmyrtjörna bogs of Rendalen
Norway, during June, July and August 1980, where __Hellichiella__ spp. were collected

	Dominant	Common	Occasional
Musci			
Sphagnum fuscum	*		
S. magellanicum	*		
Equisetaceae			
Equisetum palustre			*
Cyperaceae			
Carex vesicaria		*	
C. vulpina	*	*	
Eriophorum angustifolium	*	*	
E. vaginatum		*	
Kobresia simpliciuscula		*	
Molina coerulea	*		
Schoemus ferrugineus	*		
Scirpus caespitosus	*		
S. lacustris		*	
Ericaceae			
Andromeda polifolia		*	
Arctostaphylos alpina			*
Ledum palustre			*
Loiseleuria procumbens		*	
Vaccinium myrtillus		*	
V. oxycoccos			*
V. uliginosum			*
V. vitis-idaea			*
Empetraceae			
Empetrum nigrum			*
Menyanthaceae			
Menyanthes trifoliata			*
Primulaceae			
Trientalis europea		*	*
Ranunculaceae			
Ranunculus aceleratus		*	
R. arvensis		*	
R. repens		*	
Scrophularaceae			
Euphrasia brevipila			*
Rosaceae			
Potentilla erecta		*	
Rubus chamaemorus		*	
Comarum palustre		*	
Shrubs and Trees (in periphery of bogs)			
Alnus incana		*	
Betula nana (ubiquitous)	*		
B. verrucosa		*	
Picea abies			*
Pinus sylvestris			*
Salix caprae		*	
S. lanata		*	
S. herbacea		*	

Table 2. Water quality parameters of certain bog and stream habitats of Simuliidae in Rendalen, Norway, during June to August 1980.

	°C	pH	Cond. µS/20°	Solids <45µ	HCO_3^-	DOC	SiO_2	Cl^-	NO_3^-	SO_4^{2-}	PO_4^{3-}	Na^+	K^+	NH_4^+	Ca^{2+}	Mg^{2+}	Fe^{3+}	flow 1/min
RENDÅLEN																		
Bog max.	15.6	5.7	52.0	4.0	48.8	15.0	0.17	0.50	0.02	3.0	100.4	0.8	0.15	0.1	1.2	0.03	0.21	800
min.	12.2	5.2	27.5	1.0	6.1	5.4	0.08	0.20	0.00	0.5	0.0	0.2	0.05	0.0	0.2	0.05	0.03	20
(N=4) X̄	14.7	5.4	37.4	3.5	18.3	8.7	0.14	0.30	0.02	1.5	34.5	0.6	0.07	0.0	0.7	0.14	0.12	100
Brook #12	12.5	5.5	100.0	4.0	24.4	11.6	0.18	1.00	0.02	1.5	17.6	0.6	0.05	0.0	5.2	0.30	0.68	15
Brook #13																		
max.	15.5	5.6	32.5	1.0	48.8	6.8	0.74	0.50	0.02	1.5	34.4	0.6	0.05	0.1	0.6	0.10	0.22	400
min.	12.5	5.3	30.0	1.0	24.4	6.6	0.14	0.30	0.00	1.0	0.0	0.6	0.05	0.0	0.4	0.12	0.12	20
(n=2) X̄	14.0	5.5	31.2	1.0	36.6	6.7	0.35	0.40	0.01	1.3	22.2	0.6	0.05	0.1	0.5	0.10	0.14	60
Brook #14																		
max.	15.5	5.8	32.0	4.0	36.6	6.4	0.37	0.50	0.02	3.5	31.2	0.6	0.05	0.0	1.0	0.20	0.14	300
min.	12.5	5.4	28.5	1.0	12.2	6.3	0.04	0.16	0.02	0.5	0.0	0.6	0.05	0.0	0.4	0.10	0.14	10
(n=2) X̄	14.0	5.6	30.2	3.5	24.4	6.3	0.20	0.33	0.02	2.0	14.2	0.6	0.05	0.0	0.7	0.15	0.14	40
Brook #15	12.2	6.5	56.0	1.0	12.2	6.7	0.21	0.30	0.02	1.5	94.8	0.7	0.05	0.0	2.4	0.35	0.11	60
Rendå B.																		
SMETHYLJØRNA	12.0	7.7	25.0	4.0	24.4	11.0	0.57	0.20	0.00	3.0	0.0	0.9	0.35	0.0	5.4	1.15	0.15	>10⁴
Lower bog																		
max.	15.6	5.9	74.0	2.5	12.2	15.0	0.60	0.30	0.02	0.6	34.0	1.0	0.35	0.2	4.2	0.35	0.90	300
min.	12.2	5.4	38.0	2.0	12.2	10.8	0.11	0.22	0.02	0.1	0.0	0.9	0.05	0.0	1.2	0.15	0.28	10
(n=2) X̄	14.4	5.6	56.0	2.2	12.2	12.9	0.35	0.26	0.02	0.4	15.3	1.0	0.20	0.1	2.7	0.25	0.59	60
Upper bog																		
max.	15.6	5.6	74.0	4.0	12.2	16.8	0.20	0.52	0.02	3.0	47.6	0.8	3.20	0.2	1.8	0.25	1.90	100
min.	12.2	5.4	41.0	4.0	12.2	13.8	0.16	0.16	0.00	2.0	4.0	0.6	0.05	0.0	1.6	0.20	0.98	1
(n=3) X̄	14.4	5.5	58.3	4.0	15.2	15.2	0.18	0.37	0.02	2.7	29.5	0.7	1.80	0.1	1.7	0.22	1.20	10

mg/l

* PO_4^{3-} in 10^{-3} mg/l

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Hellichiella and Other Simuliid Species

from Renådalen and Åsmyrtjörna

Renådalen Bog

The first larvae of Hellichiella from Renådalen bog were found in streams 12, 13 and 14 in the second and third weeks of June 1979 associated with mature larvae and pupae of Greniera brachiata Rubtsov. The low density of simuliids in these streams led to finding their bog origin and discovery of the breeding source of Hellichiella in this habitat. The relative abundance of simuliids in these three streams and bog during June and July 1979 is summarized in Table 3. These preliminary results, based on random collections, show that H. rendalense was the dominant species, comprising 61.2% of six species present in the bog, but it was less than half as abundant in each of the three streams. The other species followed nearly the same trend, being more abundant in the bog than in the streams; the apparent absence of Greniera brachiata from the bog is attributed to its early development, with adults having completely emerged before June 27, the time of first collection from the bog. Both E. aureum (Fries) and S. noelleri Friederichs occurred as young developing larvae, up to 5th instars, in early July; hence no pupae or adults of these two species were found.

The proportions of H. rendalense and H. near dogieli, based on the 1979 collections (Table 3), are shown in Tables 4,5. Identifications

of last instar larvae (Table 4) showed that H. rendalense was the
dominant species in 1979, comprising 92.2% of Hellichiella larvae from
the bog, and 63.6%, 85.7% and 80.0% from streams 12, 13 and 14 respectively.
The dominance of H. rendalense over H. near dogieli is evident also from
identifications of reared adults (Table 5) which occurred in nearly
identical proportions as the larvae. These results indicate also that
these two species develop simultaneously without significant temporal
or spatial separation. Mature larvae, with small fat bodies, and pupae
of both species were found in about the same proportions from the third
week of June to the second week of July 1979. There was no evidence
of a second larval generation nor of reared adults developing eggs in
captivity without a blood meal. However, one of the four larval collections
of June 29 (Table 4) showed an equal proportion of the two species of
Hellichiella, indicating a microhabitat preference by these two species.
Since this collection was made about 10 m further up into the bog, it
appears that larvae of H. near dogieli occur preferentially in the
outer bog seepages while those of H. rendalense are distributed primarily
at the edge of the bog.

The results of random collections of larvae from Renådalen
bog of the 1980 season are shown in Table 6. The proportion of
H. rendalense s. l. in this season was again the highest, comprising
about 35% of the eight species found in the bog. However, this
proportion is about half that of the previous season because of the
larger populations of the other species encountered over the longer
collecting period in 1980. The relative abundance of E. vernum remained
essentially unchanged from the previous season. G. brachiata was
the dominant species, occurring as penultimate and last instar larvae

Table 3. Relative abundance of simuliid species from the Renådalen bog biotope based on collections of June 9, 15, 24, 26, 27, 28, 29 and July 1, 2, 4, 7, 11, 1979.

Taxon	Bog la	pa	ex	adults ♂	♀	Total	%	Brook #12 la	pa	ex	adults ♂	♀	Total	%	Brook #13 la	pa	ex	adults ♂	♀	Total	%	Brook #14 la	pa	ex	adults ♂	♀	Total	%
Cnephia																												
Gr. brachiata s.l.	0	0	0	0	0	0	0	3	3	3	2	0	11	8.7	27	2	1	0	2	32	4.2	24	4	0	3	1	29	5.4
St. duodecimata	14	8	0	4	4	30	1.1	17	0	0	0	0	17	13.5	27	4	1	0	2	34	4.5	8	4	0	1	1	14	2.6
Eusimulium																												
E. aureum	302	0	0	0	0	302	11.2	0	0	0	0	0	0	0	105	0	0	0	0	105	13.8	147	0	0	0	0	147	27.3
Hellichiella																												
Renådalens s.l.	1158	226	38	105	120	1647	61.2	29	9	0	6	3	47	37.3	31	9	5	4	6	55	7.2	14	4	0	2	3	23	4.3
Nev. bicorne	0	0	0	0	0	0	0	0	0	0	0	0	0	0	106	19	0	10	8	143	18.8	32	7	0	4	3	46	8.6
Nev. vernum s.l.	590	34	3	20	12	689	25.6	41	0	0	0	0	41	32.5	305	40	2	22	17	386	50.7	205	34	0	16	18	273	50.1
Simulium																												
S. noelleri	24	0	0	0	0	24	0.9	0	0	0	0	0	0	0	6	0	0	0	0	6	0.8	5	0	0	0	0	5	0.9
						2692							**126**							**761**							**537**	
Number of collections						10							4							12							7	

* Date of first collection from the bog

la = larvae; pa = pupae; ex = exuviae; adults reared from pupae

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Table 4. Relative abundance of Hellichiella rendalense and H. near dogieli based on instar larvae collected in the Renådalen bog biotope during June and July 1979

	June					July						Total	%
	24	26	27	28	29	1	2	4	7	9	11		
Bog													
rendalense	62	71	33	64	32	129	198	105	117	72	9	892	92.2
nr. dogieli	3	3	2	26	1	3	13	14	6		0	75	7.8
Stream #12													
rendalense	4	3										7	63.6
nr. dogieli	4	0										4	36.4
Stream #13													
rendalense				6		3			3			12	85.7
nr. dogieli				2		0			0			2	14.3
Stream #14													
rendalense	0	2	1			5						8	80.0
nr. dogieli	1	1	0			0						2	20.0

Table 5. Relative abundance of *Hellichiella* rendalense and *H.* near dogieli based on pupae and reared adults collected in the Renådalen bog biotope in June and July 1979

	June					July					Total	%
	24	26	27	28	29	1	2	4	7	11		
Bog												
rendalense ♂	6	9	3	3	6	28	5	28	5	4	97	93.3
♀	2	12	8	2	6	16	14	31	12	10	113	
nr. dogieli ♂	1	3				1	2			1	8	6.7
♀	0	2				2	2			1	7	
Stream #12												
rendalense ♂			1				2			1	4	77.8
♀			1			1	1				3	
nr. dogieli ♂	2										2	22.2
♀	0										0	
Stream #13												
rendalense ♂			1						2		3	90.0
♀			1			1			4		6	
nr. dogieli ♂										1	1	10.0
♀											0	
Stream #14												
rendalense ♂	1	1									2	80.0
♀	1	1									2	
nr. dogieli ♂	0	0									0	20.0
♀										1	1	

Table 6. Relative abundance of simuliid species based on larvae from the Renådalen bog during the summer of 1980

Taxon	June						July								Aug	Total	%
	4	5	6	10	14	25	1	6	12	15	21	23	25	30	6		
Greniera																	
brachiata s.l.	67	106	229	212	68	0	14	0	0	0	0	0	0	0	0	696	7.8
Stegopterna																	
duodecimata	12	5	9	5	26	40	61	0	7	1	0	0	0	0	0	192	2.1
Hellichiella																	
rendalense s.l.	87	92	165	386	148	435	322	696	615	60	103	47	14	5	0	3175	35.4
crassum	0	0	0	0	0	0	0	17	3	9	10	7	8	6	0	60	0.7
Nevermannia																	
vernum s.l.	62	70	60	25	131	320	486	108	237	304	184	199	82	72	70	2426	27.0
Eusimulium																	
aureum	0	0	0	0	0	0	44	160	111	202	291	217	152	181	22	1538	17.2
Simulium																	
noelleri	0	0	0	0	0	0	7	60	28	143	26	160	11	113	26	692	7.7
rotundata	0	0	0	0	0	0	5	0	2	0	0	0	0	37	146	190	2.1
																8969	

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during the first week of June, showing that this species also breeds in the bog. In July, when the earlier species had declined, larvae of other species, such as _E. aureum_ and _S. noelleri_, became more numerous. Hence, this seasonal species succession is a factor affecting the proportion of _H. rendalense_ s.l. The results of larval collections from the three streams issuing from Renådalen bog for the 1980 season are shown in Table 7. The relative abundance of _H. rendalense_ s.l. was about half of that from the bog and less than half of that of _N. vernum_ s.l. which comprised about 50% of the eight species from all three streams.

The proportions of _H. rendalense_ and _H._ near _dogieli_ based on mature larvae from both rubber strips and random collections of 1980 from bog and streams are shown in Table 8. The first mature larvae of these two species occurred in the second week of June and the last larvae in the second week of July. From a total of 1164 last instar larvae of _Hellichiella_, 25.8% were identified as _H. rendalense_ and 74.2% as _H._ near _dogieli_. This proportional difference was generally maintained through the season, without evidence of temporal succession between species. The same results were obtained from stream 13, while the proportion of larvae in stream 14 was found to be nearly equal between the species, with a difference of about 12% more larvae of _H._ near _dogieli_. In the latter two streams larvae of _H. rendalense_ occurred for about one week longer into early July, and in the bog one week longer into mid July, indicating a slightly protracted period of larval development for this species relative to that of _H._ near _dogieli_. This greater proportion of _H._ near _dogieli_ larvae in 1980 is the reverse of that of the previous season (Table 4) when larvae of _H. rendalense_ were the more abundant. This indicates that the relative abundance

Table 7. Relative abundance of simuliid species based on larvae from various points along three streams originating from the Renådalen bog in June and July 1980

Taxa	Brook #12					Book #13					Brook #14									
	June 4	June 12	June 14	Total	%	June 4	June 12	June 14	Total	%	June 4	June 6	June 8	June 12	June 14	July 30	July 6	July 21	Total	%
Greniera brachiata s.l.	10	2	0	12	2.7	9	0	0	9	1.5	7	106	12	12	0	0	0	0	137	4.5
Stegopterna duodecimata	7	40	56	103	23.4	7	12	19	38	3.2	4	11	21	14	4	0	0	0	54	1.1
Helichiella crassum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	26	1	0	27	0.9
rendalense s.l.	35	4	55	94	21.4	10	76	86	172	14.4	15	101	118	242	92	20	0	0	588	19.2
Nevermannia bicorne	0	0	2	2	0.5	0	63	82	145	12.1	0	172	112	171	84	15	0	0	554	18.1
vernum s.l.	26	5	153	184	41.9	124	329	371	824	68.8	44	274	268	346	155	36	47	0	1170	38.2
Eusimulium aureum	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	31	251	186	479	15.7
Simulium noelleri	0	0	44	44	10.0	0	0	0	0	0	0	7	2	0	0	0	25	16	50	1.6
				439					1182										3059	

Table 8. Relative abundance of <u>Hellichiella</u> <u>rendalense</u> and H. near <u>dogieli</u> based on last instar larvae collected in the Renådalen bog biotope during June and July 1980

	June					July			Total	%
	11	14	18	25	26	1	6	14		
Bog										
rendalense	5	42	90	24	14	59	60	6	300	25.8
nr. dogieli	75	239	231	212	51	42	14	0	864	74.2
Stream #13										
rendalense	0	0	2	0	1	0	3	0	6	15.4
nr. dogieli	7	8	18	0	0	0	0	0	33	84.6
Stream #14										
rendalense	25	3	11	0	1	20	0	0	60	44.1
nr. dogieli	38	18	19	0	1	0	0	0	76	55.9

between these species may vary between seasons.

The proportion of these two species in 1980 determined from reared adults is shown in Table 9. H. rendalense comprised 85.7% and H. near dogieli 14.3% of adults from the bog, with similar proportion for stream 14. These results also show that the proportion of reared females to males was about 1.5:1 for H. rendalense and 6:1 for H. near dogieli. Hence, the expected sex ratio of 1:1 obtained for Hellichiella spp. in 1979 (Table 5) was not obtained for the bog population in 1980. This is the converse of 1980 results of larval collection where H. rendalense was only 25.8% and H. near dogieli 74.2% (Table 8). The higher proportion of H. near dogieli larvae should have produced the expected equally higher proportion of reared adults of this species, but the results show the opposite, namely, H. rendalense adults were the more abundant. Considering that immatures and adults of both species were identified correctly, the above anomalies may be explained simply as follows: On June 18 most Hellichiella larvae were in their final instar, particularly male larvae which develop earlier than females, thus they were more susceptible to drift before pupating. At this time, the five days of continuous rain from June 18 to 24 (Fig. 5) that flooded the bog and resulted in a ten-fold increase in water flow, washed downstream a significant number of the earlier maturing male larvae. The corresponding decrease of male pupae resulted in a lower proportion of reared males relative to females. The 1:1 proportion of H. rendalense males and females reared from stream 14 (Table 9) lends support to this explanation; larvae drifting downstream were more successful in reattaching onto substrates than larvae at the bog's edge, thus pupating in preferred water microcurrents in the stream

Table 9. Relative abundance of _Hellichiella_ _rendalense_ and _H._ near _dogieli_ adults reared from pupae from Renådalen bog and stream #14 in 1980.

	June		July						Total	%
	18	25	1	6	11	16	23	25		
Bog										
rendalense ♂	1	2	9	50	7	11	0	0	80	85.7
♀	4	3	8	70	20	13	5	1	124	
near dogieli ♂	0	0	1	4	0	0	0	0	5	14.3
♀	0	4	3	11	10	2	1	1	29	
Stream #14										
rendalense ♂	2	0	38	14		0			54	91.9
♀	0	0	12	36		0			48	
near dogieli ♂	0	0	2	0		0			2	8.1
♀	0	0	2	5		0			7	

bed.

Åsmyrtjörna Bog

The results of larval collections from Åsmyrtjörna bog are shown in Table 10. These results reveal, among other pertinent information, that the development of simuliids at this site was seasonally more advanced than that at Renådalen bog. Both G. brachiata and St. duodecimata, two early species which occurred mainly as mature larvae and pupae in the second week of June in Renådalen, had already emerged in Åsmyrtjörna on June 9, as indicated by the absence of larvae and presence of exuviae of these two species at this site. Similarly, nearly 50% of H. rendalense and H. near dogieli larvae were in their last instar and about 5% had pupated (Table 11); by contrast in Renådalen the first pupae of Hellichiella spp. occurred about one week later.

The more numerous species showed significant differences in abundance of larvae between the two sampling sites in Åsmyrtjörna. H. rendalense and H. near dogieli combined, comprised 19% of seven species sampled from the edge of the bog, compared to 66% of six species from mid bog. The other species, particularly H. crassum, E. vernum, E. bicorne and S. noelleri occur preferentially at the periphery of the bog, and are thus considered here as peripheral bog species, while E. aureum shows no significant preference for either site.

The proportions of H. rendalense and H. near dogieli based on identifications of mature larvae and adults reared from pupae are shown in Table 11. At the edge of the bog a total of 216 larvae consisted of 31% H. rendalense and 69% H. near dogieli. In mid bog a total of 934 larvae consisted of 3.2% H. rendalense and 96.8% H. near

Table 10. Relative abundance of simuliid species based on number of larvae from Åsmyrtjörna, edge and mid bog, during the summer of 1980
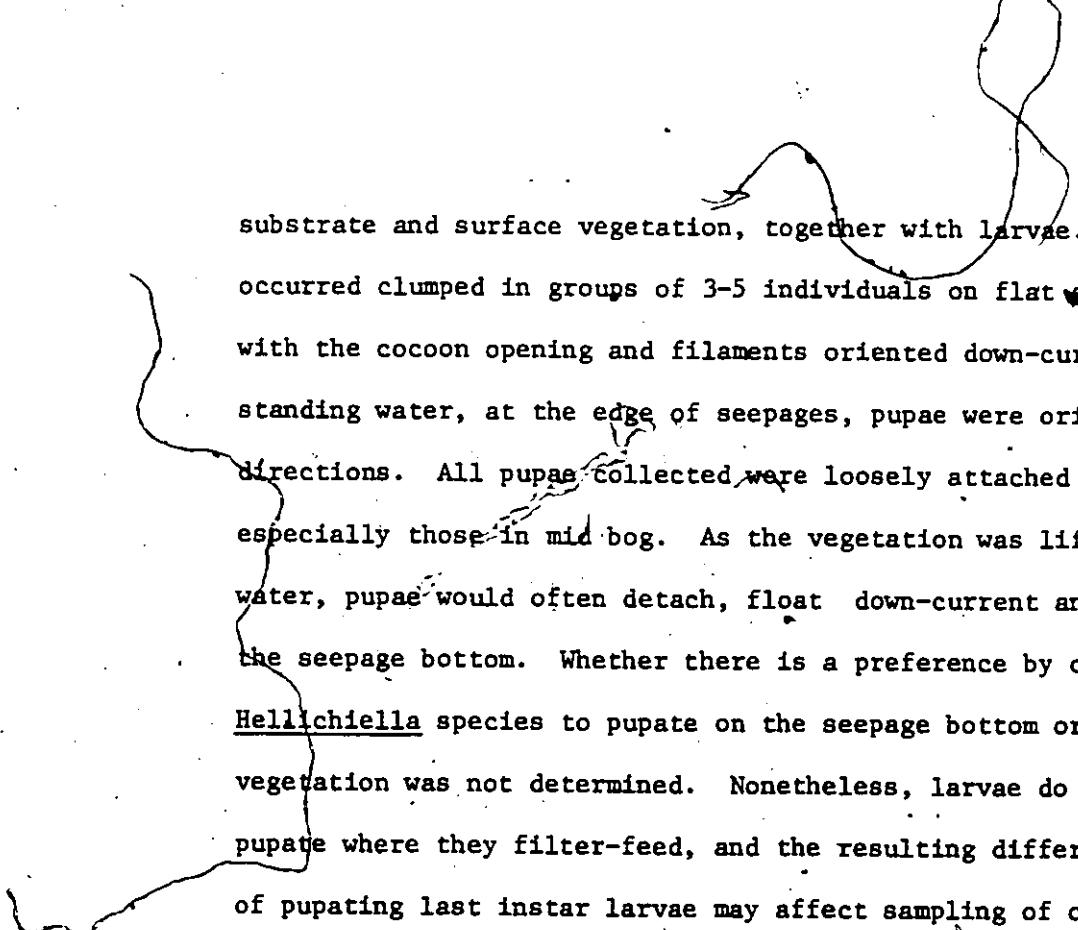
Taxon	Edge Bog June 9	16	23	July 2	18	Aug 1	Total	%	Mid Bog June 9	16	23	July 2	18	Total	%
Grenicra brachiata s.l.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stegopterna duodecimata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hellichiella rendalense s.l.	227	210	233	2	8	0	683	18.6	227	293	360	530	296	1730	66.9
crassum	0	0	2	133	65	110	310	8.4	0	0	0	0	3	3	0.0
Nevermannia vernum s.l.	321	323	322	66	201	46	1280	34.8	85	35	87	95	63	453	16.8
bicorne	22	85	296	0	0	0	403	11.0	0	0	0	0	0	0	0.0
Eusimulium aureum	0	0	0	81	115	163	359	9.8	0	0	3	88	257	348	13.5
Simulium noellieri	2	98	262	135	63	15	581	15.8	0	0	27	0	0	27	1.1
rotundata	0	0	0	39	23	4	66	1.8	0	0	26	0	0	26	1.1
							3681							2587	

* Mid Bog nearly dried up on Aug. 1

Table 11. Relative abundance of *Hellichiella rendalense* and *H.* near *dogieli* mature larvae and adults reared from pupae from Åsmyrtjörna bog in 1980.

| | Larvae | | | | | | | Adults | | | | | |
| | June | | | July | | | | June | | | July | | |
	9	16	23	2	Total	%		9	16	23	2	Total	%
Edge of Bog													
rendalense	17	50	0	0	67	31.0	♂	0			0	0	
							♀	1			0	0	
nr. dogieli	102	37	2	8	149	69.0	♂	1			1		
							♀	0			0	0	
Mid Bog													
rendalense	6	16	12	0	30	3.2	♂	5	79	22	37	143	29.7
							♀	3	16	54	56	159	33.0
nr. dogieli	206	390	284	24	904	96.8	♂	0	6	9	49	54	11.2
							♀	0	1	4	121	126	26.1

dogieli . This shows that H. near dogieli was the more abundant species
and occurred preferentially in mid bog, while H. rendalense occurred
preferentially at the periphery of the bog.

