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A study of the community gradient of the benthic insects of Wilbur Creek in Glacier National Park Montana

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A STUDY OF THE COMMUNITY GRADIENT OF THE BENTHIC INSECTS

OF WILBUR CREEK IN GLACIER NATIONAL PARK, MONTANA

By

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This work is dedicated to my parents, and to the "wee beasts" who were subjected to my scrutiny.

CHAPTER I

INTRODUCTION

The concept of community structure is not new to biologists. Victor E. Shelfield (1935) recognized that in a given habitat, taxa found seem to occur in non-random patterns, with certain limiting factors setting boundaries to these patterns. Odum (1971) defines a community as "any assemblage of populations living in a prescribed area or habitat".

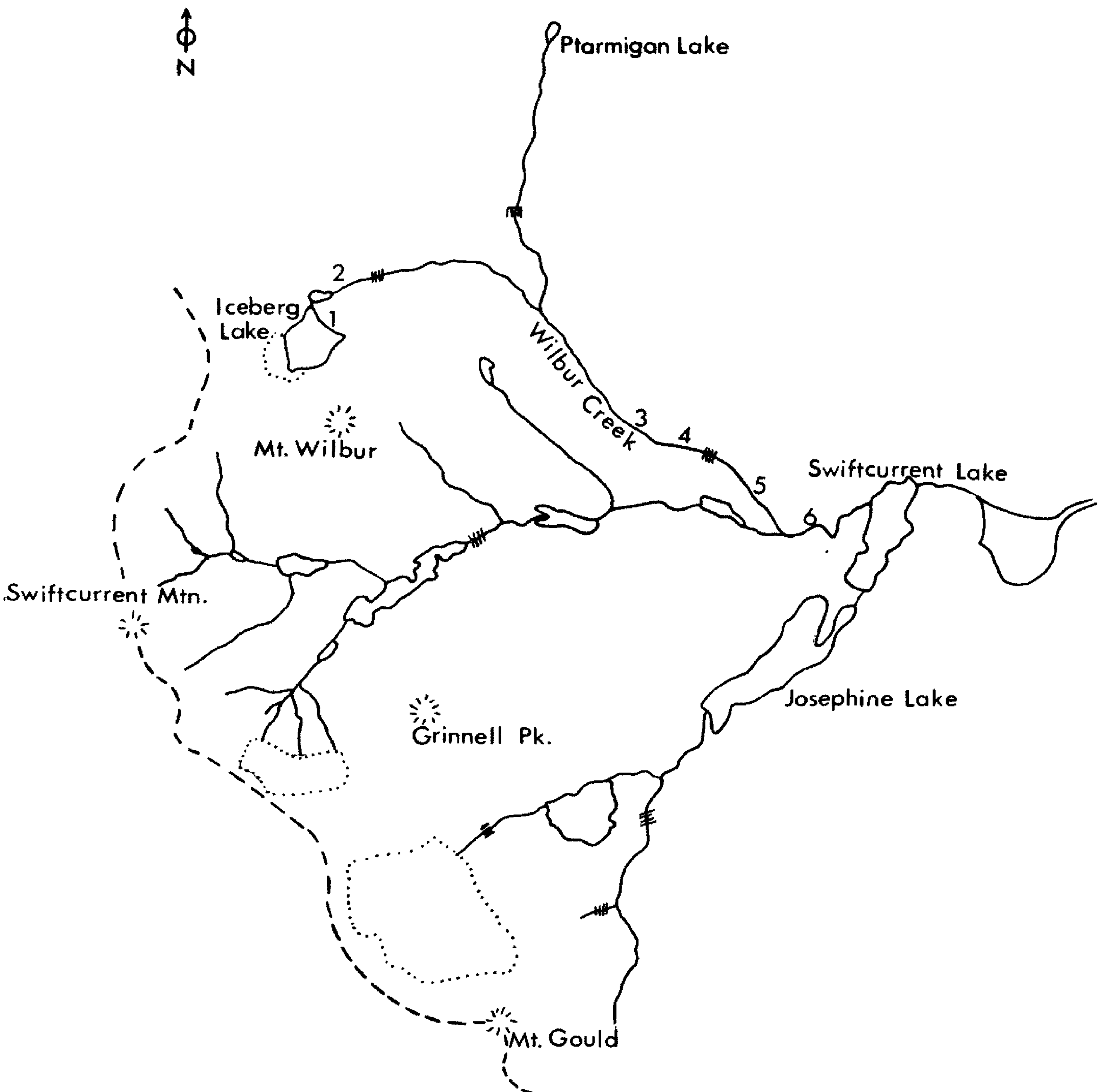
A number of methods for analyses of community structure have been used. Among the more common is the index of dominance in which the importance value of each species is mathematically determined. The index of similarity between two samples and various indices of specific diversity rely upon numbers of individual species (i.e., the variety or richness indices, the evenness index, the Shannon index).