This microhabitat preference by these two species is not
readily apparent from results of reared adults. Pupae of both species,
and therefore reared adults, were relatively scarce at the edge of the
bog (Table 11), probably due to mature larvae drifting beyond the upper
seepages where all the samples were taken (Fig. 28). Larval drift
occurred also with E. aureum and S. noelleri whose larvae in late July
were primarily in the upper seepages at the bog's edge, while most
pupae occurred in drainage stream 10 to 20 m farther below the seepages.
The proportions of adults from mid bog shows that a sample of 482
reared specimens consisted of 63% H. rendalense and 37% H. near dogieli;
these proportions are the opposite from what would be expected by the
relative abundance of larvae. In addition, the sex ratio of H. rendalense
adults was nearly 1:1, while that of H. near dogieli was about 1:2 in
favour of females. These results also show that H. near dogieli began to
emerge about one week later than H. rendalense, with males pupating in
greater proportion earlier than females for both species. The greater
tendency to drift by H. near dogieli (see next section) is a factor to
be considered affecting the unexpected difference in proportion between
larvae and reared adults, as it was for similar results from Renådalen
bog. In shallower seepages, 1 to 5 cm deep, Hellichiella pupae were
usually attached to and hidden among loose, decaying leaves of Betula,
Salix and sedges in nearly standing water. In the 10 to 30 cm deep
seepage in mid Åsmyrtjörna bog, pupae were found also on the bottom

substrate and surface vegetation, together with larvae. Pupae often

occurred clumped in groups of 3-5 individuals on flat surfaces of leaves,

with the cocoon opening and filaments oriented down-current. In nearly

standing water, at the edge of seepages, pupae were oriented in all

directions. All pupae collected were loosely attached to the substrate,

especially those in mid bog. As the vegetation was lifted out of the

water, pupae would often detach, float down-current and re-settle on

the seepage bottom. Whether there is a preference by one or both

Hellichiella species to pupate on the seepage bottom or on surface

vegetation was not determined. Nonetheless, larvae do not necessarily

pupate where they filter-feed, and the resulting differential drift

of pupating last instar larvae may affect sampling of one species of

pupae selectively over another, thus contributing to the apparent

disproportion between larvae and reared adults.

A summary comparing the relative abundance of _Hellichiella_

larvae and other simuliid species from Renådalen and Åsmyrtjörna is

shown in Table 12. _Hellichiella_ spp., primarily _H._ near _dogieli_ in

1980 and _H. rendalense_ in 1979, were more abundant in Renådalen bog

than in the issuing streams. _Hellichiella_ spp. were not found in two

samples taken June 5 and 13, 1980 from stream 15 nor in one sample of

June 6 from the Renåa river, indicating that these species are absent

from streams not originating directly from bogs. One sample of 155

third to sixth instar larvae taken from Renådalen bog 2 on June 15

contained 63.6% of _Hellichiella_ spp., and 36.4% _._ _vernum_ s.l., thus

confirming that bogs in Renådalen are the primary breeding sites of

Hellichiella. In Åsmyrtjörna, _Hellichiella_ larvae were generally more

abundant in the middle than at the periphery of the bog; specifically,

H. near _dogieli_ occurred preferentially in mid bog while H. _rendalense_ occurred primarily at the edge, indicating a microhabitat preference by these two species. H. _crassum_ (Rubtsov) is also a peripheral bog species whose larvae begin to develop in early July, after the other _Hellichiella_ species have nearly completed pupating. H. _crassum_ has not been considered further in this thesis, since cytotaxonomically it is not in the same group as the other species studied.

Table 12 . Summary of the relative abundance of simuliid larvae from certain bogs and streams in Rendalen, Norway, during June to August 1980.

Taxon	Rendalen							Asmyrtjörna	
	Bog 1	stream 12	stream 13	stream 14	stream 15	Renaa River	Bog 2	Lower Bog	Upper Bog
	%	%	%	%	%	%	%	%	%
Greniera brachiata	7.8	2.7	0.9	4.5	-	-	-	-	-
Stegopterna duodecimata	2.1	23.4	3.2	1.1	1.1	-	-	-	-
Hellichiella rendalense nr. dogieli }	35.4	21.4	14.4	19.2	-	-	63.6	18.6	66.9
crassum	0.7	-	-	0.9	0.5	-	-	8.4	0.0
Nevermannia bicorne	-	0.5	12.1	18.1	9.7	0.1	-	11.0	-
vernum s.l.	27.0	41.9	68.8	38.2	51.4	-	36.4	34.8	16.8
Eusimulium aureum	17.2	-	-	15.7	37.3	-	-	9.8	13.5
Simulium noelleri	7.7	10.0	-	1.6	-	-	-	15.8	1.1
rotundata	2.1	-	-	-	-	-	-	1.8	1.1
ornatum	-	-	-	-	-	0.2	-	-	-
rostratum	-	-	-	-	-	82.6	-	-	-
Prosimulium hirtipes	-	-	-	-	-	12.4	-	-	-
Cnephia pallipes	-	-	-	-	-	4.6	-	-	-
Total number	8969	439	1182	3059	185	908	155	3681	2587
Number of collections	20	3	3	8	2	1	1	7	7

Larval Drift

Only four tests on larval drift at the edge of Renådalen bog
were obtained from June 14 to 18 before flood waters prevented additional
sieve exposure. The results, presented in Table 13, show that _Hellichiella_
spp. and other simuliids drift downstream from the bog as young and mature
larvae. Five times more last instar larvae of _H. near dogieli_ than
H. rendalense were caught drifting from the bog. This occurred during
the period when water volume flowing from the bog and streams was reduced
by drought to a minumum of about 60 litres/min. The larger proportion
of drifting _H. near dogieli_ larvae may be related to the larger larval
population of this species in 1980 (Table 8). Furthermore, the fewer
pupae and reared adults of this species in relation to _H. rendalense_
from both major bogs may reflect the effect of a higher propensity of
H. near dogieli to drift. This is the more surprising when realizing
that, in Åsmyrtjörna bog, _H. near dogieli_ occurred preferentially in
mid bog seepages (Table 11) where larvae would be expected to be less
likely swept into drainage streams at the edge of the bog. Conversely,
the smaller number of _H. rendalense_ larvae caught in the sieve indicates
a relatively lower tendency of this species to drift. This differential
larval drift may reflect the occurrence of _H. rendalense_ larvae primarily
at the edge of the bog (Table 11), thus separating these two species
into two different microhabitats.

Larvae of _St. duodecimata_, _E. vernum_ s.l.,
S. noelleri and _E. aureum_ were also found to drift from the bog (Table 13).
Larvae of _E. vernum_ comprised the largest proportion of the seven species
found in the drift samples. Considering that this was only the second
most numerous bog species (Tables 6 and 10) the many larvae caught

Table 13. Number of simuliid larvae drifting from Renådalen bog, sampled by 30 cm diameter sieve placed across the drainage brook just below the bog in mid June 1980.

Taxon	Instars	14**				15*				17***				18**				Total
		II-III	IV-V	VI	VII	II-III	IV-V	VI	VII	II-III	IV-V	VI	VII	II-III	IV-V	VI	VII	
Stegopterna duodecimata		0	3	34	2	0	10	17	0	0	0	0	8	0	0	0	19	55
Hellichiella renadalense		0	3	21	0	1	14	0	0	0	0	3		0	0	9		51
nr. dogieli													1				2	3
													10				5	15
Nevermannia vernum s.l.		2	77	99	0	0	47	43	0	0	29	39	26	1	28	33	20	444
Eusimulium aureum		0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	3
Simulium noelleri		13	0	0	0	0	0	0	0	4	28	9	0	0	17	0	0	71

Exposure time of sieve

* 12 hours

** 24 hours

*** 48 hours

drifting from the bog reflects this species' high tendency to disperse downstream from its breeding site. The lower proportion of _E. aureum_ and _S. noelleri_ larvae in the drift samples may be related to the smaller incipient population of these two species in mid June.

Larval Density

Assessment of larval density at the edge of Renådalen bog and ensuing streams is reported in Tables 14, 15 and 16. The numbers of larvae of each species from each strip shown in the above tables were divided by the surface area of the strip (25 x 1.2 = 30 cm^2). The results are presented in Figs. 7, 8, 9, 10 and 11, and show the spatial and seasonal distribution of larval densities of each species or species complexes. The values for each sampling date at the bog origin are averages of the number of larvae/cm^2 collected on each of the six strips. The values for each sampling date and site at 10 m, 20 m, and 30 m downstream from the bog are averages of larval densities from two strips, one each from stream 13 and 14, at each distance from the bog. The absence of larvae on the strips on June 21 is associated with the five days of continous rain which reflooded the bog and streams. The resulting increase in water flow and current above the optimal limit for the species (Fig. 12) flushed the larvae from the edge of the bog and prevented their reattachment further downstream. Although a few larvae remained on submerged vegetation in the bog, their density was significantly below that of the pre-flood period. Other workers have found that rainfall modifies stream discharge and the resulting changes in discharge affects rates of larval colonization and detachment. This influences directly estimates of simuliid abundance (Carlsson 1967; Disney 1972; Merritt et al. 1978; Pegel and Rühm 1976; Ross and Merritt 1978).

Larval density of H. rendalense and H. near dogieli combined was highest in the bog and became lower downstream (Fig. 7). The density in the bog increased gradually during the season to a maximum average of 4.0 ± 1 larvae/cm^2 on June 18 and decreased therafter to less than 1 larva/cm^2; after July 15 no more Hellichiella larvae were found on the strips. This gradual increase in larval density is attributed to three factors. 1) The first collection was made with whole or unfrilled rubber strips which were less efficient for attachment of larvae than the modified frilled strips used for subsequent tests. Higher densities of larvae on narrow strips than on wide ones has been observed also for other simuliid species (Pegel and Rühm 1976). 2) Increase in number of larvae in all stages of development. The first two collections from June 5 to 8 contained all young larvae, up to the sixth instar, which are more difficult to collect, while on June 18 when the first Hellichiella pupae were collected, nearly 80% of larvae were in the last instar, the rest being in the fourth to sixth instars. Larval instars were distinguished by the size of the head capsule, following Fredeen (1981). 3) Increase in concentration of larvae near the edge of the bog, related to a decrease in water flow from the bog during the dry period of June 7 to 18 (see above). By contrast the density of larvae in the drainage streams 13 and 14 below the bog was consistently less than 1 larva/cm^2.

Larvae of E. vernum s.l. also occurred in higher density in the bog than in the drainage streams below the bog (Fig. 8). A peak of 3.3 larvae/cm^2 occurred around June 12, nearly one week before the peak reached by Hellichiella larvae. However, the density of E. vernum larvae below the bog was comparatively higher than those of Hellichiella.

Table 14 . Number of simuliid larvae collected on rubber strips, each 25 cm by 1.2 cm, floated in seepages at the edge of Renådalen bog, June and July 1980.

Strip # & Taxon	June							July			
	5	8	11	14	18	21	26	6	14	22	31
Strip #1											
G. brachiata	5	3	1	1	2	0	0	0	0	0	0
St. duodecimata	17	12	3	13	19	0	6	0	0	0	0
H. rendalense } H. nr. dogieli	7	24	58	113	145	0	11	8	4	0	0
H. crassum	0	0	0	0	0	0	0	2	3	1	0
N. vernum s.l.	20	49	123	109	64	0	51	29	21	0	0
E. aureum	0	0	0	0	3	0	12	12	54	13	15
S. noelleri	0	3	0	4	0	0	0	7	16	32	4
Strip #2'											
G. brachiata	0	0	1	0	0	0	0	0	0	0	0
St. duodecimata	0	11	33	21	6	0	5	0	0	0	0
H. rendalense } H. nr. dogieli	0	22	83	162	96	0	5	8	3	0	0
H. crassum	0	0	0	0	0	0	0	0	1	6	2
N. vernum s.l.	0	48	175	150	43	0	74	17	8	3	0
E. aureum	0	0	15	7	0	0	13	25	58	60	18
S. noelleri	0	1	4	4	0	0	0	0	0	0	1
Strip #3											
G. brachiata	0	0	0	0	0	0	0	0	0	0	0
St. duodecimata	0	1	2	1	1	0	0	0	0	0	0
H. rendalense } H. nr. dogieli	0	1	62	52	49	0	2	0	0	0	0
H. crassum	0	0	0	0	0	0	0	0	0	0	0
N. vernum s.l.	0	2	11	33	24	0	0	0	0	0	0
E. aureum	0	0	9	4	68	0	0	0	6	0	0
S. noelleri	0	0	0	14	14	0	0	0	0	0	0

Table 14 . Continued

Strip # & Taxon	June						July			
	8	11	14	18	21	26	6	14	22	31
Strip #4										
G. brachiata	0	2	0	0	0	0	0	0	0	0
St. duodecimata	0	0	0	0	0	0	0	0	0	0
H. rendalense	0	18	53	22	0	26	13	2	0	0
H. near dogieli } H. crassum	0	0	5	0	0	2	20	1	1	0
N. vernum	0	3	5	29	0	7	3	1	6	0
E. aureum	0	0	0	30	0	3	6	4	43	3
S. noelleri	0	0	0	0	0	0	0	0	3	0
Strip #5										
G. brachiata	1	0	0	0	0	0	0	0	0	0
St. duodecimata	7	0	5	4	6	0	0	0	0	0
H. rendalense	52	33	20	106	0	7	0	2	0	0
H. near dogieli } H. crassum	0	0	0	0	0	8	2	0	1	0
N. vernum	40	0	52	64	0	11	2	0	0	0
E. aureum	0	0	4	13	0	0	14	19	0	0
S. noelleri	0	0	0	4	0	0	0	0	0	0
Strip #6										
G. brachiata	0	0	1	0	0	0	0	0	0	0
St. duodecimata	0	0	9	13	0	2	0	0	0	0
H. rendalense	0	2	43	0	0	50	8	1	0	0
H. near dogieli } H. crassum	0	0	0	0	0	0	7	5	2	1
N. vernum	0	30	90	95	0	9	20	50	1	0
E. aurerum	0	0	14	0	0	8	15	35	13	2
S. noelleri	0	14	0	206	0	2	22	0	15	93

Table 15 . Number of simuliid larvae collected on rubber strips, each 25 cm by 1.2 cm, floated in stream
#13 at 10 m, 20 m and 30 m from Renådalen bog, June and July 1980.

Strip # & Taxon	June							July			
	5	8	11	14	18	21	26	6	14	22	31
Strip #1 @ 10 m											
G. brachiata	2	0	0	0	0	0	0	0	0	0	0
St. duodecimata	0	1	1	0	0	0	0	0	0	0	0
H. rendalense	7	9	0	0	0	0	0	0	0	0	0
H. near dogieli }	0	0	0	0	0	0	0	0	0	0	0
H. crassum	0	0	0	0	0	0	0	1	0	0	0
N. vernum s.l.	29	31	37	45	10	0	0	1	1	0	0
E. aureum	0	0	0	0	0	0	0	1	3	0	0
S. poelleri	0	0	5	0	0	0	0	1	0	0	0
Strip #2 @ 20 m											
G. brachiata	2	0	0	0	0	0	0	0	0	0	0
St. duodecimata	0	3	7	1	0	0	0	0	0	0	0
H. rendalense	6	2	4	6	10	0	0	0	0	0	0
H. near dogieli }	0	0	0	0	0	0	0	0	0	0	0
H. crassum	0	0	0	0	0	0	0	0	0	0	0
N. vernum s.l.	49	37	44	20	49	0	0	0	0	0	0
E. aureum	0	0	0	0	0	0	0	0	0	0	0
S. noelleri	0	0	0	0	5	0	0	0	0	0	0
Strip #3 @ 30 m											
G. brachiata	3	2	0	0	0	0	0	0	0	0	0
St. duodecimata	2	1	1	2	0	0	0	0	0	0	0
H. rendalense	8	18	0	13	18	0	0	0	0	0	0
H. near dogieli }	0	0	0	0	0	0	0	0	0	0	0
H. crassum	0	0	0	0	0	0	0	0	0	1	0
N. vernum s.l.	36	16	18	41	38	0	24	3	1	2	0
E. aureum	0	0	0	5	9	0	0	2	3	13	0
S. noelleri	0	0	0	4	3	0	1	6	0	1	1

Table 16 . Number of simuliid larvae collected on rubber strips, each 25 cm by 1.2 cm, floated in stream #14 at 10 m, 20 m and 30 m from Renådalen bog, June and July 1980.

Strip # & Taxon	June							July			
	5	8	11	14	18	21	26	6	14	22	31
Strip #1 @ 10 m											
G. brachiata	1	0	0	0	0	0	0	0	0	0	0
St. duodecimata	1	0	0	0	2	0	0	0	0	0	0
H. rendalense	1	0	7	7	5	0	1	0	0	0	0
H. near dogieli}											
H. crassum	0	0	0	0	0	0	0	2	0	0	0
N vernum s.l.	17	3	2	14	11	0	0	6	0	0	0
E. aureum	0	0	0	0	4	0	0	0	2	0	0
S. noelleri	0	0	0	4	0	0	1	4	0	0	0
Strip #2 @ 20 m											
G. brachiata	0	0	0	0	0	0	0	0	0	0	0
St. duodecimata	0	3	3	7	0	0	0	0	0	0	0
H. rendalense	3	2	5	27	20	0	0	0	0	0	0
H. near dogieli}											
H. crassum	0	0	0	0	0	0	0	11	1	0	0
N. vernum s.l.	6	15	16	32	3	0	8	7	0	0	0
E. aureum	0	0	0	0	4	0	3	50	4	1	0
S. noelleri	0	0	0	0	0	0	0	6	0	0	0
Strip #3 @ 30 m											
G. brachiata	1	1	0	0	0	0	0	0	0	0	0
St. duodecimata	1	2	1	0	0	0	0	0	0	0	0
H. rendalense	1	10	6	6	13	0	1	2	0	0	0
H. near dogieli}											
H. crassum	0	0	0	0	0	0	0	0	0	0	0
N. vernum s.l.	23	26	23	7	13	0	4	3	0	0	0
E. aureum	0	0	0	0	11	0	1	3	10	1	0
S. noelleri	0	0	0	0	0	0	0	0	0	0	0

Figs. 7 to 11 Spatial and seasonal distribution of simuliid larvae
(third to last instars) at the edge of Renådalen bog
and 10 m, 20 m and 30 m downstream from the bog.
Larval density at each point is based on the average
number of larvae collected on six strips in the bog
and two strips, one each in stream 13 and 14, at
each distance downstream (see Tables 14, 15 and 16).
Note, the absence of larvae on 21 June is related
to the five days of rainfall that flooded the bog
and streams (see text).

Fig. 7 _H. rendalense_ and _H._ near _dogieli_ larvae combined.

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H. rendalense s.l.

Fig. 7
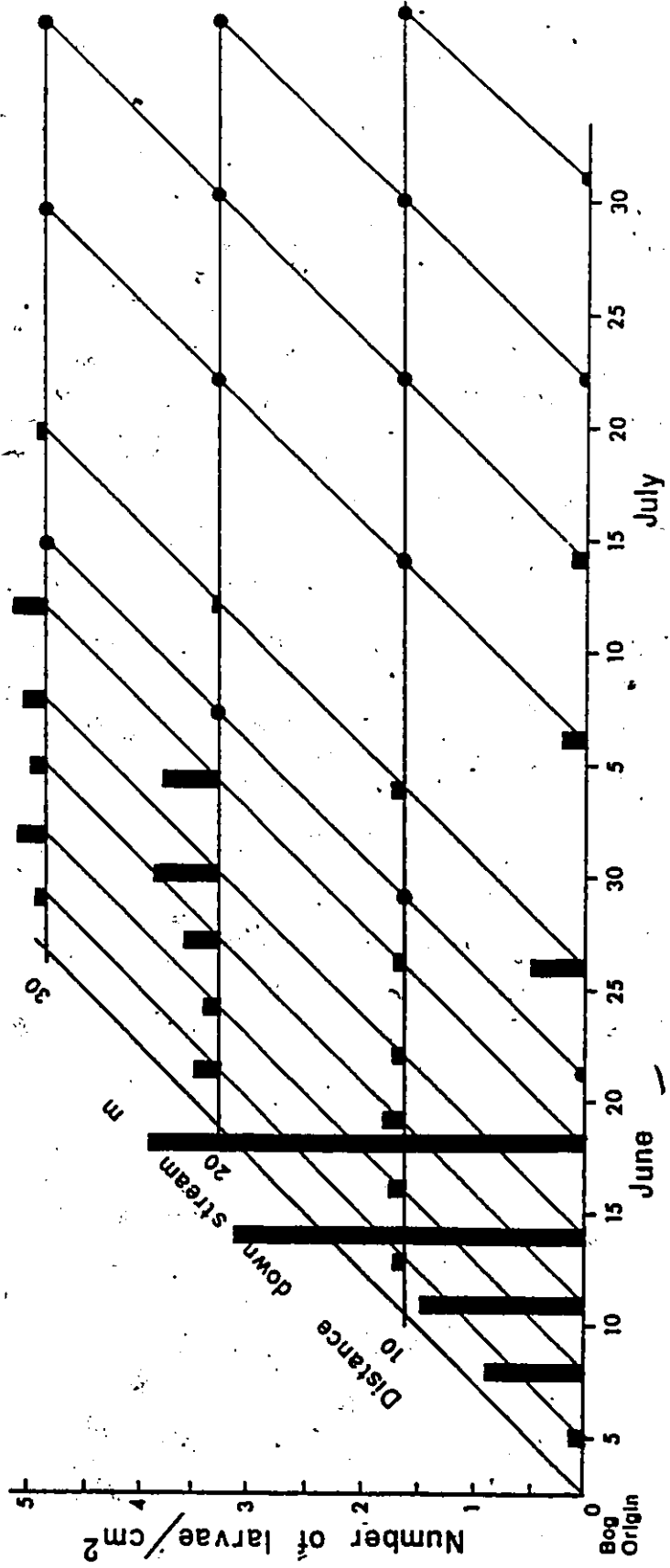
Fig. 8   Spatial and seasonal distribution of _E. vernum_ s.l. larvae.