In the last few years, the phi coefficient has gained in useage. Mathematically, calculation of phi will give the probability that upon finding species A in one sample, species B will also be found.. When 40 species are computed two at a time through a 2x2 contingency table, a symmetrical matrix containing 800 possible combinations occurs (because the probability that AxB equals the probability that BxA, only one-half of the 1600 possible combinations are needed). The aid of a computer was enlisted, and the data from the phi coefficient matrix was plotted using the unweighted pair group method of cluster

analyses as outlined by Roback, Cairns, and Kaesler (1969). The resulting dendrograms display various levels of associations occurring among groups or aggregations of individual species.

The purpose of this investigation was to describe a community of benthic insects taxonomically, and to discover associations among individual species. Biological associations were worked out by analyzing the stomach contents of the insects. Statistical associations were found using the correlation coefficient phi (ϕ). Similarity of sites was determined using a similarity index (S). The stream selected for study was Iceberg (Wilbur) Creek, which flows east from Iceberg Lake in the Many Glacier Valley in Glacier National Park, Montana. The total distance studied was approximately 5.5 miles. The stream dropped approximately 1500 feet in elevation between its origin at the lake and the bottom of the Many Glacier Valley. An alpine stream was selected for two reasons: first, an alpine situation should represent the most primitive type of community structure. The relative geologic youth, precambrian rock substrata, and cold temperatures act to slow the evolution of the community. Second, the area is in pristine condition and still relatively unaltered by man.

Map no. 1. The Many Glacier valley. Sample sites along Wilbur creek shown at numerals.



MAP 1. MANY GLACIER VALLEY

CHAPTER II

DESCRIPTION OF STUDY SITES

The Many Glacier Valley lies on the east slope of the Continental Divide in the Northeast sector of Glacier National Park, Montana. Iceberg Creek originates at Iceberg Lake in a small alpine cirque at 6080 feet elevation in the Many Glacier Valley. The lake is amictic and remains frozen most of the year, the ice cover retreating for only a few weeks during August. There are nearly always large pieces of ice floating about in the lake, and the temperature rarely rises above two or three degrees Celsius. The lake lies in a small cirque formed by walls of precambrian argellitic limestone rocks of the Belt series, particularly Siyeh limestone, which rise about 1,000 feet above the lake. Along the trail from Iceberg Lake the other layers of rock in the Belt series become apparent: red Grinnell argillite, green Appekunny argillite, and Altyn limestone forming the base of the valley.

The area exhibits typical alpine vegetation with Krumholz communities of alder (Alnus sp.) and whitebark pine (Pinus albicaulis) dominating the cirque vegetation. As one progresses toward Swiftcurrent Lake, a transition to vegetation typical of the Canadian biome becomes apparent with Engelmann spruce (Pices englemanni) and Douglas fir (Pseudotsuga menziesii) communities dominating.

Five of the original sites were selected for statistical and biological analyses. Site 1, at Iceberg Lake, was omitted because this investigation was designed to include the stream-dwelling forms

only. See map number one for placement of sites. The terms used in describing substrate at each site are described by Lagler (1952) in his publication, "Freshwater Fishery Biology".

Site Two

Site 2 was established approximately 30 meters below the outlet from the lower section of Iceberg Lake proper. The substrate is composed mainly of sheets of argillitic bedrock, rocks, and some rubble. Small riffles and runs predominate. There are a few large boulders and a little gravel on the substrate. The stream is wide and shallow and the water of uniform depth. Alder (Alnus sp.), various sedges, and the monkey flower(Mimulus) are found along the bank.

Site Three

Site 3 was located approximately 4.16 kilometers downstream from site 2. It is easily reached by following the service road from the campground to a point along the stream which houses the concrete intake flume which is the major water source for the Many Glacier Hotel and campground complex. The stream is narrow with large boulders and rocks forming the substrate. Rapids and riffles predominate. There are few pools. The water is not of uniform depth. Alder bushes and lodgepole pine (Pinus contorta) provide much shade to this stretch of stream.