Fig. 8

E. vernum s.l.
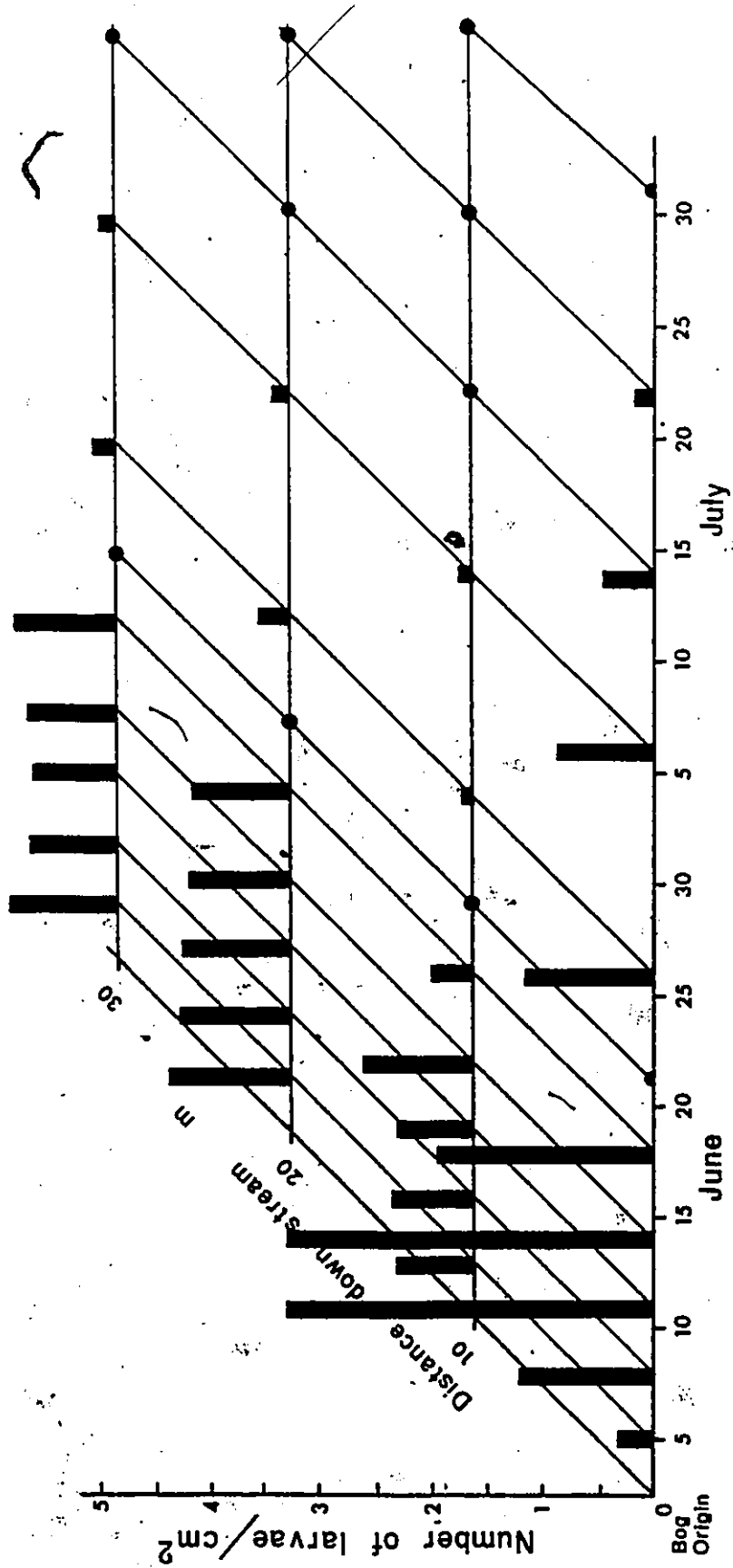
Fig. 9 Spatial and seasonal distribution of <u>St. duodecimata</u> larvae.

Fig. 9

St. duodecimata

174
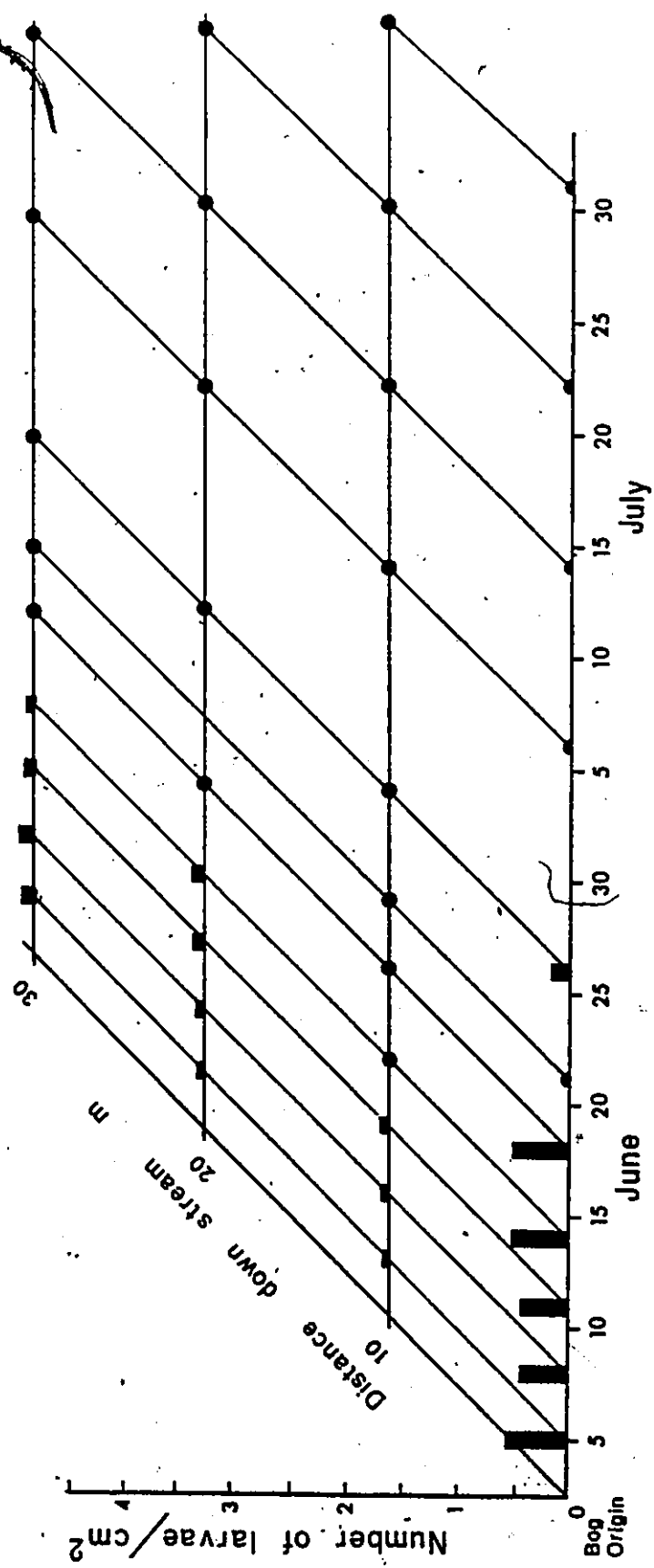
Fig. 10 Spatial and seasonal distribution of E. aureum larvae.

E. aureum

Fig. 10

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Number of larvae/ cm²

4
3
2
1
0

Bog Origin

30
20
10

Distance down stream   m

5   10   15   20   30   5   10   15   20   25   30

June   July
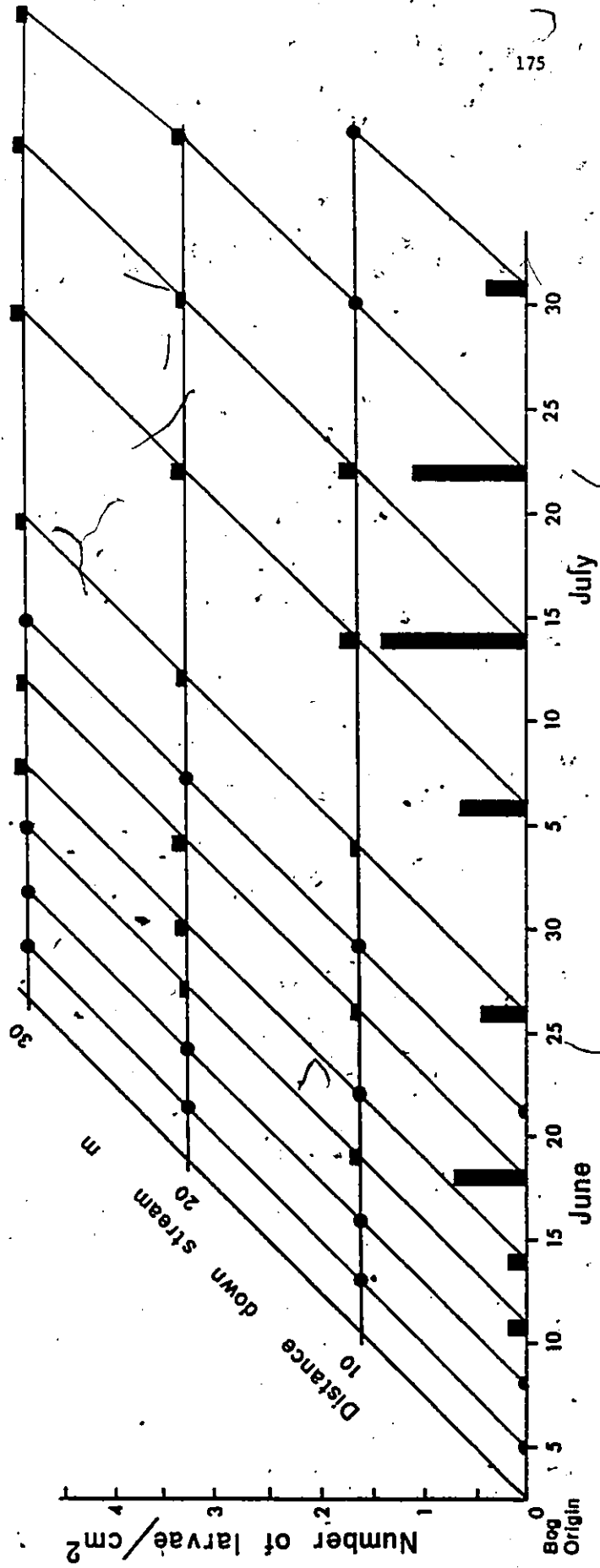
Fig. 11   Spatial and seasonal distribution of _S. noelleri_ larvae.

Fig. 11

S. nölleri

Number of larvae/cm^2

Distance down stream m

Bog Origin

June   July
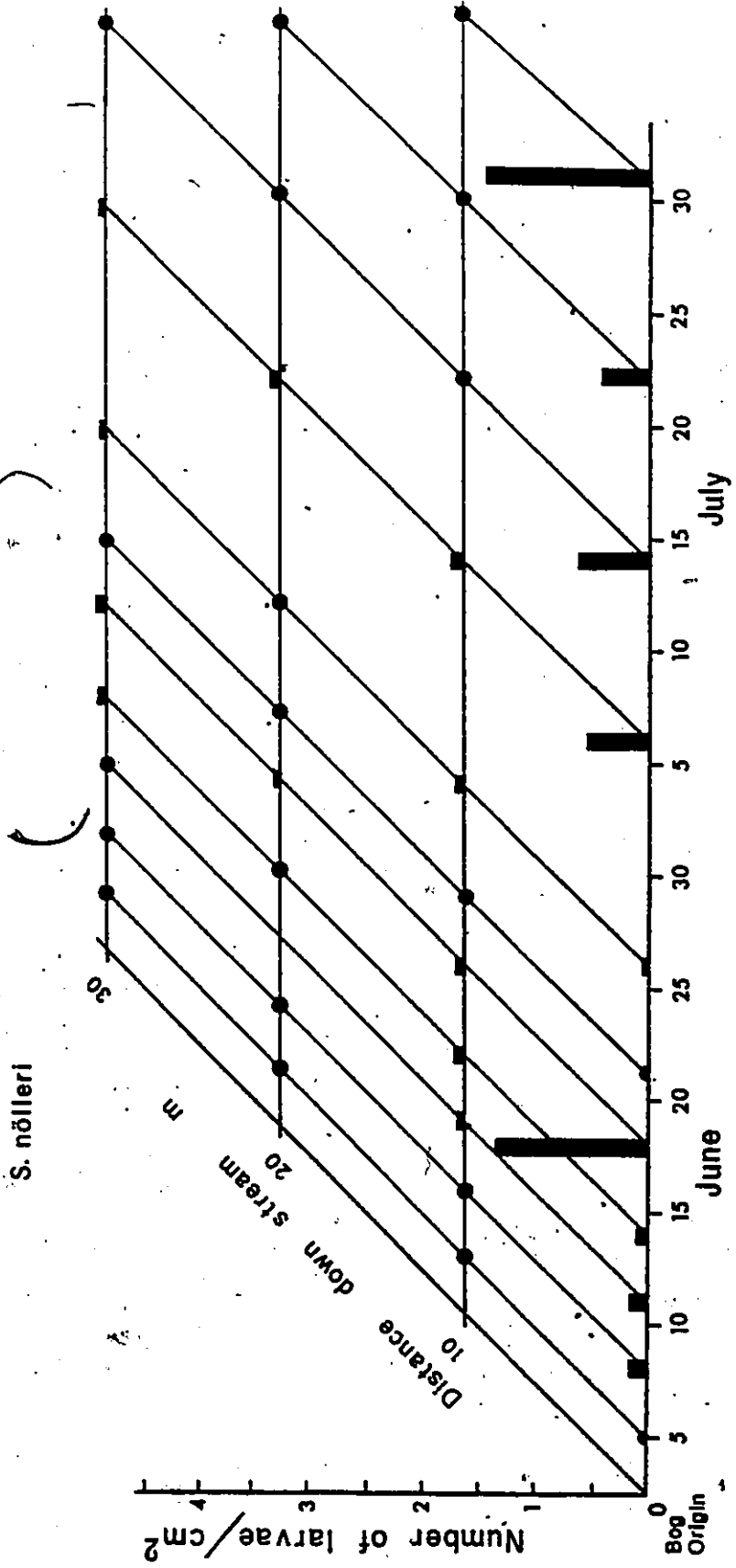
This reflects the higher tendency of <u>E. vernum</u> larvae to drift from the bog (see Table 13) and their relatively greater tolerance for higher water currents (see next section).

Current Preference

The relative abundance of larvae on strips exposed in different water currents at the edge of Renådalen bog are reported in Tables 17 and 18 and illustrated in Figs. 12, 13, 14 and 15. In general, species of <u>Eusimulium</u> s.l. showed similar preferences, with peak abundance occurring in water currents of about 20 cm/sec. In particular, 23% of larvae of <u>H. rendalense</u> and <u>H.</u> near <u>dogieli</u> combined occurred in currents of 0 to 10 cm/sec., although no larvae were found filter-feeding in completely stationary water. The lower proportion of larvae of both <u>E. vernum</u> s.l. and <u>E. aureum</u> in currents between 0 and 25 cm/sec. reflects their tolerance for a wider range in water current. About 25% of <u>E. vernum</u> and 23% of <u>E. aureum</u> larvae occurred in currents of 50 to 60 cm/sec. compared to a negligible 0.5% of <u>Hellichiella</u> larvae. By contrast, larvae of <u>S. noelleri</u> showed a specifically different current preference. Larval density of this species was directly related to water current; only about 2% occurred in currents of 0 to 10 cm/sec., about 23% in 15 to 25 cm/sec. and about 75% in 50 to 60 cm/sec. This requirement for high water current restricted <u>S. noelleri</u> larvae at specific sites at the edge of the bog and drainage streams where relatively fewer larvae of other species occurred. Although specific measurements of current preferences between <u>H. rendalense</u> and <u>H.</u> near <u>dogieli</u> larvae were not made, it is notable that the higher mean number of primary head fan rays in larvae of <u>H.</u> near <u>dogieli</u> (see Chapter 2) may reflect their adaptation for more efficient filter-feeding in mid bog seepages where

water currents are generally lower than at the bog's edge.

Thus, current preferences may reflect, in general, the distribution of larvae of sympatric species in particular microhabitats in the bog biotope. Larvae of _Hellichiella_ species, with lowest current preferences, develop specifically in the bog, and occur in first order streams draining the bog only secondarily as larvae drift from their primary habitat. Larvae of _E. vernum_ s.l., with a higher tolerance for water current, occur at the edge of the bog and actively migrate to streams draining the bog. _E. aureum_ and _S. noelleri_ are also sympatric but both develop about one month later than the other two groups of species; their larvae are separated in microhabitats with water currents optimal for the species. Several workers have reported that water speed is one of the most important ecological factors influencing the distribution and abundance of simuliid larvae and pupae, mainly because water current carries food, supplies oxygen and help larvae migrate to more suitable sites in their habitat. (Wu 1931; Dalmat 1955; Carlsson 1962, 1967; Usova 1961; Hynes 1970; Colbo and Moorhouse 1978; Gersabeck and Merritt 1979; Mohsen and Mulla 1982). Therefore, factors that minimize competition for food and space among aquatic stages of _Hellichiella_ and other bog species include 1) microhabitat specificity related to water current preferences of larvae, and 2) differences is seasonal development.

For additional evidence of seasonal succession of bog simuliids, it would have been desirable to analyse the emergence cage collections of adults from Renådalen. However, the data from larval and pupal collections presented in this thesis give sufficient evidence to show that abundance of different species depends on microhabitat and seasonal development.

Table 17. Abundance of larvae (third to last instar) of H. rendalense s.l. and N. vernum s.l. collected on 25 x 1.2 cm² strips* in various water currents at the edge of Renådalen bog. (See Figs. 12 and 13).

water current & collection #	rendalense and near dogieli									vernum s.l.								
	8-VI No.	%	11-VI No.	%	14-VI No.	%	18-VI No.	%	$\bar{x}$ ± Sx	8-VI No.	%	11-VI No.	%	14-VI No.	%	18-VI No.	%	$\bar{x}$ ± Sx
0-5 cm/sec 1	1	3.0	0	0.0	53	23.2	22	1.6	6.9 ± 4	2	4.2	0	0.0	5	1.9	29	14.0	5.0 ± 3
5-10 cm/sec 1	0		18		52		49			0		3		33		24		
2			33		20									52				
$\bar{x}$		0.0	25	23.8	36	16.1		25.8	16.4 ± 6		0.0	3	2.2	42	15.7		11.7	7.3 ± 4
15-25 cm/sec 1	24		58		113		145			49		123		109		64		
2	22		83		162		96			48		175		150		43		
3	52		62				106			40		11				64		
$\bar{x}$	33	97.0	68	64.8	136	60.7	119	62.6	71.3 ± 9	46	95.8	103	75.7	130	48.7	57	28.0	62.5 ± 15
50-60 cm/sec 1	0	0.0	2	1.9	0	0.0	0	0.0	0.5	0	0	30	22.1	90	33.7	95	46.3	24.7 ± 10

*These collections are derived from Table 14 and correspond to dates when water current speeds were recorded.

Table 18. Abundance of larvae (third to last instars) of E. aureum and S. noelleri collected on 25 x 1.2 cm^2 strips* in various water currents at the edge of Renådalen bog. (See Figs. 14 and 15).

water current & collection #	aureum							noelleri						
	6-VII		14-VII		22-VII		$\bar{x}$ ± Sx	18-VI		6-VII		22-VII		$\bar{x}$ ± Sx
	No.	%	No.	%	No.	%		No.	%	No.	%	No.	%	
0-5 cm/sec														
1	0	0.0	6	8.1	0	0.0	2.7 ± 2	0	0.0	0	0.0	0	0.0	0.0
5-10 cm/sec														
1	6	15.8	19	25.7	0	0.0	13.8 ± 7	14	6.3	0	0.0	0	0.0	2.1 ± 2
15-25 cm/sec														
1	12		54		13			0		7		32		
2	25		58		60			4		0		3		
3	14		35		43									
$\bar{x}$	17	44.7	49	66.2	32	71.1	61.1 ± 8	2	0.5	4	16.0	17	53.1	23.2 ± 15
50-60 cm/sec	15	39.5	0	0.0	13	28.9	22.8 ± 12	206	93.2	22	84.0	15	46.9	74.7 ± 14

* These collections are derived from Table 14 and correspond to dates when water current speeds were record.

Figs. 12 and 13   Abundance of larvae (third to last instars)
                  of H. rendalense and H. near dogieli combined
                  (Fig. 12) and E. vernum s.l. (Fig. 13) relative
                  to water current in Renådalen bog. (See
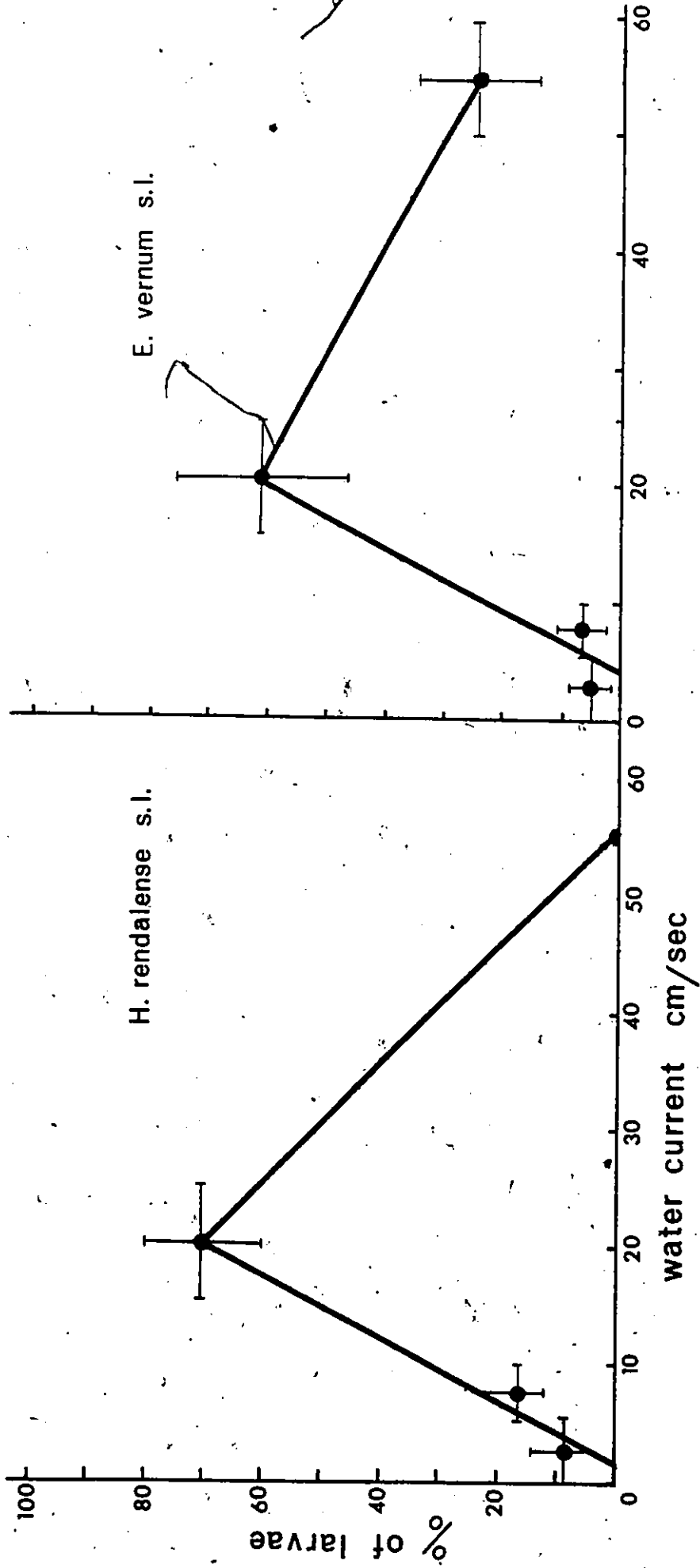   Table 17)

Fig. 13

E. vernum s.l.

Fig. 12

H. rendalense s.l.

water current cm/sec

% of larvae

Figs. 14 and 15   Abundance of larvae (third to last instars)
of _E. aureum_ (Fig. 14) and _S. noelleri_ (Fig. 15)
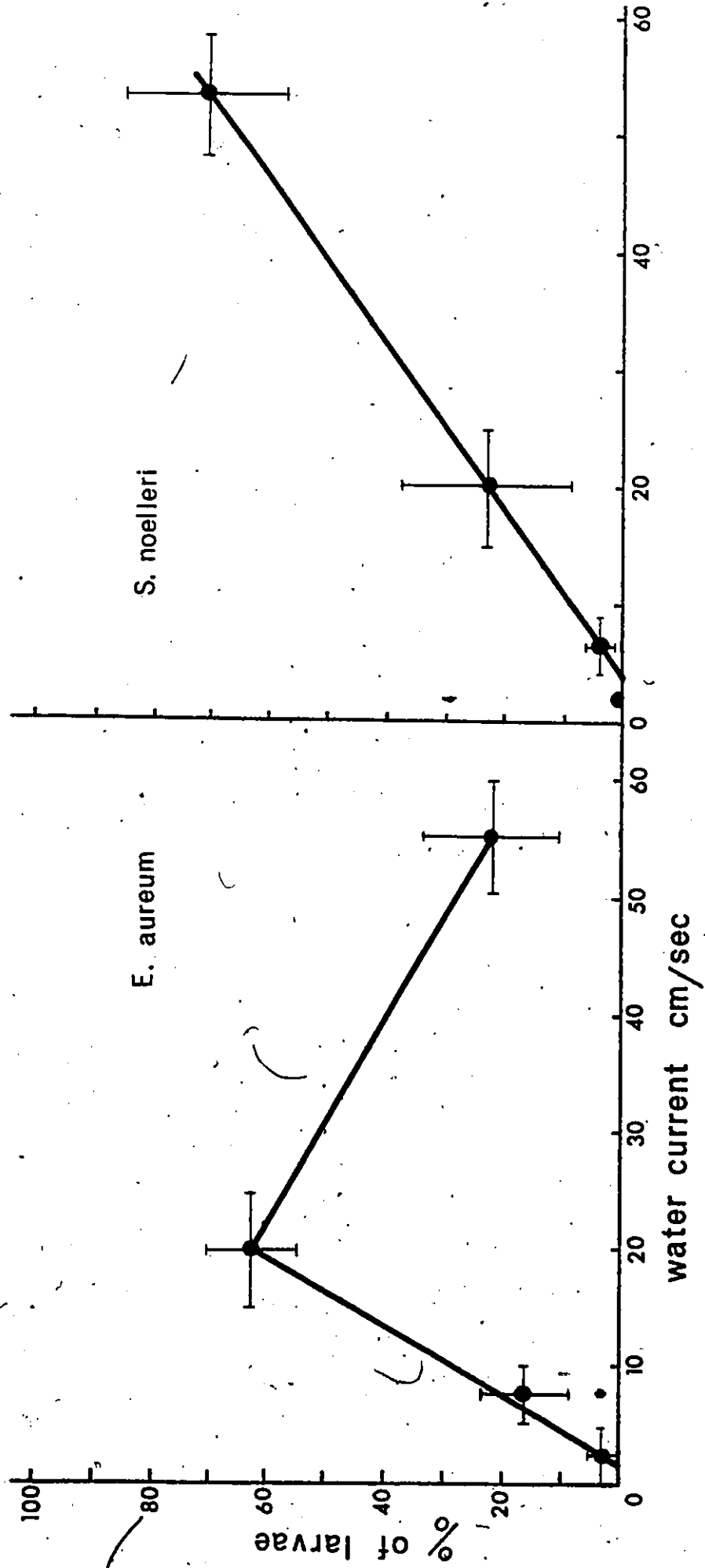relative to water current in Renadalen bog.
(See Table 18)

Fig. 15

Fig. 14

S. noelleri

E. aureum

water current cm/sec

% of larvae

Geographical Distribution

Occurrence of _Hellichiella_ spp. in Ontario and other Regions.

The relative abundance of larval simuliids in bog-like habitats in southern Ontario is reported in Table 19. Two of the 16 sites examined are shown in Figs. 30 and 31. These sites are described in terms of water quality, reported in Table 20, and type of vegetation for two typical sites, reported in Table 21. The 16 sites examined for _Hellichiella_ spp. consist of small marshes with surface water draining through seepages (5-20 cm deep and 30-50 cm wide) containing simuliid larvae in water current of 1 to 30 cm/sec. These sites are generally fed by snow melt water and, in the absence of recurrent rains, normally become dry before early summer. In May these marshes are focal breeding sites of _Aedes_ (_Ochlerotatus_) mosquitoes and some species of _Anopheles_ in summer after reflooding by rains. During May overwintered females of _Anopheles earlei_ Walker were frequently netted while attracted to the author at these sites. These wetland habitats where _Hellichiella_ and other _Eusimulium_ species were found, are typically small (10 to 50 m^2) in southern Ontario, often appearing as roadside drainages covered with emergent vegetation. Unlike the more extensive bog habitats in higher latitudes, as in Norway, these southern miniature wetlands generally lack _Sphagnum_ mosses. Notable differences in water quality of sites in southern from those of central Ontario were in pH, conductivity.and concentration of cations (Table 20). Water samples from the Bruce Trail (Hamilton), Bruce Peninsula and Caledon had nearly neutral pH, and relatively higher conductivity and cation concentration, reflecting their location on limestone region of southern Ontario. In the other sites in Muskoka and Algonquin Park, on the Precambrian shield, the water is typically acidic and conductivity

and concentration of cations correspondingly lower. Water samples of rivers from Algonquin Park were included (Table 20) as examples of habitats with water quality similar to bogs in this region but lacking species of _Hellichiella_.

The 14 species of simuliids found in these bog seepages (Table 19) include H. _anatinum_, H. _innocens_, H. _excisum_ and H. _rivuli_. These _Hellichiella_ species occurred in relatively low concentration in 13 of the 16 sites examined. H. _anatinum_ was found exclusively on the Precambrian shield north of Muskoka and comprised 2.0% of the 13 species from that region; H. _innocens_ and H. _excisum_ occurred primarily in the limestone region south of Muskoka and comprised about 3% of 10 species, while H. _rivuli_ comprised about 2% of the species south and about 6% north of Muskoka.

The influence, if any, of water chemistry on the distribution of _Hellichiella_ species in bog habitats remains to be determined. The ubiquitous occurrence of _Sphagnum_ mosses in bog habitats of these species in Norway is significant. These plants not only regulate the hydrology of these bogs by their great capacity to hold water, but Sphagna have also a high capacity to extract small quantities of nutrients in the rain that falls on them, giving up hydrogen ions in exchange. Thus, they actively acidify their habitat (Walker 1970, in Barber 1981).

However, the dominant factors which reflect the distribution of these species are biotic and physical, as in other simuliids (Ross and Merritt 1978; Carlsson 1972; Usova 1961; Colbo and Moorhouse 1978).

Low water volume and current are the most obvious factors associated with immature stages of _Hellichiella_ in Norway. Additional observations in Ontario indicate that similar species are limited to

bog seepages also by these two factors. In England H. latipes is
confined also to shallow marshy seepages with sluggish water current
(Fig. 32 and Table 22). This type of habitat is similar to that reported
by Doby et al. 1958 for this species in France. They found fortuitously
larvae of H. latipes (their subexcisum) in nearly standing water,
associated with mosquito larvae of Aedes (Ochlerotatus) spp., Culex spp.,
Theobaldia spp. and Anopheles maculipennis Meigen. Additionally, larvae
and pupae of H. saccai were initially found fortuitously among decaying
vegetation in nearly standing water, by Prof. G. Sacca, during an
ecological study of residual Anopheline mosquitoes in the Agro Pontino
region of Italy (Rivosecchi 1967, 1978). Immature stages of H. dogieli
have been reported to occur in streams with exceptionally faster water
current of 30-50 cm/sec, in north-eastern Europe (Rubtsov 1956; Usova 1961).
However, this may reflect collection of this species in drainage streams,
as they were found on stones and grass, rather than from bog seepages.

It should be noted that Hellichiella species are not unique
among simuliids in their requirements for low water current. Most species
of Eusimulium, Greniera and Parahelodon also occur in shallow seepages with
low water current, as observed during this study and by other workers.
Species of the E. aureum group are generally adapted to seepages with
nearly standing water. One of these species, E. paludiculum Rivosecchi,
bears witness to its adaptation to marshy habitats (Rivosecchi 1978).
In the Ethiopian region S. ruficorne Maq. also occurs in shallow streams
with slow moving water (Van Someren 1944; Freeman and DeMeillon 1953;
Crosskey 1960, 1969).

However, the significance of adaptation of Hellichiella species

to slow water current is related to the distribution of certain species,
such as H. rendalense s.l. and H. anatinum, in extensive sedge-Sphagnum
bogs in the Boreal region which are generally unknown as primary habitat
of simuliids. Studies on distribution of simuliids in the subarctic and
Boreal regions do not refer specifically to bogs as habitats of these
insects (Rubtsov 1959-64, 1973; Usova 1961; Shewell 1958; Downes 1965;
Peterson 1970). Twinn (1936) shows the habitat of H. excisum (his
subexcisum) as a shallow stream, about 1 m wide, draining a raised bog,
but apparently was unaware of the bog as a potential breeding habitat.
These wetlands cover extensive areas in this region (Fig. 33) where
annual precipitation exceeds evaporation and the flat land topography
retards water drainage (Sjörs 1961; P'yavchenko 1958; Romanov 1961;
Radforth and Brawner 1977; Jeglum et al. 1979). These rain-fed or
ombrotrophic bogs in the U.S.S.R. cover an area of about 71.4 million
acres (m.a.), equivalent to about 70% of the world's total; in Canada
9.6 m.a., Finland 9.5 m.a., Sweden 6.0 m.a., Norway 2.1 m.a. and south
central Europe the remainder of about 2 m.a. (Romanov 1961). The extent
of colonization of these areas by Hellichiella spp. can be deduced from
few available collection records listed in Table 23 and shown in Figs.
34 to 39.

Of particular significance is the distribution of H. anatinum
(Fig. 36) which is clearly centered essentially around the Hudson Bay
lowlands where the largest area of Sphagnum bogs occurs in North America.
This is also the habitat of Opinaga new cytotype (see Chapter 1). In his
ecological study of simuliids of Quebec, C. Back (pers. comm.) found high

concentrations of H. anatinum larvae in certain bog sites east of James Bay. One collection from Opinaga in May 29, 1978 consisted of 66% H. anatinum and 33% N. vernum; this proportion is similar to that of related species from bogs in Rendalen. This and other distribution records of Hellichiella species from Murmansk, Ural-Ob River basin and Novosibirsk Siberian wetlands (Rubtsov 1959-64, 1973; Usova 1961; Patrusheva 1962, 1971) indicate that the ombrotrophic peat bogs of the Boreal region contains the largest concentration of Hellichiella species. South of this region, in both Nearctic and Palaearctic, most species occur in small isolated habitats which, due to drier climate, are mere vestiges at the fringe of the more extensive bogs in higher latitudes.

Distribution and Habitat Specificity Related to Host Specificity

In addition to being habitat specific, certain species of Hellichiella, whose feeding habit of females is known, are also host-specific, feeding either on woodland birds or aquatic birds (Bennett 1960; Anderson and DeFoliart 1961; Golini 1975; Herman et al. 1975). In South-Central Ontario, Michigan and Eastern U.S.A. species of Hellichiella known to feed on and transmit Leucocytozoon simondi to ducks and geese are primarily H. anatinum (Bennett 1960; Fallis and Smith 1964; Fallis and Bennett 1966; Anderson 1968), H. innocens (Herman et al. 1975; Tarshis, pers. comm.) and H. congareenarum (Stone 1964; Stone and Snoddy 1969). The incidence of females of these species feeding on these birds is generally low at these latitudes (Fallis and others pers. comm.) compared to the much larger number at higher latitudes (Golini 1975). This is attributed to the fact that both simuliids and hosts are more

numerous in the Boreal region and reproduce in the same extensive bog habitats. In Rendalen, Åsmyrtjörna lakelet on the upper reaches of the bog (Figs. 1 and 2) contains in the summer flocks of reproducing ducks and other aquatic birds during the emergence period of H. rendalense s.1. Birds seen and known to nest in this bog (A. Kiaer, pers. comm.) include ducks such as the golden-eye Bucephala clangula clangula, the osprey Pandion haliatus haliatus and waders such as Charadinus apricarius, Calidrius alpina and Tringa nebularis.

The occurrence of L. simondi in domestic and wild ducks in this region (Eide et al. 1969; Eide and Fallis 1972) shows that these simuliids feed on wild aquatic birds in this region as they do on domestic ducks (Golini 1975).

The open wetlands of the Boreal region of North American are the primary reproductive habitats and summer feeding grounds of flocks of ducks and geese, such as Canada goose (Branta canadensis) (Fig. 40) black duck (Anas rubripes) (Fig. 41) and common golden-eye (Bucephala clangula americana) (Fig. 42) (Bellrose 1976). This breeding range corresponds with the known distribution of H. anatinum (Fig. 35) including H. innocens and Opinaga sibling in the bogs around Hudson Bay lowlands and of H. minus (Fig. 39) in the west. The first two of these simuliid species are known indirectly to feed on the Anseriformes of this region by the occurrence of L. simondi in the young of these birds (Laird and Bennett 1970; Bennett and MacInnes 1972). Interestingly, Downes (1965) indicates that simuliids in the tundra are adapted, as adults, to fly close to the ground to minimize the resistance of wind. In fact, low flying is inherent also in the host-seeking behaviour of duck-feeding

simuliids, such as <u>H. anatinum</u> and <u>H. rendalense</u> s.1. (Fallis and

Bennett 1966; Golini 1975). Thus in the open Boreal wetlands this low

flight imparts a double advantage in these ornithophilic simuliids.

Conversely, the distribution of the autogenous <u>Hellichiella</u> species,

<u>H. crassum</u> and <u>H. baffinense</u>, in subarctic wetlands also relects their

adaptation to this biotope by their loss of the host-seeking flight.

      Furthermore, the distribution of <u>Hellichiella</u> spp. is linked

also with the migration routes and winter feeding grounds of various

aquatic hosts. Particularly, the distribution of <u>H. congareenarum</u>

along the south-eastern states (Fig. 37) and that of <u>H. minus</u> in the

west (Fig. 39) clearly reflects the migration routes and winter feeding

ranges of several species of aquatic birds (Belbrose 1976). Thus, the

low incidence of <u>Hellichiella</u> spp. in southern Ontario is related not

only to the fewer suitable breeding habitats but also to fewer hosts

which migrate from or briefly stop in transit in this region. The comments

of Rivosecchi (in litt.) are notable. He interprets the occurrence of

<u>H. saccai</u> in the Agro Pontino region as an isolated case of a habitat

linked with the migration routes of aquatic birds whose normal breeding

grounds are in northern Europe and winter feeding habitats in North Africa.

Since avian hosts of <u>H. saccai</u> and <u>H. latipes</u> are not known, their geo-

graphical distribution, and also that of <u>H. rendalense</u> s.1., in relation

to their hosts remains to be determined. However, the occurrence of

<u>H. simondi</u> in wild ducks, <u>Anas</u> <u>crecca</u> L. and <u>A. platyrhynchos</u> L., in Rendalen

(Eide et al. 1969) indicates not only that these birds are normal hosts of

<u>Hellichiella</u> species in this region, but also that the distribution of

<u>Hellichiella</u> spp. in the Palaearctic is also linked to that of their hosts

and breeding habitats.

The Palustrine Biotope, the Unifying Factor

in the Epizootiology of Haemosporidia

The association of <u>Hellichiella</u> species and other simuliids
with bog habitats brings these flies closer ecologically to mosquitoes
and other biting flies which normally breed in bogs and marshes. Particularly,
certain species of Anopheline mosquitoes, such as <u>Anopheles freeborni</u> Aitken,
are known to breed in marshes with some water current (Bates 1954; James and
Harwood 1969). Species of this subfamily of mosquitoes are also known vectors
of <u>Plasmodium</u>. The main vector of malaria in the Philippines, <u>A</u>. <u>minimus</u>
Theobald, breeds in small flowing streams in the foothills (Russell 1932,
in James and Harwood 1969). Therefore, certain species of both simuliids and
culicids are adapted in the ecotone between lentic and lotic habitats.
Significantly, these nematocerous flies not only breed in similar habitats,
but they are also capable of transmitting haematozoa parasites: <u>Leucocytozoon</u>
spp. by simuliids, primarily <u>Hellichiella</u> spp. (Fallis and Bennett 1960;
Anderson 1968; Eide and Fallis 1972; Herman et al. 1975; Golini 1975)
and <u>Plasmodium</u> spp. by <u>Anopheles</u> spp. (Jucci 1952; James and Harwood 1969).
In addition, some species of biting midges (Ceratopogonidae),which also breed
in bog-like habitats and shallow edges of streams, are vectors of <u>Akiba</u>
and <u>Parahaemoproteus</u> (Fallis and Bennett 1960; Bennett et al. 1965). The
ability of these insects to transmit these blood parasites indicates that
the breeding habitat may be the unifying ecological factor in the epizoo-
tiology of haemosporidia. This suggests the the corollary that haemosporidia
parasites evolved in the palustrine biotope in association with nematocerous
flies, through a monoxenic Coccidia ancestor, some of which became vectors
to vertebrate hosts.

Table 19. Relative abundance of simuliid species based on number of larvae from some bog-like habitats in southern and central Ontario expected to contain <u>Hellichiella</u> spp., 23 April to 20 May 1980.

Taxon	Southern					Central				
	Hamilton Bruce Trail	Bruce Penins.	Caledon	Total	%	Algonquin Park	Muskoka	New Griffin Huntsville	Total	%
Cnephia										
Cn. dacotensis			1093	1093	53.1		2	60	62	3.4
Gren. denaria						1			1	0
Steg. mutata	296	2		298	14.5	232	17		249	13.6
Eusimulium										
E. aureum		1		1	0	21	12	16	49	2.7
Hellichiella										
anatinum						25		12	37	2.0
excisum			71	71	3.4			1	1	0
rivuli	44			44	2.1	32	5	76	113	6.2
Nevermannia										
croxtoni		163		163	7.9	90			90	4.9
vernum		135		136	6.6	196	103	191	490	26.8
Prosimulium										
Parahel. gibsoni			34	34	1.7	230			230	12.6
decemarticulatum						93		20	113	6.2
Simulium										
S. tuberosum							8		8	0.2
S. venustum	210	135	11	355	17.2	220		275	495	27.1
				2059					1827	
Number of collections	4	3	2	9		6	3	2	11	
Number of Bogs	1	3	1	5		6	3	1	10	

H. innocens   43   from Valens marsh, Dundas, 7 May 1981

N. croxtoni   369

N. vernum   61

Table 20. Water quality parameters of certain bog and stream habitats of Simuliidae in Southern Ontario during May 1980.

mg/l (except PO_4^{3-} in 10^{-3} mg/l)

(Hamilton)	°C	pH	Cond. μS/cm	HCO_3^-	DOC	SiO_2	Cl^-	NO_3^-	SO_4^{2-}	PO_4^{3-}	Na^+	K^+	Ca^{2+}	Mg^{2+}	Fe^{3+}	O_2	flow l/min
BRUCE TRAIL																	
Bog max.	14.4	7.5	650	305	5.0	0.11	9.0	0.12	22.0	10.8	30.0	3.25	91.0	16.0	0.09	8.5	~100
min.	8.5	7.2	590	244	3.4	0.05	2.2	0.00	13.0	0.0	14.5	2.60	73.0	4.5	0.02	8.1	0
(n=4) X̄	11.5	7.4	630	268	4.2	0.08	4.4	0.05	16.0	3.6	15.5	2.83	84.0	15.5	0.06	8.3	~10
BRUCE PEN.																	
max.	15.3	8.4	340	287	10.2	0.26	0.8	0.18	9.0	44.0	8.2	2.90	51.0	31.0	0.22	10.0	~40
min.	7.9	7.2	230	207	2.1	0.08	0.0	0.04	1.5	21.6	0.7	0.15	25.0	2.0	0.03	6.4	0
4 Bogs X̄	11.2	7.6	303	256	7.8	0.15	0.4	0.21	4.1	28.5	3.8	1.00	32.3	19.0	0.09	7.7	~15
OAKRDON Bog	22.2	6.5	560	281	6.9	0.02	3.0	0.52	2.5	0.0	27.0	0.80	63.0	20.5	0.02	-	~5
MUSKOKA																	
Brooks max.	11.0	5.6	88.0	18.3	4.3	0.16	8.0	0.18	5.5	4.0	17.0	1.35	11.0	2.0	0.28	9.7	~20
min.	9.0	4.8	37.0	12.2	2.3	0.13	0.1	0.04	2.5	0.0	1.1	0.30	4.8	0.4	0.01	8.9	0
(n=4) X̄	10.0	5.3	54.7	15.3	3.4	0.15	4.7	0.10	4.0	1.5	8.6	0.80	7.5	1.1	0.19	9.2	~5
GRIFFIN Bog	9.7	5.5	45.0	18.3	18.1	0.15	0.1	0.04	4.0	7.6	2.0	0.15	5.6	0.8	0.66	8.8	~5
ALGONQUIN PK.																	
max.	11.0	5.6	85.0	30.5	12.6	0.13	0.6	0.64	5.5	6.0	2.8	0.85	13.6	1.30	0.18	-	~100
min.	7.1	5.2	33.5	6.1	2.8	0.11	0.0	0.06	3.5	2.4	1.3	0.35	3.8	0.8	0.04	-	~5
4 Bogs X̄	8.5	5.4	63.7	18.1	8.6	0.12	0.3	0.32	4.3	4.0	1.8	0.64	8.9	1.1	0.12	-	~20
MADAWASKA R#1	8.1	5.2	29.0	3.7	9.1	0.02	0.0	0.00	4.0	7.2	1.5	0.90	5.8	1.5	0.14	-	>10^4
MADAWASKA R#2	9.4	5.5	47.0	30.5	5.6	0.19	2.3	0.08	2.5	4.4	1.5	0.65	10.0	0.9	0.08	-	>10^4
OXTONGUE R	9.4	5.3	44.5	6.1	4.6	0.08	0.0	0.20	3.5	17.6	2.1	0.55	5.2	1.2	0.06	-	>10^4
COSTELLO CR	11.0	5.1	44.0	7.3	5.8	0.08	0.5	0.08	5.0	2.0	3.6	0.55	5.2	1.2	0.09	-	>10^3

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Table 21. Vegetation occurring in two small bogs in southern Ontario during late spring and summer where _Hellichiella_ spp. were collected.