Site Four

Site 4 was located about 900 meters above the Many Glacier Campground. The stream at this point is wide, shallow, and of uniform depth. Few boulders are present and many riffles and runs predominate. The substrate material is mostly glacial till which was deposited by the receding glacier. The substrate is unstable because of its recent geologic past and still bears scars from recent shifting of the stream

course.

Site Five

Site 5 was just behind and upstream from Many Glacier Campground. Geologically it exhibits an unstable substrate which is composed of boulders, rocks, rubble, and sand. There are riffles, runs, and a few deep areas in which some sand and silt have accumulated. In 1964 the spring period of high water deposited logs and boulder material which are still evident along the banks upstream from this point to a point approximately 250 meters below site 3.

Site Six

Site 6 was located at the eastern tip of the campground. The stream is wide, with variable depth, and also exhibits shifting substrate because of glacial till composition. There are sandbars at various points along the flow. The substratte is dominated by riffles, runs, and deep pools, although areas of mud and silt deposition occur.

CHAPTER III

METHODS AND MATERIALS

Sampling the Biota

The insect fauna was sampled with a hand screen. The investigator kicked up benthic material and collected insects from the net with BB forceps, storing them immediately in 4-dram shell vials containing 70% ethyl alcohol to which 10 ml glycerin had been added per gallon of alcohol. The addition of glycerin insured pliability of the insects which aided in taxonomic determination. One dowel of the hand screen was calibrated to 1-centimeter units to allow recording of the average depth at each site. Maximum and minimum depths of sample areas were taken and the average recorded. A 50-foot piece of 500 lb. test nylon line was calibrated to meters to measure the stream widths.

Chemical Analyses

Chemical analyses were accomplished by using wet chemicals from the Hach Co. At each site dissolved oxygen, methyl orange and phenolphthalein alkalinities, and free carbon dioxide were recorded. The air and water temperatures were taken. (See Table 3) At each site the number of screenings depended on the biomass and diversity recovered. The investigator screened until convinced that all possible habitats had been collected at each site.

Identification

Identification of the insect fauna included the use of a Bausch and Lomb dissecting microscope.

Sampling

Physical and chemical parameters were recorded at each sampling period. Each site was visited at least four times during the period from July 9, 1972, to April 24, 1973. The first sampling took place July 9, the second July 17, the third July 24, the fourth August 3, the fifth September 2, the sixth October 2, and the seventh on April 27 of the following spring. Each sampling period consisted of two days. On the first day, sites 5 and 6 were sampled. The second day was required to complete the five mile hike into Iceberg cirque.

Weather Conditions

The summer of 1972 was cooler than normal. The first three sampling periods took place under sleet and blizzard conditions. The water temperature remained at or near 0° Celsius presumably for a longer than normal period. Because water temperature is thought to be one of the critical factors controlling insect emergence, it is possible that the emergence patterns were later than normal.

Statistical Analyses

Two statistical tests were used to discover associations between the aquatic insects.

The Similarity Coefficient (S)

The similarity coefficient (S) was computed using the formula:

$$S = \frac{2C}{A+B}$$

Where A = Number of species in site A
Where B = Number of species in site B
Where C = Number of species common to both

This coefficient was chosen as it appears in Fundamentals of Ecology (Odum, 1972) and was selected because of its simplicity.

The Association Coefficient

The association coefficient phi (ϕ) was also chosen because of its

relative simplicity. It is based on the decision that either a species is present, or is not, and eliminates a great deal of time that might otherwise be spent counting insects. On the other hand, one must keep in mind that he is limited to the type of frequency data he can obtain from this formula. The coefficient was computed using the following function:

	+	−	
+	A	B	(A+B)
−	C	D	(C+D)
	(A+B)	(B+D)	N

$$\phi = \sqrt{\frac{AB-BC}{(A+B)\ (C+D)\ (A+C)\ (B+D)}} = \sqrt{\frac{X^2}{N}}$$

A computer program was then written (see Appendix B) for the function: $\sqrt{\frac{X^2}{N}}$ which would compute the phi coefficient. The same program printed out the resulting coefficients in order of magnitude from least (0.000) to highest probability (1.000). Dendrograms were then constructed to illustrate the clustering of the species. The phi coefficient yields the probability that given species A, species B will appear in the same sample.

CHAPTER IV

RESULTS

Abiotic

Chemical Analyses

Chemical analyses were done to make certain that the chemical environment remained constant. The results of the analyses indicate that the chemical conditions did not vary to a significant degree and fell into normal range for oligotrophic waters. These data compare favorably with tests run during the summer of 1970 by the Park Sanitarian (Sonstelie 1970). Ranges of values for Wilbur Creek appear in Table 1. All concentrations are recorded in parts per million (ppm).