Bog #1. New Griffin, Hwy #11, ca. 15 Km south of Huntsville

Equisetaceae
  Equisetum arvense

Alismataceae
  Sagittaria latifolia

Balsaminaceae
  Impatiens capensis

Compositae
  Aster simplex
  Bidens cernua
  Solidago graminifolia

Cyperaceae
  Carex lurida

Gramineae
  Glyceria canadensis
  Leersia oryzoides
  Phalaris arundinaceae

Juncaceae
  Juncus effusus

Labiatae
  Lycopus virginicus

Leguminosae
  Lotus corniculatus

Myricaceae
  Myrica gale

Polygonaceae
  Polygonum hydropiper

Rubiaceae
  Galium boreale
  G. tinctorium

Sparganiaceae
  Sparganium chlorocarpum

Shrubs and Trees
  Betula sp.
  Salix sp.

Table 21. (cont.)

Bog #2. Bruce Trail between Hamilton and Ancaster

Equisetaceae
  Equisetum arvense

Cyperaceae
  Carex cristatella
  C. retrosa
  Eleocharis palustris
  Scirpus atrovirens

Gramineae
  Elymus virginicus
  Glyceria canadensis
  Phalaris arundinacea
  Phleum pratense

Compositae
  Cardus acanthoides
  Solidago graminifolia

Lemnaceae
  Lemna minor

Onagraceae
  Epibolium palustre

Ranunculaceae
  Caltha palustre

Typhaceae
  Typha latifolia
Shrubs and Trees
  Betula sp.
  Salix sp.

Table 22. Some more common vegetation from the breeding habitat of

Hellichiella latipes from Knebworth, Sussex, England in mid August 1980.

Species	Common Name
Dioscoraceae	
Tamus communis L.	Black Briony
Gramineae	
Phragmites sp.	Grass
Lemnaceae	
Lemna minor L.	Duckweed
Onagraceae	
Epibolium hirsutum L.	Great Willow Herb
E. angustifolium L.	Rose-Bay Willow Herb; Fireweed
Polygonaceae	
Rumex hydrolapathum Hudson	Dock
Ranunculaceae	
Ranunculus aquatilis	Water Crowfoot
Rosaceae	
Rubus fructicusus L.	Blackberry
Rubiaceae	
Galium aparine L.	Goose Grass
Solanaceae	
Atropa bella-donna L.	Deadly Nightshade
Umbelliferae	
Anthiscus sylvestris (L.) Bern.	Cow Parsley
Urticaceae	
Urtica diodica L.	Stinging Nettle
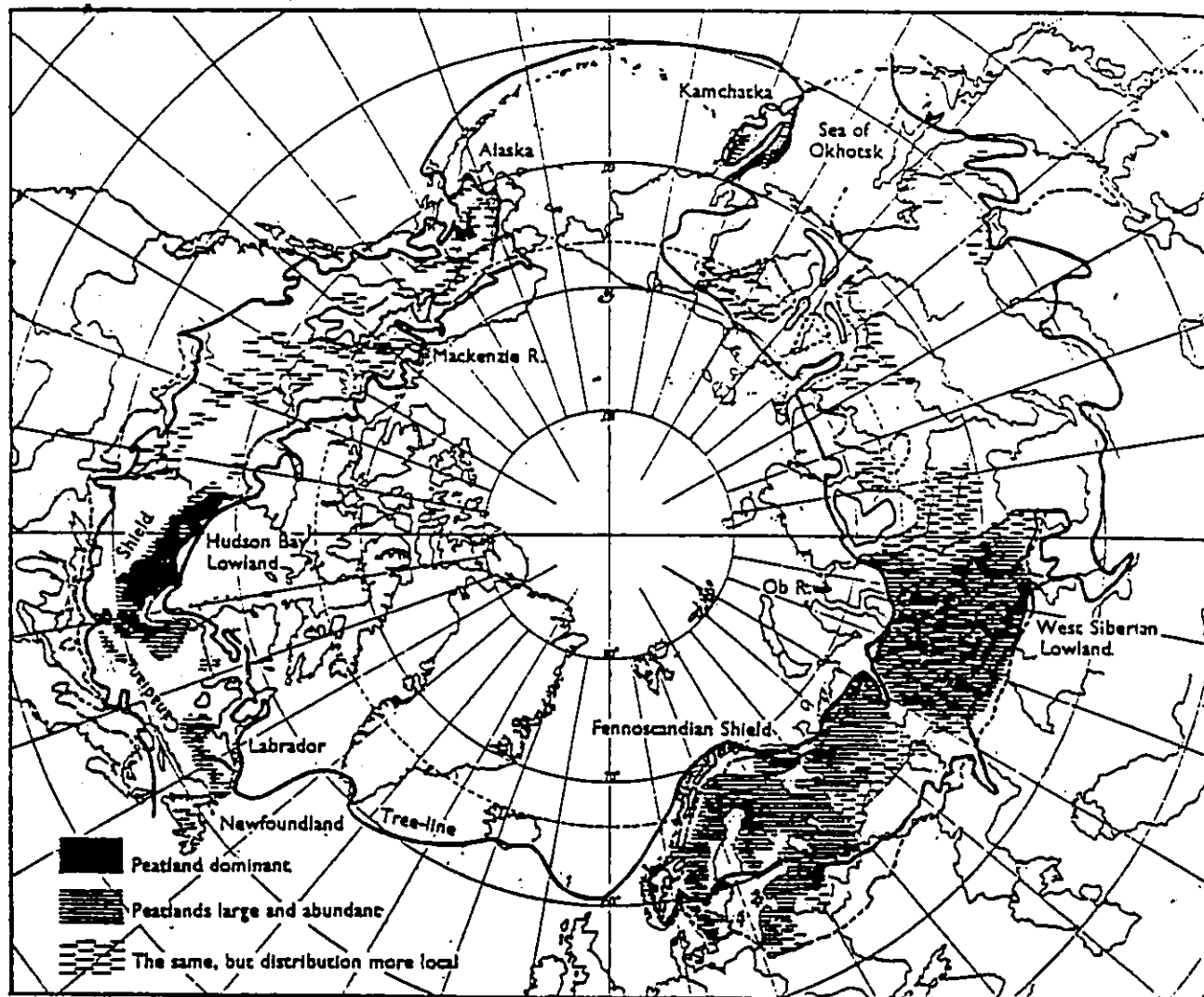
Fig. 33. Polar projection of northlands showing areas of abundant bogs
and peatland in the Boreal zone; transational regions reach
the broken lines.

(Reproduced from Sjörs 1961. Endeavur 20, p. 220, Fig. 13)

This zone includes the largest habitat area of Hellichiella spp.
and other bog simuliids, and corresponds to the northern
breeding habitat of aquatic bird hosts.

Table 23.

Geographical Distribution of <u>Hellichiella</u> species of the <u>congareenarum</u> Groups A & B

EUROPE

Species	Locality	Reference
<u>dogieli</u> Rubtsov	U.S.S.R. Karelia Urals, Ob R. basin	Ussova 1961 Rubtsov 1959-64, 1956 Patrusheva 1962, 1976
	Finland Enontekio Finnish Lapland	Kuusela 1971
	Norway	Raastad & Davies 1977
near <u>dogieli</u>	Norway Rendalen	Golini 1975, 1982
<u>fallisi</u> Golini	Norway Rendalen	Golini 1975, 1982
<u>latipes</u> Meigen (syn. <u>subexcisum</u> Edw.)	Great Britain	Edwards 1915 L. Davies 1966, 1968 Crosskey & Bass pers. comm. 1981-82
	France Poitier, Rambouillet, Le Plessis-Trevise Belle-Ile, Queberon	Grenier 1953 Doby et al. 1958
<u>rendalense</u> Golini	Norway Rendalen	Golini 1975, 1982
<u>saccai</u> Rivosecchi	Italy Lazio	Rivosecchi 1967, 1978, pers. comm.
<u>yerburyi</u> Edwards	England	Edwards 1920
	France ?	Grenier 1953
	U.S.S.R. Kola Pen. ? South Yamal	Rubtsov 1962 Patrusheva 1971

Table 23. (cont.)

NORTH AMERICA

Species	Locality	Reference
anatinum Wood	Canada	
	Goose Bay, Labrador	Shewell 1955-
	Churchill, Manitoba	Dunbar 1962, 1967
	Quebec, Ungava Bay	Laird & Bennett 1970
	Opinaga, Montreal	Back & Harper 1978
	McConnell R., N.W.T.	Bennett & MacInnes'72
	Ontario	Wood 1963, Wood et al 1963, Golini 1982
	Vancouver Is., B.C.	Mahrt J.L. pers. com.
	U.S.A.	
	Maine	Bauer & Granett 1979
	New Hampshire	J. Burger pers. comm.
Opinaga	Opinaga, Quebec	Golini 1982 (C. Back coll.)
congareenarum Dyar & Shannon	U.S.A. North Carolina, N.Y. Island, Virginia, Connecticut, Georgia, Louisiana, Florida, Alabama, Delaware	Dyar & Shannon 1927 Jamnback & Stone 1957 Stone 1964 Stone & Snoddy 1969 R. Lake pers. comm.
	Canada Ontario	Davies et al.1962 Wood et al.1963
congareenarum 'b'	Ontario	Dunbar 1962, 1967
excisum Davies, Peterson & Wood	Canada Ontario	Twinn, 1936, Davies et al.1962, Wood et al.1963, Golini 1982, Dunbar, 1967
	Quebec	Back & Harper 1978, 1979
	Newfoundland	Lewis & Bennett 1973

Table 23. (cont.)

NORTH AMERICA

Species	Locality	Reference
excisum Davies Peterson & Wood	Canada	
	Kalso, B.C.	Wood pers. comm.
	U.S.A.	
	Maine	Bauer & Granett 1979
	Michigan	Merritt et. al. 1978
innocens Shewell	Canada	Dunbar, 1967,
	Ontario	Shewell 1952, Davies
	British Columbia	et al. 1962, Wood et al
		1963, Golini 1982
	Opinaga, P.Q.	C. Back & Wood pers. comm.
	U.S.A.	
	Maine	Bauer & Granett 1979
	Michigan	Herman et al. 1975
		Merritt et al. 1978
minus Dyar & Shannon	U.S.A.	
	Yosemite, California	Dyar & Shannon 1927
	College, Alaska	Stone 1952
	Moscow, Idaho	
	Belton, Montana	
	Glacier, Washington	
	Yellowstone Pk. Wyoming	
	Canada	
	Cariboo, British Columbia	Hearle 1932
	Kalso, Vancouv. Is. B.C.	Wood pers. comm
		Williams et al. 1980
rivuli Twinn	Canada	
	Ontario	Twinn 1936, Davies et al 1962, Wood et al. 1963, Golini 1982
	U.S.A.	
	New Hampshire, Connecticut,	Stone 1964
	Maine	Bauer & Granett 1979

EUROPE
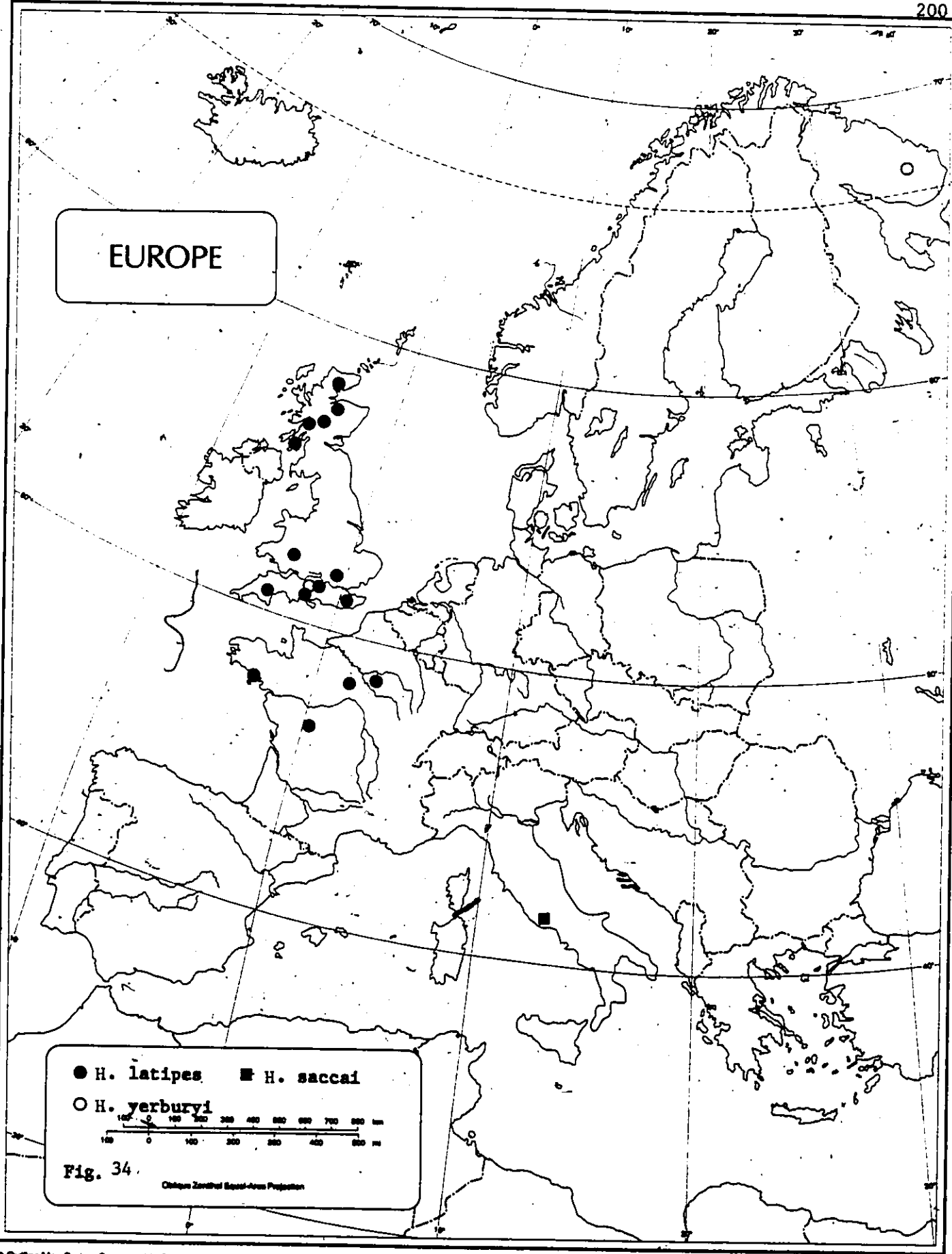
● H. latipes   ■ H. saccai

○ H. yerburyi

Fig. 34
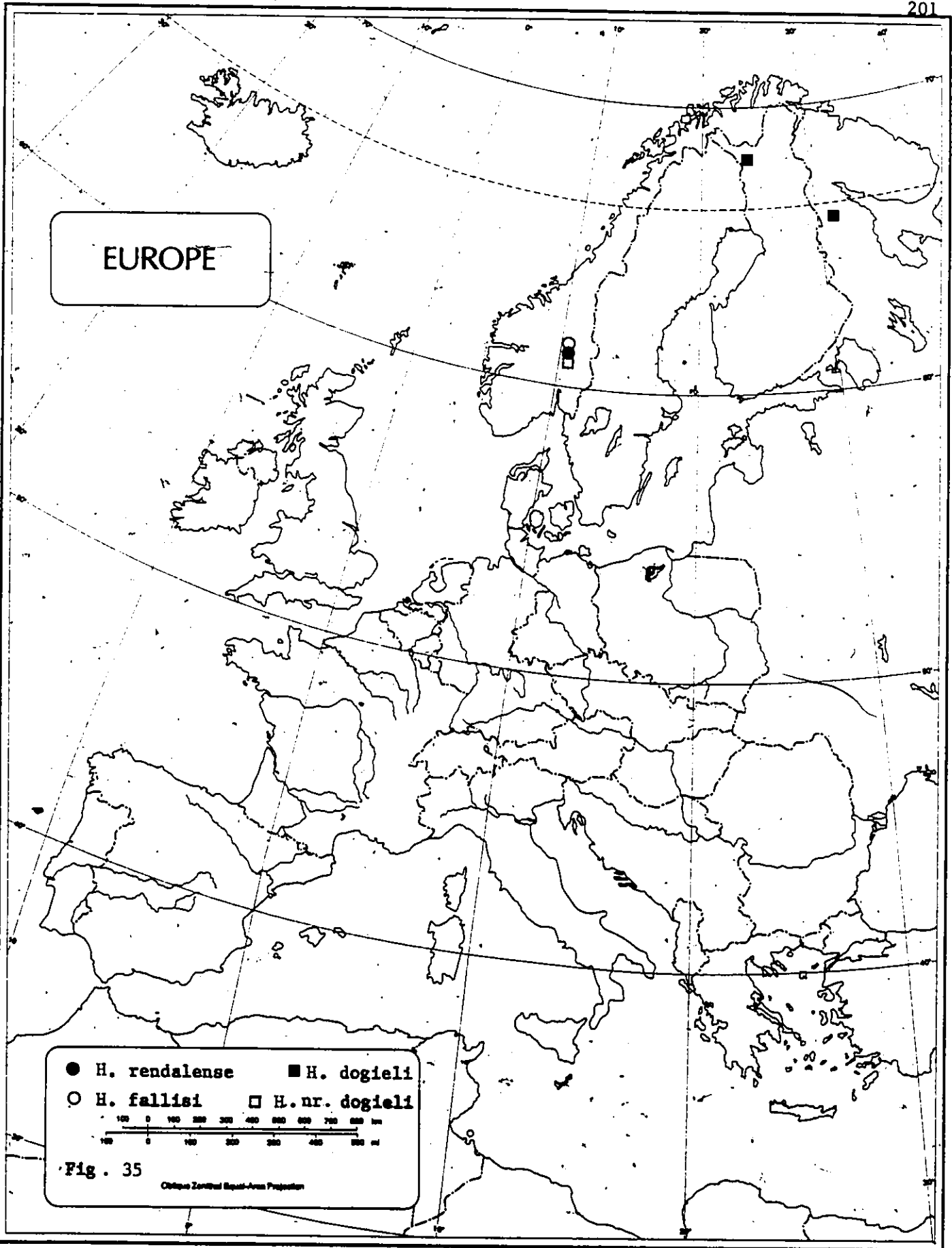
EUROPE

● H. rendalense	■ H. dogieli
○ H. fallisi	□ H. nr. dogieli
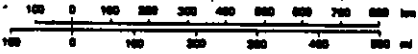
Fig . 35
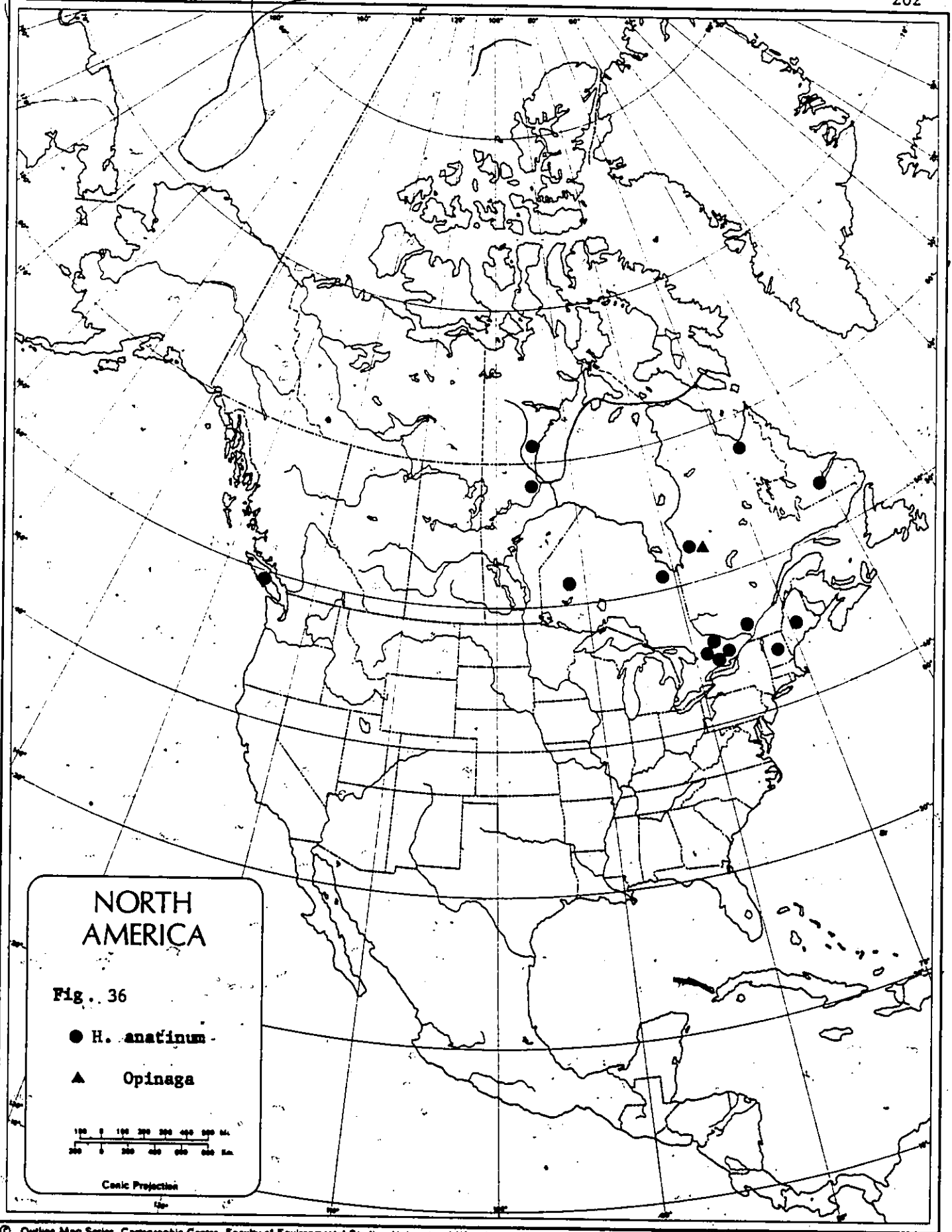
NORTH
AMERICA

Fig. 36

● H. anatinum

▲ Opinaga

Conic Projection

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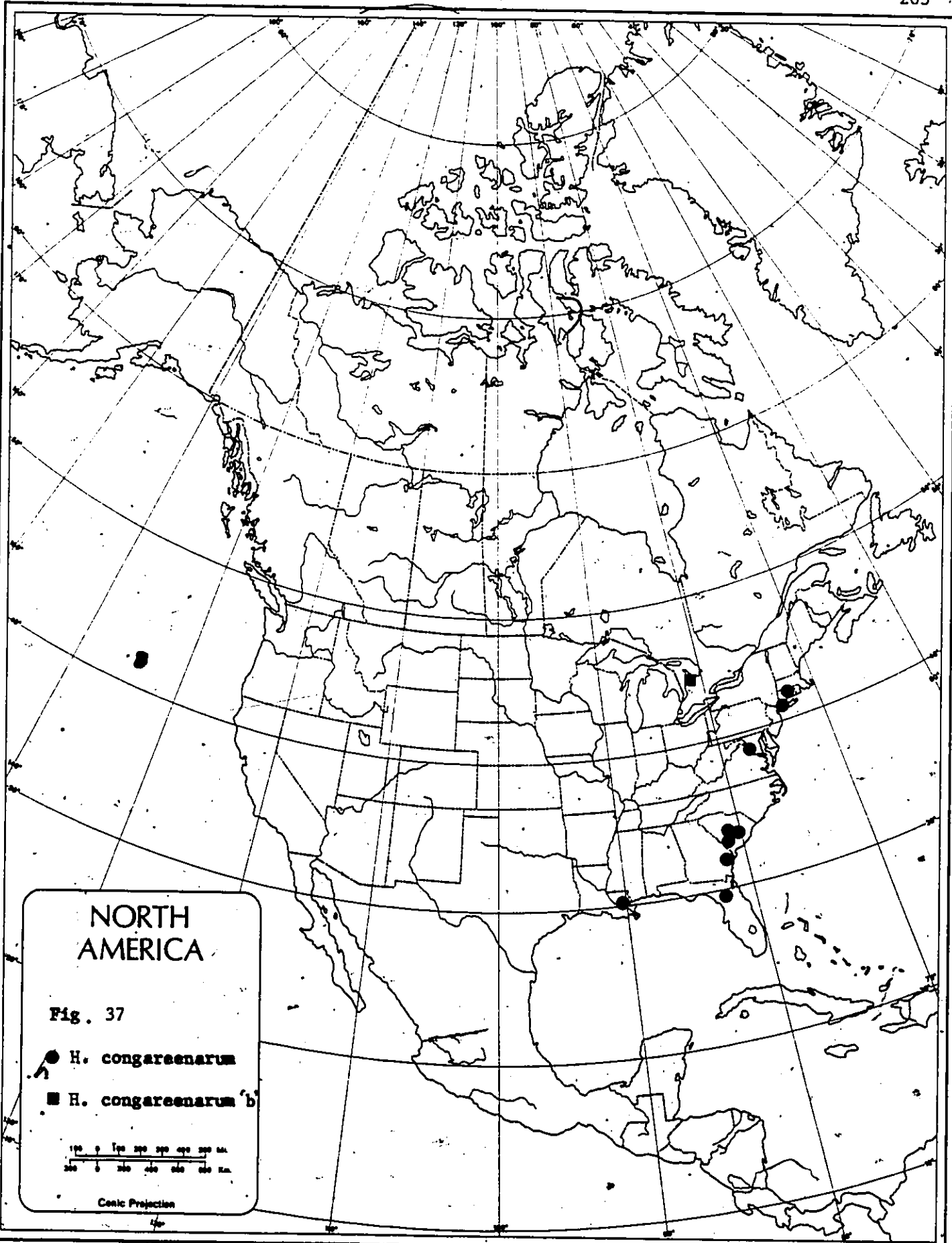
NORTH
AMERICA

Fig. 37

● H. congareenarum

■ H. congareenarum 'b'
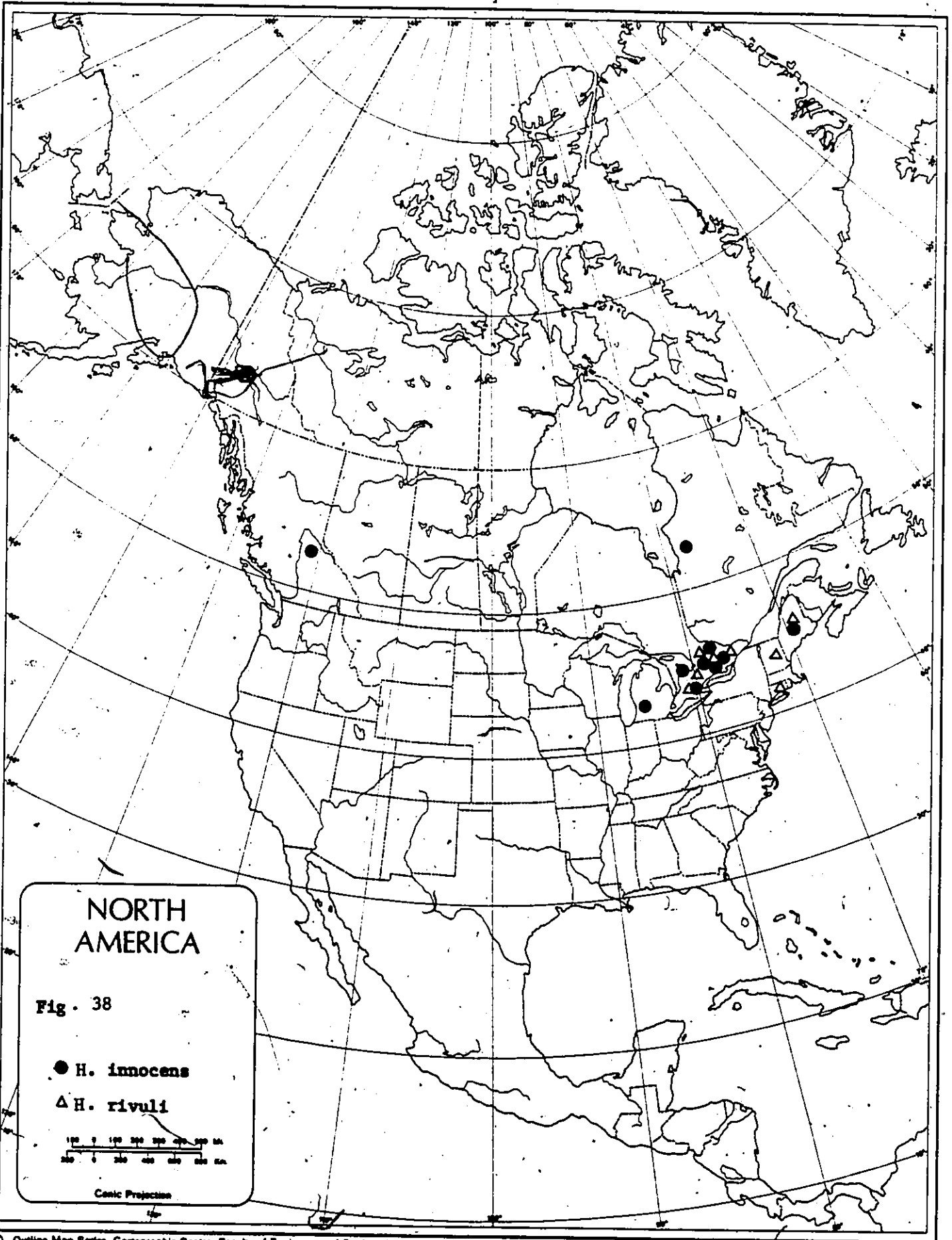
Conic Projection

NORTH
AMERICA

Fig. 38

● H. innocens

△ H. rivuli

Conic Projection

NORTH
AMERICA

Fig. 39

● H. minus

■ H. excisum

Conic Projection

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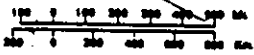
Table 24A. Species of Simuliidae Reported in this Study.

Most of these species occur in the palustrine biotope except those marked
with an asterisk *.

Palaearctic Region

Prosimulium
    Prosimulium hirtipes Fries*

Cnephia
    Metaenephia pallipes Fries*
    Stegopterna duodecimata Rubzov Δ
    Greniera brachiata ?Rubzov (probable new entity)Δ

Eusimulium
    Hellichiella dogieli Rubzov
    H. near dogieli ?Ussova (probable new entity)
    H. crassum Rubzov
    H. fallisi Golini
    H. latipes Meigen (auct. *subexcisum* Edw.)
    H. rendalense Golini
    H. saccai Rivosecchi
    H. yerburyi Edwards
    Parahellichiella annulum Lundström*
    P. annuliforme Rubzov*
    P. olonicum Ussova*
    Nevermannia vernum s.l. Macquatt
    N. bicorne Dorogostaiskii, Rubzov and Vlasenko*
    Eusimulium aureum Fries

Simulium
    Odagmia ornatum Meigen*
    O. rotundata Rubzov Δ
†   *Argentisimulium noelleri* Friederichs.

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† *Argentisimulium* Rubzov and Yankovskyi, 1982
Δ Species records new to Scandinavia

Table 24B.   (con't.)

Nearctic Region

Prosimulium
   Parahelodon gibsoni   Twinn
   P. decemarticulatum   Twinn

Cnephia
   Cnephia dacotense   Dyar and Shannon
   Stegopterna mutata   Malloch
   Greniera denaria   Davies, Peterson and Wood

Eusimulium
   Hellichiella anatinum   Wood
   H. congareenarum   Dyar and Shannon
   H. congareenarum "b" (cytospecies, Dunbar 1967)
   H. excisum   Davies Peterson and Wood
   H. innocens   Shewell
   H. minor   Dyar and Shannon
   H. rivuli   Twinn
   H. Opinaga (cytospecies, new entity)
   Parahellichiella canoniculum   Dyar and Shannon*
   P. clarum   Hart*
   P. euryadminiculum   Davies*
   P. emarginatum   Davies, Peterson and Wood*
   P. johannseni   Dyar and Shannon*
   Nvermannia croxtoni   Nicholson and Mickel
   N. vernum   s.l. Macquart
   Eusimulium aureum   Fries

Simulium
   † *Archesimulium tuberosum*   Lundström
   Simulium venustum   Say

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†*Archesimulium*   Rubzov and Yankovskyi, 1982

SUMMARY

The relationship among simuliid species in the genus <u>Hellichiella</u> from Europe and North America was studied on the basis of their salivary gland chromosomes, morphology and ecology. The banding pattern of polytene chromosomes of eight species was examined and compared with that of <u>H. congareenarum</u> defined by Dunbar (1967) as the standard. Species studied for the first time are <u>H. rendalense</u> (from Norway), <u>H. latipes</u> (<u>subexcisum</u> syn. from Britain) and <u>H. saccai</u> (from Italy) and the undescribed cytospecies "Opinaga" (from James Bay region, Quebec) and <u>H.</u> near <u>dogieli</u> (from Norway). <u>H. congareenarum</u>, <u>H. anatinum</u> and <u>H. innocens</u> were restudied. These species are distinguished by the following inversions relative to the standard.

1) <u>H. anatinum</u>: one fixed inversion, IIS-1, and the sex differential segments IIL-1 (X_1) and IIL-1,2 (X_2).

2) "Opinaga" cytospecies: with fixed inversions IS-1 associated with the sex differential segment IS-1,2 (Y); IIS-2 and IIIL-1.

3) <u>H. rendalense</u>: with complexly rearranged IIIL-4,5,8 and sex differential segments IIS-3 (Y_1), IIS-3,4 (Y_2), IIS-5 (X_1) and IIS-5,6 (X_2).

4) <u>H.</u> near <u>dogieli</u>: with fixed inversion IIS-3, corresponding to the Y differential segment in <u>H. rendalense</u>.

5) <u>H. latipes</u>: with fixed inversions IL-1; complexly rearranged

IIIL-9,10,11 and the H-band at the base of IIS, expressed in chromosomes
of female larvae (X:Hb$^+$) but not in those of male larvae (Y:Hb$^-$).

      6) <u>H. saccai</u>: with fixed inversion IL-1; expression of the
nucleolar organizer in females (X:NO$^+$) but not in males (Y:NO$^-$); Hb$^+$/Hb$^-$
is autosomal, and complexly rearranged IIIL-9,10,11 which is similar to
that of <u>H. latipes</u>.

      Furthermore, preliminary evidence indicates that <u>H. yerburyi</u>
is not a distinct species from <u>H. latipes</u>. It is concluded that <u>H. innocens</u>
conforms in all respects with Dunbar's (1967) description and that the
sibling distinction between <u>congareenarum</u> and <u>congareenarum</u> 'b' is not
valid. The possibility exists that the IIIL-1 sequence of "Opinaga"
leads to the first step of the complexly rearranged IIIL-4,5,8 of
<u>H. rendalense</u>, thus being phylogenetically intermediate between the
Palaearctic and Nearctic species of <u>Hellichiella</u>.

      The genus <u>Hellichiella</u> Riv.&Card. is redefined according to
its type species <u>H. saccai</u>, and includes all the species examined cytologically
in this study, as well as those included in Dunbar's (1967) <u>congareenarum</u>
subgroup B. Thus this genus is distinguished morphologically and
ecologically from the <u>annulum</u>-group sensu stricto which is represented
by the taxon <u>Parahellichiella</u> subg. n. Described for the first time
are the larvae, pupae and males of <u>H. rendalense</u> and <u>H.</u> near <u>dogieli</u>,
and the female of <u>H.</u> near <u>dogieli</u> and pupa of <u>H. fallisi</u>. The female
and pupa, but not the male, of <u>H. fallisi</u> are distinguished from those
of <u>H. rendalense</u>.

      These <u>Hellichiella</u> species are compared morphologically with
each other, and sister species are shown to differ by few but discrete

character differences. The original description of H. dogieli as
reported by Rubtsov (1956) is reproduced in translation, and it is
concluded that a) this species is a senior homonym of H. dogieli sensu
Usova (1959), and b) H. near dogieli is different from both H. dogieli
(Rubtsov) and H. dogieli sensu Usova.

The larvae and pupae of H. rendalense and H. near dogieli occur
in ombrotrophic, sloping sedge-Sphagnum bogs in Norway, developing in
shallow seepages with water current 1-30 cm/sec and temperature $10^{\circ}- 16^{\circ}C$.
This habitat is further described in terms of water quality and vegetation
from the bog surface. H. rendalense larvae occur primarily at the
bog's edge, while those of H. near dogieli occur normally in mid bog.
This microhabitat preference substantiates the differences between
these species confirmed by chromosomal and morphological evidence. Data
presented on larval drift and water current and on microhabitat preferences
show that water current is a major factor influencing microhabitat specifi-
city. Certain Sphagnum bogs in Norway are the source of Hellichiella
larvae and the origin of first order drainage streams which are secondarily
colonized by these and other simuliids.

The distribution of other Hellichiella species in Ontario and
other regions show that these simuliids occur in similar palustrine
habitats. Their primary distribution is located in the boreal region,
and is associated with the breeding and feeding habitat of aquatic bird
hosts. These species, some of which are known as vectors of Leucocytozoon,
are compared ecologically for the first time with other vectors of
haematozoa, such as Anopheline mosquitoes and Ceratopogonid flies. It is
theorized that the breeding habitat is the unifying ecological factor in
the epizootiology of Haemosporidia. A list of species considered in this
thesis is given in Tables 24A and 24B.

References

Anderson, J.R. and DeFoliart, G.R. 1961. Feeding behavior and host preference of some black-flies (Diptera; Simuliidae) in Wisconsin. Ann. Ent. Soc. Amer. 54: 716-729

Anderson, R.C. 1968. The simuliid vectors of Splendidofilaria fallisensis of ducks. Can. J. Zool. 46, 610.

Back, C. and Harper, P.P. 1978. Les mouches noires (Diptera:Simuliidae) de deux ruisseaux des Laurentides, Québec. Ann. Soc. ent. Québec 23, 55-66.

Back, C. and Harper, P.P. 1979. Succession saisonnière, émergence, voltinisme et repartition de mouches noires des Laurentides (Diptera:Simuliidae). Can. J. Zool. 57, 627-639.

Barber, K.E. 1981. Peat Stratigraphy and Climatic Change. A.A. Balkema, Rotterdam, 219 pp.

Basrur, P.K. 1962. The salivary gland chromosomes of seven species of Prosimulium from Alaska and British Columbia. Can. J. Zool. 40: 1019-33.

Bauer, L.S. and Granett, J. 1979. The blackflies of Maine. Maine Life Sciences and Agricultural Station Technical Bulletin 95, 1-18.

Bedo, D.G. 1977. Cytogenetics and evolution of Simulium ornatipes Skuse, I, Sibling speciation. Chromosoma 64, 37-65.

Beermann, W. 1955. Geschlechtsbestimmung und Evolution des genetischen Y-chromosomen bei Chironomus. Biol. Zbl. 74, 525-544.

Bellrose, F.C. 1976. Ducks, Geese and Swans of North America . Stackpole Books, Harrisburg, Pa.

Bennett, G.F. 1960. On some ornithophilic blood-sucking Diptera in Algonquin Park, Ontario, Canada. Can. J. Zool. 38, 377-389.

Bennett, G.F. 1961. On the specificity and transmission of some avian trypanosomes. Can. J. Zool. 39, 17-33.

Bennett, G.F. and Fallis, A.M. 1960. Blood parasites of birds in Algonquin Park, Canada, and a discussion of their transmission. Can. J. Zool. 38, 261-273.

Bennett, G.F. and MacInnes, C.D. 1972. Blood parasites of geese of the McConnell River, N.W.T. Can. J. Zool. 50, 1-4.

Carlsson, G. 1962. Studies on Scandinavian black flies (Fam. Simuliidae). Opuscula Entomol. Suppl. 21, 1-280.

Carlsson, G. 1967. Environmental factors influencing black fly populations. Bull. WHO 37, 139-50.

Chubareva, L.A. and Petrova, N.A. 1979. Basic karyotypic characteristics of black flies (Diptera Simuliidae) of the world. In Karyosystematics of the Invertebrate Animals. Acad.Sci. U.S.S.R. Leningrad, pp. 58-95.

Crosskey, R.W. 1960. A taxonomic study of the larvae of West African Simuliidae (Diptera:Nematocera) with comments on the morphology of the larval black-fly head. Bull. Brit. Mus. (Nat. Hist.) 10, 1-74.

Crosskey, R.W. 1969. A re-classification of the Simuliidae (Diptera) of Africa and its islands. Bull. Brit. Mus. (Nat. Hist.), Suppl. 14, 1-195.

Crosskey, R.W. 1981. Simuliid Taxonomy - The contemporary scene. In Blackflies, ed. M. Laird. Acad. Press, pp. 3-18.

Crosskey, R.W. and Davies, L. 1972. The identifies of Simulium lineatum (Meigen), S. latipes (Meigen) and S. vernum Macquart (Diptera Simuliidae). Entomol. Gaz, 23, 249-258.

Dalmat, H.T. 1955. Black Flies (Diptera, Simuliidae) of Guatemala and their Role as Vectors of Onchocerciasis. Smiths. Misc. Collect. 125, 425 pp.

Davies, D.M. 1949. Description of Simulium euryadminiculum, a new species of black fly (Simuliidae:Diptera). Can. Ent. 81, 45-49.

Davies, D.M., Peterson, B.V. and Wood, D.M. 1962. The black flies (Diptera:Simuliidae) of Ontario. Part I. Adult identification and distribution with descriptions of six new species. Proc. Ent. Soc. Ont. (1961) 92, 70-154.

Davies, L. 1966. The taxonomy of British black-flies (Diptera:Simuliidae) Trans. Roy. ent. Soc. Lond. 118, 413-511.

Davies, L. 1968. A key to the British species of Simuliidae in the larval, pupal and adult stages. Fresh wat. Biol. Assoc. Sc. Publ. 24, 1-126.

Disney, R.H.L. 1972. Observations on sampling pre-imaginal populations of black flies (Diptera, Simuliidae) in West Cameroon. Bull. ent. Res. 61, 485-503.

Dunbar, R.W. 1958. The salivary gland chromosomes of two sibling species of black flies included in Eusimulium aureum Fries. Can. J. Zool. 36, 23-44.

Doby, J.M., David, F. and Rault, B. 1958. Contribution a l'etude faunistique et ecologique des culicidés et simuliidés (Diptera Nematocera) de Belle-Isle (Morbihan). Cahiers Natur. Bull. N.P., 14: 94-98.

Dunbar, R.W. 1962. Cytotaxonomic studies in Simuliidae. Ph.D. Thesis, University of Toronto, Toronto, Ontario.

Dunbar, R.W. 1967. The salivary gland chromosomes of six closely related black flies near Eusimulium congareenarum (Diptera: Simuliidae). Can. J. Zool. 45, 377–396.

Dyar, H.G. and Shannon, R.C. 1927. The North American two-winged flies of the family Simuliidae. Proc. U.S. Nat Museum, 69, 1–54.

Edwards, R.W. 1915. On the British species of Simulium. I. The adults. Bull. ent. Res. 6_, 23–42.

Edwards, F.W. 1920. On the British species of Simulium. II. The early stages; with corrections and additions to part I. Bull. ent. Res. 11, 211–246.

Edwards, F.W. 1939. Simuliidae. In British blood-sucking flies. Brit. Mus. Nat. Hist.

Eide, A., Fallis, A.M., Brinkman, A. Jr., Allen, T. and Eligh, D. 1969. Hamematozoa from Norwegian birds. Acta Univ.-Bergensis Ser. Mat. Nat. 6, 1–8.

Eide, A. and Fallis, A.M. 1972. Experimental studies of the life cycle of Leucocytozoon simondi in ducks in Norway. J. Protozool. 19, 414–416.

Fallis, A.M. and Bennett, G.F. 1960. Sporogony of Leucocytozoon and Haemoproteus in simuliids and ceratopogonids and a revised classification of the haemosporiida. Can. J. Zool. 39, 215–228.

Fallis, A.M. and Bennett, G.F. 1966. On the epizootiology of infections caused by Leucocytozoon simondi in Algonquin Park, Canada. Can. J. Zool. 44, 101–112.

Fallis, A.M. and Smith, S.M. 1964. Ether extracts from birds and CO_2 as attractants for some ornithophilic simuliids. Can. J. Zool. 42, 724–730.

Fredeen, F.J.H. 1981. The seven larval instars of Simulium (Phosterodoros) luggeri (Diptera: Simuliidae). Can. Ent. 113, 161–165.

Freeman, P. and DeMeillon, B. 1953. Simuliidae of the Ethiopian Region. London, 224 pp.

Gersabeck, E.F. and Merritt, R.W. 1979. The effect of physical factors on the colonization and relocation behavior of immature black flies (Diptera:Simuliidae). Environ. Ent. 8, 34–39.

Glatthaar, R. 1978. Verbreitung und Ökologie der Kriebelmücken (Diptera: Simuliidae) in der Schweiz. Vjschr. naturf. Ges. Zürich 123, 71–124.

Gleason, H.A. and Cronquist, A. 1963. <u>Manual of Vascular Plants of Northeastern United States and Adjacent Canada</u>. Litton Educ. Publ., Inc. 810 pp.

Golini, V.I. 1970. Observations on some factors involved in the host-seeking behaviour of simuliids in Ontario and Norway. M.Sc. Thesis, McMaster University, Hamilton.

Golini, V.I. 1975. Simuliidae (Diptera) of Rendalen, Norway, I – <u>Eusimulium</u> <u>rendalense</u> n.sp. and <u>E. fallisi</u> n.sp. feeding on ducks. Ent. Scand. <u>6</u>, 229-239.

Golini, V.I. 1981. A simple technique for rearing pupae of Simuliidae and other Diptera. Ent. scand. <u>12</u>, 426-428.

Grenier, P. 1953. Simuliidae de France et d'Afrique du Nord. Encycl. ent. Ser. A. <u>29</u>, 7-170.

Grenier, P. and Rageau, I. 1960. Simulies (Diptera:Simuliidae) de Tahiti remarquees sur la classification des Simuliidae. Bull. Soc. Pathol. Exot. <u>53</u>, 727-742.

Grunewald, J. 1981. Hydrochemical and physical characteristics of the larval sites of species of the <u>Simulium</u> <u>damnosum</u> complex. In, Blackflies, ed. M. Laird, Acad. Press pp. 227-235.

Hearle, E. 1932. The blackflies of British Columbia (Simuliidae, Diptera). Proc. Ent. Soc. B.C. <u>29</u>, 5-19.

Herman, C.M., Barrow, J.H. and Tarshis, I.B. 1975. Leucocytozoonosis in Canada geese at the Seney National Wildlife Refuge. J. Wildl. Dis. 11, 404-411.

Hynes, N.B.N. 1970. <u>The Ecology of Running Waters</u>. University Toronto Press.

Jamnback, H. and Stone, A. 1957. A first record of <u>Simulium</u> (<u>Eusimulium</u>) <u>congareenarum</u> (D. & S.) from New York with descriptions of the male, female, pupa and larva. Ann. Ent. Soc. Amer. <u>50</u>, 395-399.

Jeglum, J.K., Boissonneau, A.N. and Haavisto, V.G. 1974. Towards a wetland classification for Ontario. Can. Forest. Serv., Info. Rep. O-X-215, Envir. Can. 54 pp.

Jucci, C. 1952. Citogenetica degli Anofeli: sua importanza per la malariologia. Symposia Genetica In Pleiotropic geniche e polimorfismi cromosomici Pavia, 1952.

Kuusela, K. 1971. Preliminary notes on the black fly species (Diptera Simuliidae) of Finland. Ann. Entomol. Fenn. <u>37</u>, 190-194.

Laird, M. and Bennett, G.F. 1970. The subarctic epizootiology of Leucocytozoon simondi. J. Parasitol. 56: 198.

Lewis, D.J. and Bennett, G.F. 1973. The blackflies (Diptera: Simuliidae) of insular Newfoundland. I. Distribution and bionomics. Can. J. Zool. 51, 1181-1187.

Lowther, J.K. and Wood, D.M. 1964. Observations on the specificity displayed by the black-fly, Simulium euryadminiculum Davies, toward its host, the common loon. Can. Ent. 96, 911-913.

Merritt, R.W., Ross, D.H. and Peterson, B.V. 1978. Larval ecology of some lower Michigan black flies (Diptera:Simuliidae) with keys to the immature stages. Great Lakes Entomol. 11, 177-208.

Mohsen, Z. and Mulla, M.S. 1982. The ecology of black flies (Diptera: Simuliidae) in some southern California streams. J. Med. Ent. 19, 72-85.

Osvald, O. 1954. Sloping mires in north-western Norway. Bot. Tidskr. 51, 274-280.

Patrusheva, V.D. 1962. Simuliidae of the middle part of the Ob River basin. Izv. Sib. otd. AN SSSR 3, 94-110.

Patrusheva, V.D. 1971. New and rare species of black flies of the group annulum Lundstr. (Simuliidae, Eusimulium) from Yamal. In, New and Little-known Species in the Siberian Fauna, 5 (1971), 82-88. Nauk Novosibirsk.

Pegel von M. and Rühm, W. 1976. Investigations on arrival of preimaginal stages of blackflies on artificial substrates. Z. ang. Ent. 82, 65-71.

Peterson, B.V. 1970. The Prosimulium of Canada and Alaska (Diptera: Simuliidae). Memoirs Ent. Soc. Can. No. 69, 216 pp.

Procunier, W.S. 1975. A cytological study of two closely related black fly species: Cnephia dacotensis and Cnephia ornithophilia. Can. J. Zool. 53, 1638-47.

P'yavchenko, N.I. 1958. Peat Bogs of the Russian Forest Steppe. Akad. Nauk SSSR, (IPST 1964) 156 pp.

Raastad, J.E. 1979. Fennoscandian black-flies (Diptera, Simuliidae): Annotated list of the species and their gross distribution. Rhizocrinus, No. 11, 27 pp. Zool. Mus Univ. Oslo.

Raastad J.E. and Davies, D.M. 1977. Black flies (Dipt., Simuliidae) new to Norway. Norw. J. Ent. 24, 33-34.

Radforth, N.W. and Brawner, C.O. 1977. Muskeg and the Northern Environment in Canada. Univ. Toronto, 399 pp.

Rivosecchi, L. 1967. Contributo alla conoscenza dei simulidi italiani. XV – Un nuovo Eusimulium del gruppo annulum. Riv. Parassit. 28, 63-70.

Rivosecchi, L. 1978. Simuliidae. Diptera: Nematocera. In, Fauna D'Italia, Vol. XIII, 534 pp. Ed. Calderini, Bologna.

Rivosecchi, L. and Cardinali, R . 1975. C.C.S.I. XXIII – Nuovi dati tassonomici: Riv. Parassit. 36, 55-78.

Romanov, V.V. 1961. Hydrophysics of Bogs. Leningrad (IPST 1968) 299 pp.

Ross, D.H. and Merritt, R.W. 1978. The larval instars and population dynamics of five species of black flies (Diptera:Simuliidae) and their response to selected environmental factors. Can. J. Zool. 56, 1633-42.

Rothfels, K.H. 1956. Black flies: Sibling, sex and species-grouping. J. Heredity. 47, 113-122.

Rothfels, K.H. 1979. Cytotaxonomy of black flies (Simuliidae). Ann. Rev. Entomol. 24, 507-39.

Rothfels, K.H. 1980. Chromosomal variability and speciation in black flies. In Insect Cytogenetics, ed. Blackman, Hewitt and Ashburner, Symp. roy. Entomol. Soc. Lond. 10, 207-224.

Rothfels, K.H. 1981. Cytological approaches to the study of black fly systematics and evolution. Symp. Ent. Soc. Amer. (1980).

Rothfels, K.H. and Dunbar, R.W. 1953. The salivary gland chromosomes of the black fly Simulium vittatum Zett. Can. J. Zool. 31, 226-241.

Rothfels, K.H., Feraday, R. and Kaneps, A. 1978. A cytological description of sibling species of Simulium venustum and S. verecundum with standard maps for the subgenus Simulium Davies. Can. J. Zool. 56, 1110-1128.

Rothfels, K.H. and Featherston, D. 1981. The population structure of Simulium vittatum (Zett.) I. The IIIL-1 and IS-7 sibling species. Can. J. Zool. 59, 1857-1883.

Rothfels, K.H. and Nambiar, R. 1981. A cytological study of natural hybrids between Prosimulium multidentatum and P. magnum with notes on sex determination in the Simuliidae (Diptera). Chromosoma (Berl.) 82, 673-691.

Rubtsov, I.A. 1956. Black flies (Diptera). In Fauna S.S.S.R. 6(6), 860 pp.

Rubtsov, I.A. 1959-64. Simuliidae (Melusinidae) In Die Fliegen der Palaearktischen Region. Ed. Erwin Lindner. Pt. 14 689 pp.

Rubtsov, I.A. 1971. New and little-known species of black flies. In, New and Little-known species in the Siberian Fauna, 5, 89-108.

Rubtsov, I.A. 1973. New and little-known species of black flies (Diptera, Simuliidae). In, New and Little-known Species in the Siberian Fauna 7 (1973), 120-128. Nauk, Novosibirsk.

Rubtsov, I.A. 1974. On the evolution, phylogeny and classification of black flies (Diptera:Simuliidae). Trudy zool. Inst. Leningr. 53, 230-282.

Rubtsov, I.A. and Carlsson, G. 1965. On the taxonomy of black flies from Scandinavia and northern U.S.S.R. Acta Univ. Lundensis, sec. II, no 18, 1-40.

Rubtsov, I.A. and Yankovsky 1982. New genera and subgenera of black flies (Diptera, Simuliidae). Ent. Rev. 61, 183-187.

Shewell, G.E. 1952. New Canadian black flies (Diptera:Simuliidae) I. Can. Ent. 84, 33-42.

Shewell, G.E. 1955. The identity of the black fly that attacks ducklings and goslings in Canada (Diptera:Simuliidae). Can. Ent. 87, 345-349.

Shewell, G.E. 1958. Classification and distribution of arctic and subarctic Simuliidae. Proc. 10th int. Cong Ent., Montreal 1, 635-643.

Sjörs, H. 1952. On the relation between vegetation and electrolytes in north Swedish mire waters. Oikos 2(1950), 241-258.

Sjörs, H. 1961. Surface patterns in Boreal peatland. Endeavour 20, 217-224.

Stone, A. 1952. The Simuliidae of Alaska (Diptera). Proc. Ent. Soc. Wash. 54, 69-96.

Stone, A. 1964. Simuliidae and Thaumaleidae. Guide to the Insects of Connecticut, Part VI. The Diptera or true flies of Connecticut. Bull. 97, State Geol and Nat. Hist. Surv. Conn. 126 pp.

Stone, A. and Snoddy, E.L. 1969. The black flies of Alabama (Diptera: Simuliidae). Alabama Agricultural Experi... Station, Bull. 390, 93 pp.

Thompson, P.E. and Bowen, J.S. 1972. Interaction of differentiated primary sex factors in Chironomus tentans. Genetics 70, 491-493.

Twinn, C.R. 1936. The black flies of eastern Canada (Simuliidae, Diptera). Can. J. Res. D. 14, 97-150.

Ursing, B. 1966. Norsk Farge flora. E.G. Mortensens Forlag, Oslo, 233 pp.

Usova, Z.V. 1961. Flies of Karelia and the Murmansk Region (Diptera: Simuliidae). Akad. Nauk SSSR (1961) 268 pp. (IPST 1964).

Van Someren, G.R.C. 1944. Some records of Simuliidae in Abyssinia and British Somaliland. Bull. ent. Res. 35, 113-114.

Williams, N.A. Mahrt, J.L. and Zwickel, F.C. 1980. The ecology of blood parasites in blue grouse from Vancouver Island, British Columbia. Can. J. Zool. 58, 2175-2186.

Wood, D.M. 1963. An interpretation of the phylogeny of the Eusimulium group (Diptera:Simuliidae) with description of six new species. Ph.D. Thesis, McMaster University, Hamilton, Ontario.

Wood, D.M. 1963. Two new species of Ontario black flies. Proc. Entomol. Soc. Ontario (1962) 93, 94-98.

Wood, D.M., Peterson, B.V., Davies, D.M. and Györkös, H. 1963. The black flies (Diptera: Simuliidae) of Ontario. Part II. Larval identification, with descriptions and illustrations. Proc. Entomol. Soc. Ontario (1962) 93, 99-129.

Wu, Y.F. 1931. A contribution to the biology of Simulium. Michigan Acad. Sci. Arts and Letters 13, 543-599.

Bates, M. 1954. The Natural History of Mosquitoes. McMillan Co., N.Y. 379 pp.

Bennett, G.F., Garnham, P.C.C. and Fallis, A.M. 1965. On the status of the genera Leucocytozoon Ziemann, 1898 and Haemoproteus Kruse, 1890 (Haemosporiida:Leucocytozoidae and Haemoproteidae). Can. J. Zool. 43: 927-932.

Colbo, M.H. and Moorhouse, D.E. 1978. The ecology of pre-imaginal Simuliidae (Diptera) in South-Eastern Queensland, Australia. Hydrobiologia 63: 63-79.

Downes, A.J. 1965. Adaptation of insects in the Arctic. Annu. Rev. Entomol. 10: 257-274.

James, M.T. and Harwood, R.F. 1969. Medical Entomology. McMillan Co. Toronto. 484 pp.

Usova, Z.V. 1959. A new species of Simuliidae, Hellichia dogieli n. sp. from Karelia. Trudy Karel'skogo Filiala AN SSR, 14: 110-114.

ECOLOGY

APPENDIX

Fig. 16   View of Åkerströmmen and Mistra river in Rendalen,
          showing in the background the mountain ridge linked
          with Renåskarven·and Renåfjellet beyond which is
          situated Renådalen watershed. Note, the Mistra is
          a third order river which drains also the Renådalen
          watershed through the second order Renåa river.
          Other simuliids, but not Hellichiella, breed in this
          relatively large river, e.g. Prosimulium hirtipes,
          Metacnephia pallipes, Simulium austeni, S. ornatum,
          S. rostratum. (Picture taken from Ås Gard)

Fig. 17   View of Renådalen watershed drained by the Renåa river
          showing location of the bog (arrow) surrounded by
          boreal forest (cf. Figs. 20, 22   ). Notice, other
          patches of treeless terrain in lower background have
          various degrees of surface water drainage and are
          potential breeding sites of Hellichiella. In the far
          background is Sölen mountain 1755m a.s.l. (Picture
          taken from foot of Renåfjellet, looking east)
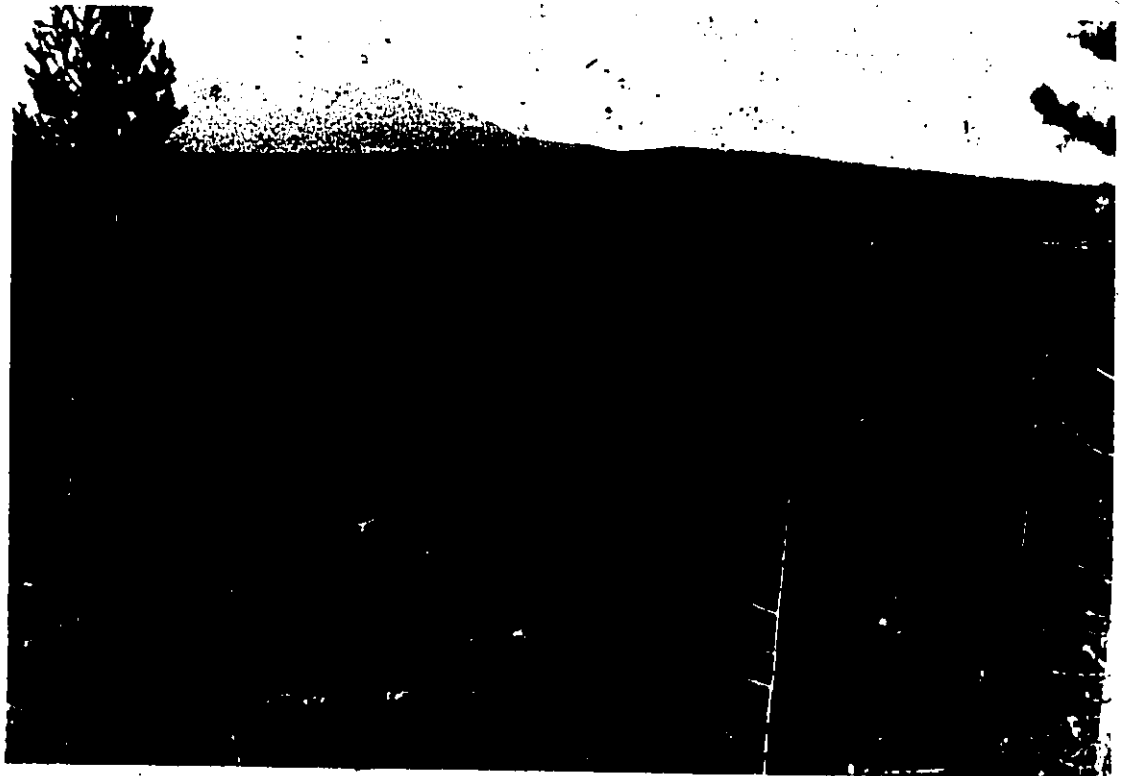
Fig. 16

Fig. 17

COLOURED PICTURES
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Fig. 18   Upper section of stream 12 with emergence cage; source·
of the brook from Renådalen bog is hidden just behind
bushes of _Salix._ Larvae and pupae of _Hellichiella_, occurring
sparingly on submerged stones and leaves, were found
initially in this stream in mid June 1979. In absence
of rain, water flow is reduced to an imperceptible
trickle or it may desiccate completely.

Fig. 19   Mid section of stream 14 just above Renådalen road and
about 10m below the bog source, showing reduced water
level and stone bottom in early June when larvae of
Hellichiella are found on submerged stones. Incipient
budding of _Betula_ and _Salix_ is concurrent with larval
development. The 40cm wide basin used to collect rain-
water and the pH meter are shown beside the brook. Note,
after 40mm of continuous rain, water volume nearly over-
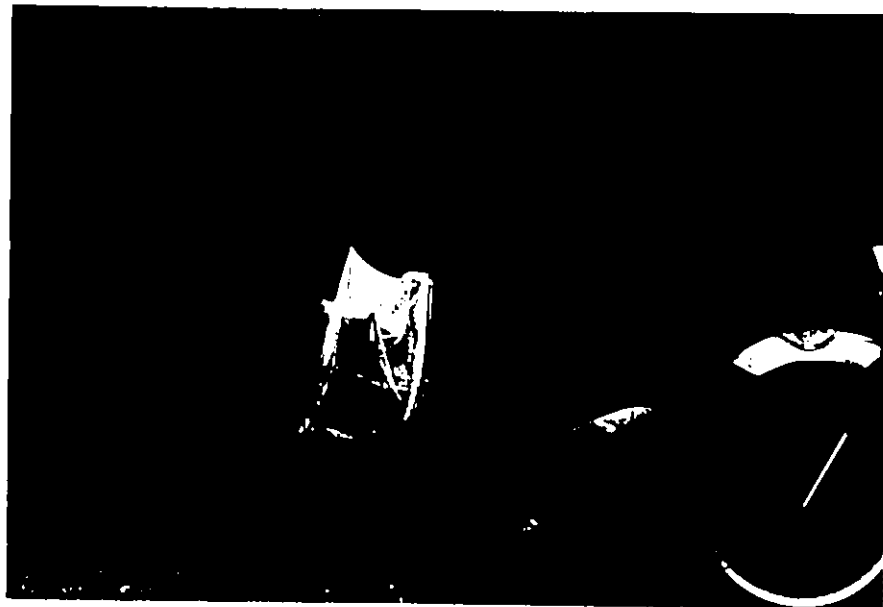flows the banks of this brook.

Fig. 18

Fig. 19

COLOURED PICTURES
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Fig. 20 Origin of stream 13 at the edge of Renådalen bog in
early June, showing normal water level from a major
seepage flowing 5 to 30 cm/sec into the right branch
of the stream. Larvae and pupae of _Hellichiella_ are
loosely attached on decaying sedges just below water
surface. Initial new growth of sedges contrasts with
partly decaying old sedges accumulating over the bog
surface. The 30 cm wide brass sieve used for larval
drift tests is shown with other collecting equipment.

Fig. 21 View of Renådalen bog, looking toward the lower
periphery in early June. Note the slightly raised
and sloping surface covered with sedges, ericaceous
plants, few lichens – _Cladina_ _rangiferina_ – on drier
upper periphery (foreground), low palsa mounds mainly
of _Sphagnum_, 30 to 50 cm high, and few dwarf pine trees.
The tops of two emergence cages in the lower background
are barely visible due to the convex bog surface.
(See Table 1 for a list of plants indigenous to this
habitat). In far higher background is Renåfjellet.
Mosquitoes (mainly _Aedes_ spp.) and biting midges
(mainly _Culicoides_ _pulicaris_ (L) and _C._ nr. _impunctatus_
Goetghebuer)[*] were collected at this and other sites
in Rendalen while biting man in mid to late June

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[*] det. A. Downes

Fig. 20

Fig. 21

COLOURED PICTURES
Images en couleur

Fig. 22   Periphery of Renådalen bog at origin of stream 13
(see Fig. 20) looking toward the stream. Notice
fully grown sedges in early July and dense vegetation
of _Betula_ and _Salix_ at the edge of the bog and
beginning of the brook. The emergence cage is set
on the seepages shown in Fig. 20 . Darker upright
sedges in foreground were inundated by flood water,
in third week of June, which reached about 10mm depth
above normal at this site.

Fig. 23   Stream 13 about 30 m from the bog and just below
Renådalen road. The stream bed is overgrown with
vegetation and water in normal flow under the
emergence cage is barely visible. Larvae and pupae
of _Hellichiella_ are relatively scarce on vegetation
trailing in the water of this brook. In third week
of June 1980 flood water level reached 1/3 the height
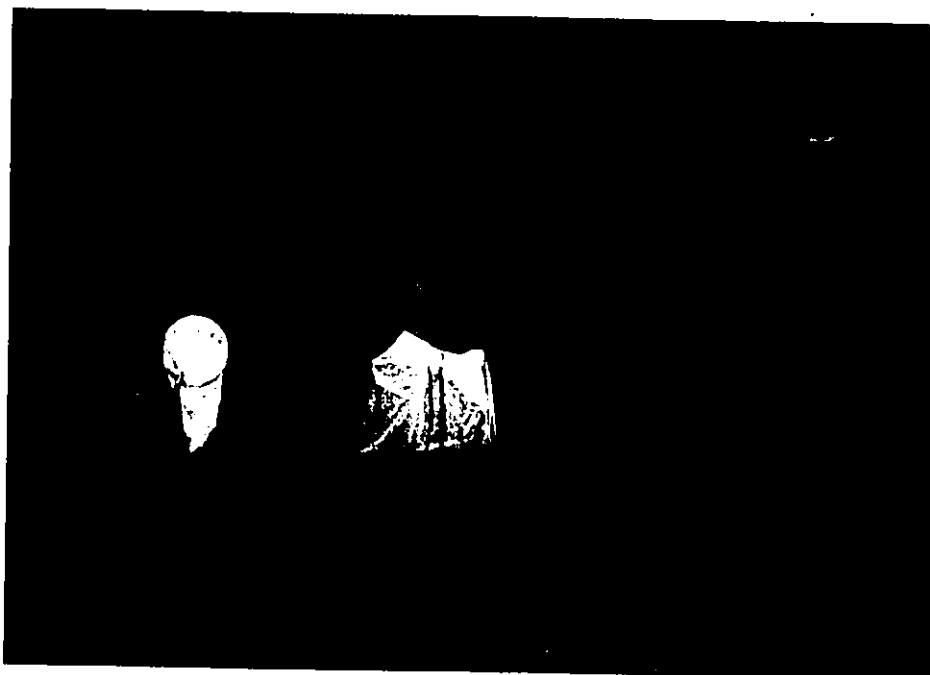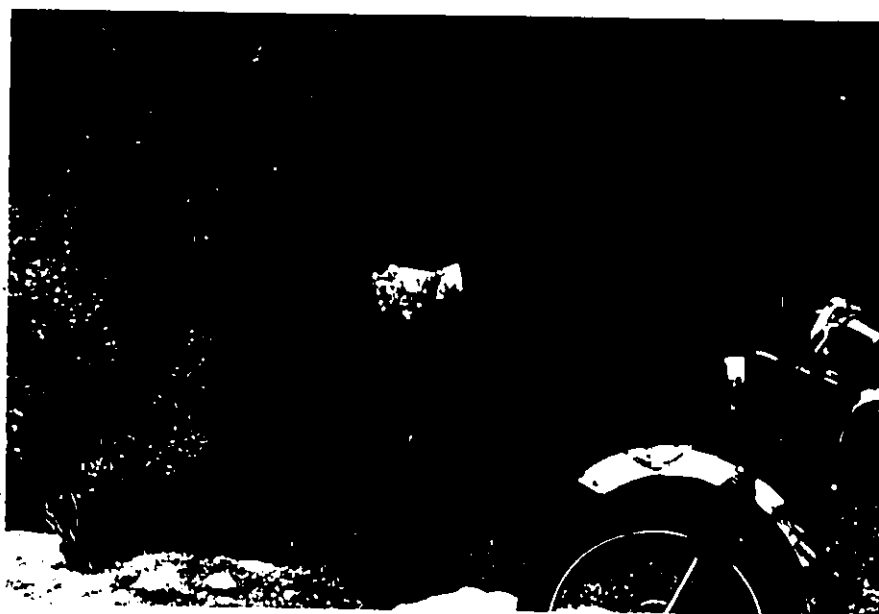of the cage which became nearly uprooted by the current.

Fig. 22

Fig. 23

COLOURED PICTURES

Fig. 24   Lower periphery of Renådalen bog showing drainage
          brook leading into stream 13. Notice the brook in
          full capacity at the end of June 1980 when water
          had receded to 1/3 flood level after 5 days of
          continuous rainfall (see text).

Fig. 25   Lower periphery of Renådalen bog showing the 30 to 60 cm
          deep drainage brook in mid June 1980, before the rains,
          barely flowing at 1/3 full capacity and nearly desiccated
          compared to the period after rainfall (Fig. 24) The
          max.-min. thermometer used to monitor daily water
          temperature is momentarily exposed on corner of
          emergence cage.
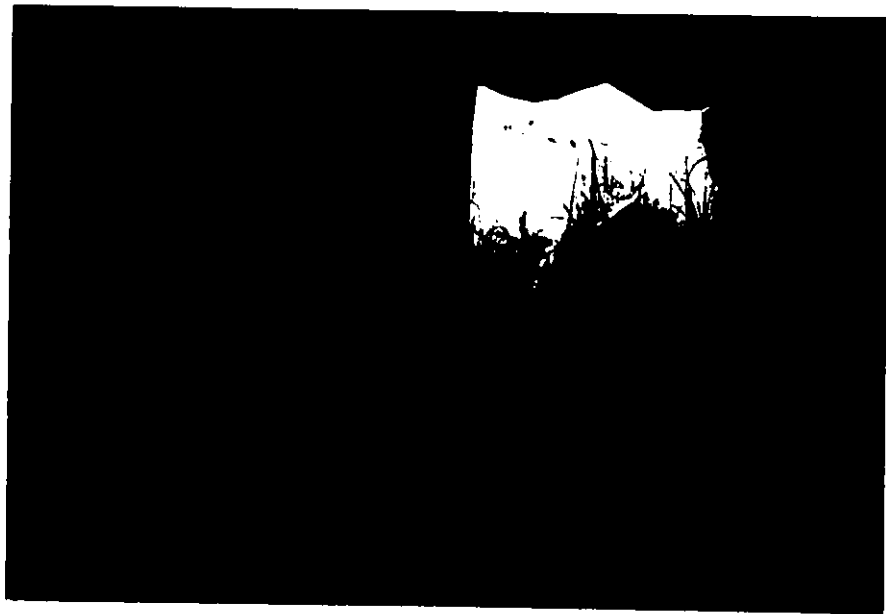
Fig. 24

Fig. 25

Fig. 26   One of the 25 cm long fringed rubber strips on which
          simuliids were collected during larval density tests.
          On the right is shown part of the sedge-covered
          seepage in Renådalen bog where the strip was floating.
          Some pupae and larvae collected on this strip are shown
          in the petri dish and in the ethanol vial respectively
          on the left.   (The fly, _Eristalis_ sp., was persistently
          attracted to the white plastic background while the
          picture was being taken.)

Fig. 27   View of Fuglåsen plateau in far background where
          Åsmyrtjörna bog is located (arrow). The picture was
          taken from highway #117 just before descent down the
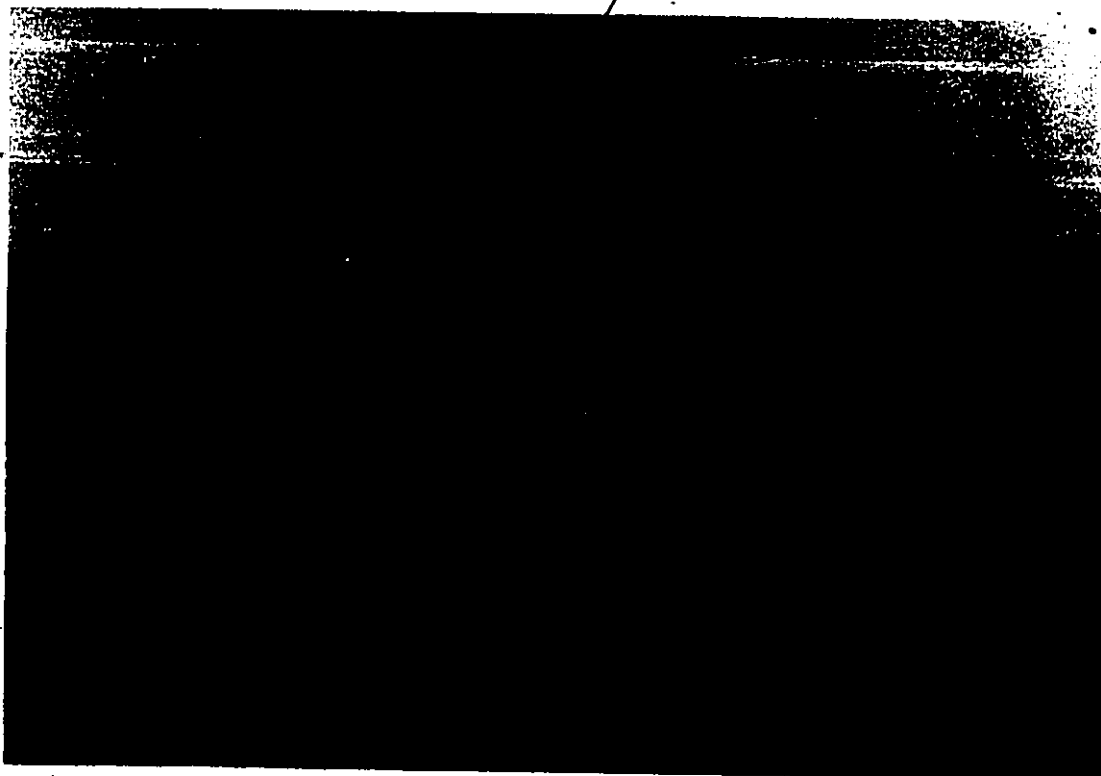   mountain shown in Fig. 16.

Fig. 26

Fig. 27

COLOURED PICTURES
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Fig. 28 The lower edge of Åsmyrtjörna bog in late June
showing seepages from raised upper level of bog
where samples of _Hellichiella_ larvae were taken
(arrows). Scarcity of pupae at these points indicates
that mature larvae may have drifted and pupated in the
flooded lower foreground just below the seepages.
Adult females of _Culicoides_ _pulicaris_ (L.) and _C_. sp.
near _impunctatus_ Goetg. were collected at this bog and
vicinity while biting man in mid to late June.

Fig. 29 Mid Åsmyrtjörna bog showing the 20 m long, 30 cm wide
and 20 cm deep rill, in early June, where mid bog
samples of _Hellichiella_ were taken. This rill originated
just below a raised area of the bog saturated with
surface water, and dissipated into the ground about 20 m
farther down (on the right). The imperceptible surface
water flow stops completely in dry periods, but some bottom
flow from peripheral seepage was sufficient to keep
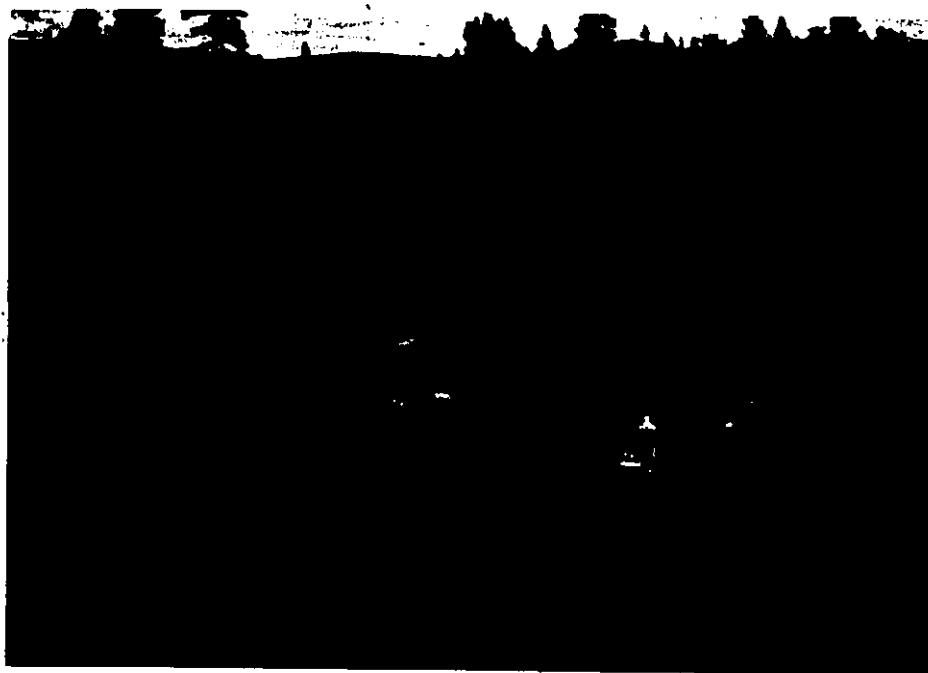larvae and pupae thriving. (In the far high background is
Renafjellet.)

Fig. 28

Fig. 29

COLOURED PICTURES

Fig. 30 The stream draining new Griffin "bog", 8 km south of
Huntsville, Ontario. Hellichiella larvae and pupae
occur sparingly on decaying sedges in 5 to 20 cm/sec
water current from early to late May. Note abundance
of sedges on margins of the 50 cm wide stream. Some
plants from this habitat are listed in Table. 21. In
the absence of rain this stream desiccates almost
completely in mid summer.

Fig. 31 A rill 20 to 30 cm wide draining a cattail marsh
in Caledon, Ontario, where H. excisum larvae and
pupae occur on vegetation in 5 to 10 cm/sec water
current in early May. In May and June this marsh
harbours an abundance of birds, likely hosts of
excisum adults. In the absence of rain the flow
from this marsh stops completely in summer.
In mid May overwintering females of Anopheles earlei
have also been collected around this site.

Fig. 30

Fig. 31

Fig. 32   The habitat of <u>H. latipes</u> in Knebworth Wood, Herts.
England, showing thick growth of vegetation covering
the stream which drains water from surrounding
farmlands.   In mid August 1980, when the picture was taken,
only a trickle of water remained and no simuliids
were found in the stream.   Dr. R. W. Crosskey, in
mid background, has collected <u>latipes</u> larvae and
pupae in this stream in March.   Some plants from this
site are listed in Table 22.

Fig. 32

Fig. 40. Abundance and migration corridors of Canada goose (Branta canadensis)
from the Boreal region breeding grounds to southern wintering areas
of North America. The distribution of H. anatinum, H. congareenarum
and H. innocens, which feed on the Anseriformes, is reflected in the
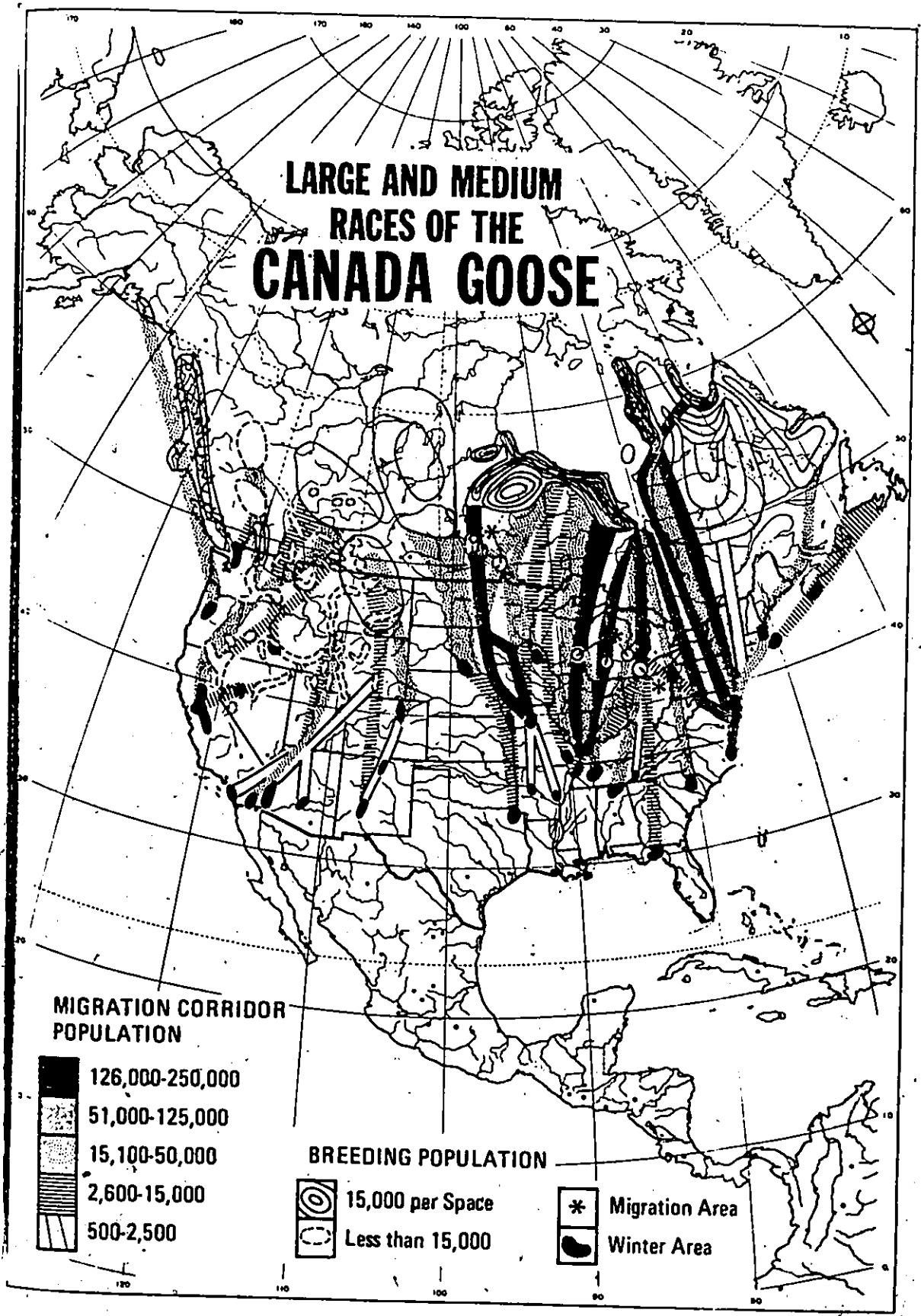distribution of these and other aquatic birds.

LARGE AND MEDIUM RACES OF THE CANADA GOOSE

MIGRATION CORRIDOR POPULATION

- 126,000-250,000
- 51,000-125,000
- 15,100-50,000
- 2,600-15,000
- 500-2,500

BREEDING POPULATION

- 15,000 per Space
- Less than 15,000

- * Migration Area
- Winter Area

Fig. 40

Reproduced from Bellrose (1976), p. 147.

Fig. 41. Abundance and migration corridors of the black duck (<u>Anas</u> <u>rubripes</u>)
from the Boreal region breeding grounds to the southern wintering
areas of North America. The distribution of <u>H</u>. <u>anatinum</u> and <u>H</u>.
<u>congareenarum</u> is reflected in the distribution of these and
other aquatic birds.

BLACK DUCK

MIGRATION CORRIDOR
POPULATION

76,000-150,000
56,000-75,000
26,000-55,000
11,000-25,000
1,000-10,000

BREEDING POPULATION

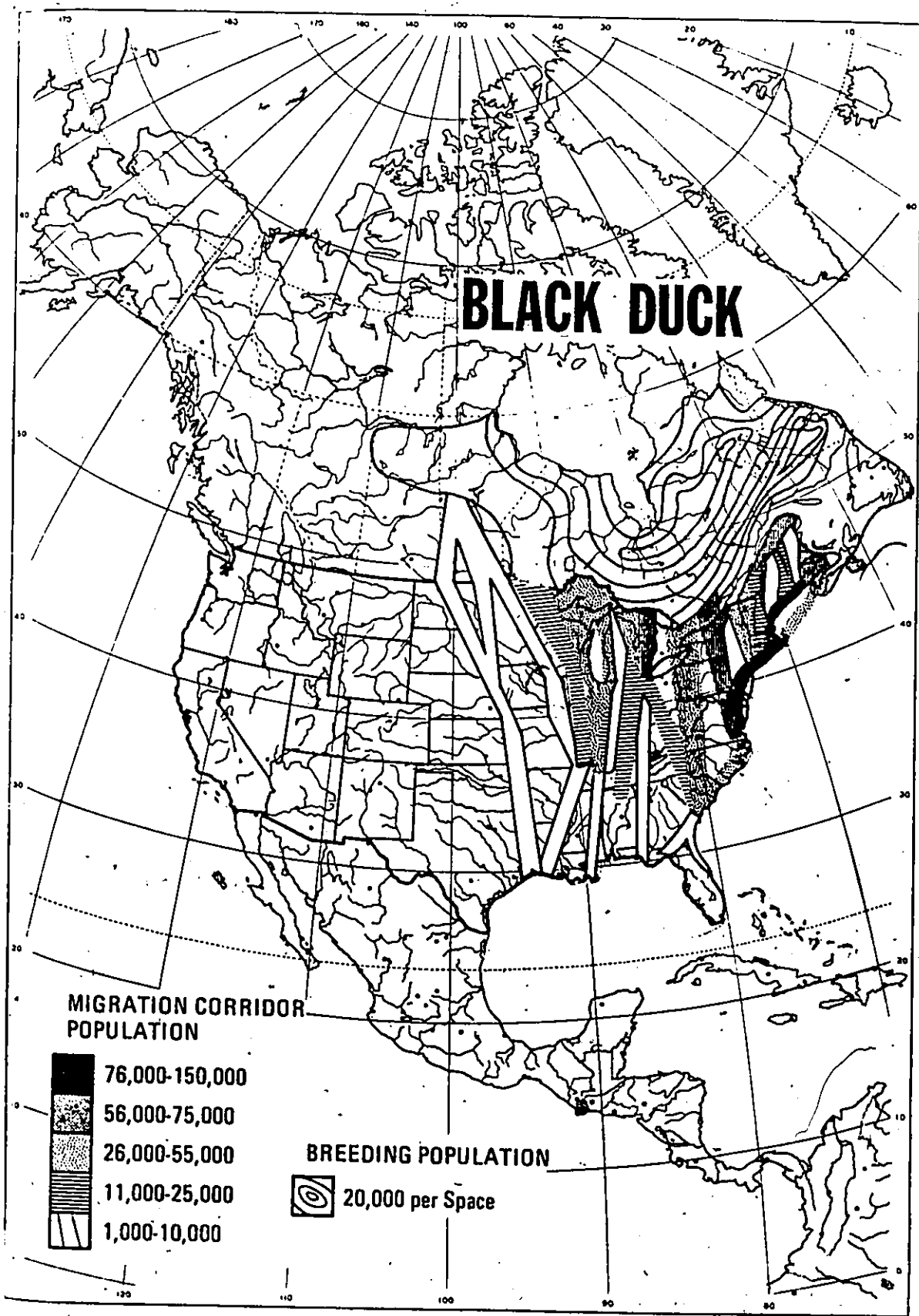20,000 per Space

Fig. 41   Reproduced from Bellrose (1976), p. 255.

Fig. 42. Abundance of the common goldeneye duck (Bucephala clangula americana)
in the Boreal region breeding grounds and southern overwintering areas.
The distribution of certain Hellichiella spp., primarily H. anatinum
and H. congareenarum, is reflected in the distribution of these and
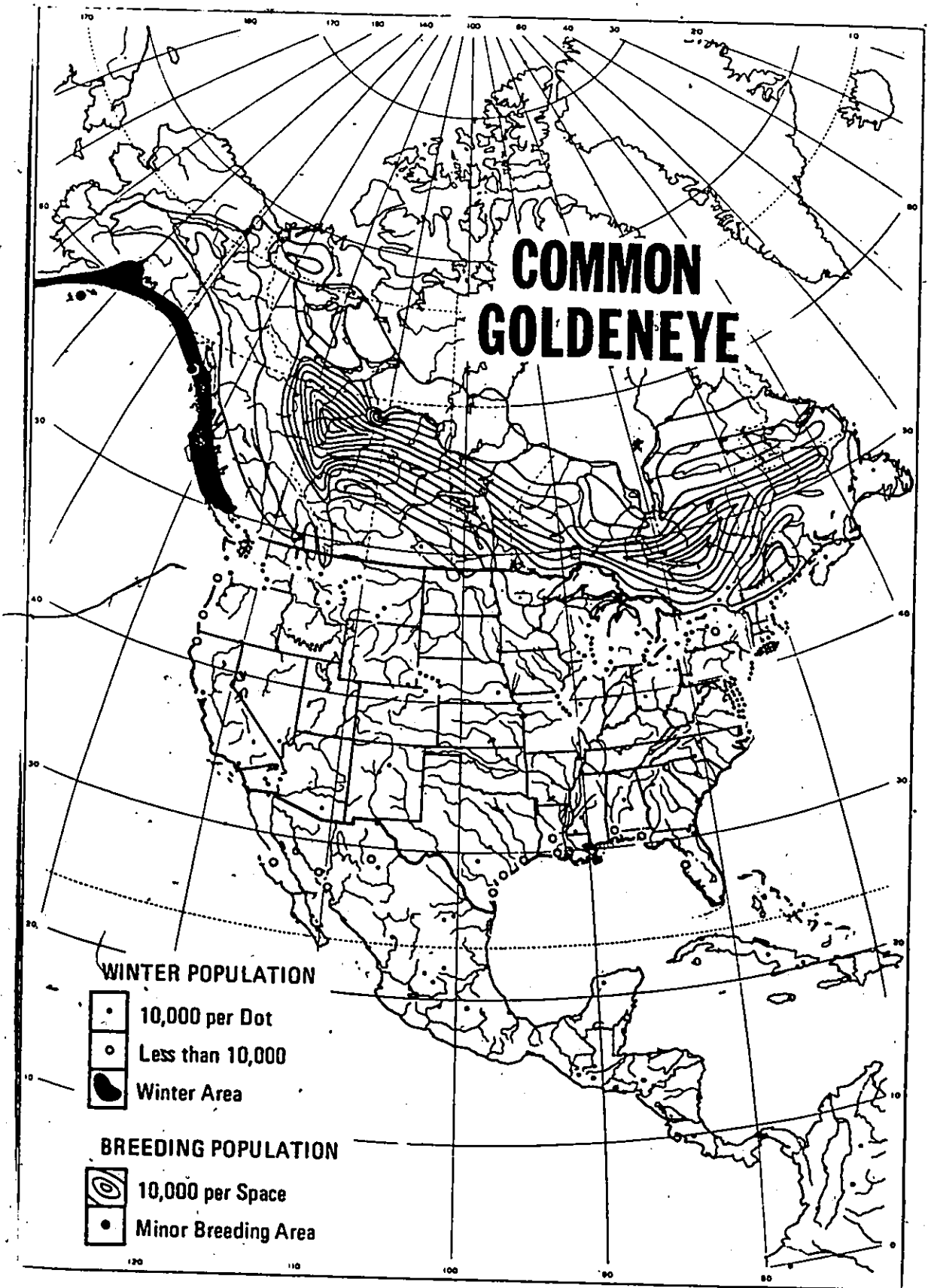other aquatic birds.

COMMON GOLDENEYE

WINTER POPULATION

- 10,000 per Dot
- Less than 10,000
- Winter Area

BREEDING POPULATION

- 10,000 per Space
- Minor Breeding Area

Fig. 42