Stream Widths and Depths

The width and average depth of the water at each station were recorded at each sampling period. The depths recorded reflect the specific area sampled. They do not indicate an accurate maximum and minimum depth of the stream as a whole, but indicate the range in which that community of insects was found. The values found during the summer of 1972 and spring of 1973 appear in Table 2.

Temperatures

Both air and water temperatures were recorded at each sampling period and appear in Table 3.

Table 1. Water chemistry analyses for Wilbur creek for the summer of 1972.

TABLE 1

WATER CHEMISTRIES

	8/2/72	9/1/72	10/2/72
Dissolved Oxygen	9.8	—	—
Free Carbon Dioxide	2.5	—	—
Phenolphthalein Alkalinity	0	—	—
Methyl Orange Alkalinity	53	—	—
pH	7.4	—	—

Site No. 3

	8/2/72	9/1/72	10/2/72
Dissolved Oxygen	8.1	9.2	—
Free CarbonDioxide	3.5	2.0	—
Phenolphthalein Alkalinity	0.0	0.0	—
Methyl Orange Alkalinity	51	51	—
pH	7.3	-	—

Site No. 4

	8/2/72	9/1/72	10/2/72
Dissolved Oxygen	9.2	10.4	—
Free Carbon Dioxide	2.0	2.0	—
Phenolphthalein Alkalinity	0.0	0.0	—
Methyl Orange Alkalinity	50	49	—
pH	7.5	-	—

Site No. 5

	8/2/72	9/1/72	10/2/72
Dissolved Oxygen	8.4	8.8	8.8
Free Carbon Dioxide	2.5	.6	tr
Phenolphthalein Alkalinity	0.0	0.0	0.0
Methyl Orange Alkalinity	53	51	52
pH	7.3	-	-

Site No. 6

Table 2. Stream widths and depths for Wilbur Creek during the summer of 1972.

Table 2

Physical Perameters

	July	August	September	October	April
STREAM WIDTH (M)	—	6.5	6.0	—	—
STREAM DEPTH (DCM)	—	2.0-5.0	1.0-3.0	—	—
STREAM WIDTH (M)	—	6.5	5.5	—	—
STREAM DEPTH (DCM)	—	1.3-3.7	—	—	—
STREAM WIDTH (M)	—	7.0	7.0	—	6.9
STREAM DEPTH (DCM)	—	2.0-3.5	1.0-2.5	—	1.5-2.0
STREAM WIDTH (M)	—	—	8.5	—	—
STREAM DEPTH (DCM)	—	—	—	—	—

Table 3. Air and water temperatures for Wilbur Creek during the summer of 1972.

		JULY 9	JULY 17	JULY 25	AUGUST 2	SEPTEMBER 2	OCTOBER 2	APRIL 29
SITE 2	AIR	38	--	58	58	--	--	--
	WATER	32.5	--	37	40	36	--	--
SITE 3	AIR	--	--	--	58	68	45	--
	WATER	--	--	--	41	49	40	--
SITE 4	AIR	--	--	--	46	67	45	28
	WATER	--	--	48	50	50	43	32
SITE 5	AIR	38	--	--	52	62	45	28
	WATER	32.5	--	48	43	49	43	32
SITE 6	AIR	38	--	--	53	68	45	28
	WATER	32.5	--	48	52	54	43	--

TABLE 3

TEMPERATURES
(Degrees Farenheit)

Biological

The results of the biological data will be considered in two phases. The first phase deals with the microscopical examination of insect stomach contents, and the second with statistical correlations.

Gut Analyses

Species which were found to contain parts of other insects only were considered strict carnivores. These included Isoperla ebria at site 2. Site 5, however, exhibited Ephemerella doddsii, Parapsyche elsis, Rhyacophila vaccua, and possibly R. tucula were found to be strict carnivores. Those stomachs examined containing both plant and animal matter were considered belonging to omnivores and occurred with greater frequency than the carnivores. These included Arcenopteryx watertoni, A. bradleyi, paraperla brevis, Rhyacophila accropedes, Rhyacophila hyalinata, and R. vaccua. If plant material only was found, the insect was deemed an herbivore, as in the case of Capnia spenceri and Cinygmula sp. Often herbivores were found to contain identifiable remnants of filamentous algae in the anterior portion of the gut indicating ingestion of living plant material as well as dead leaf material in the same region. Apparently the insects were grazing an area and consuming all plant material encountered. Included in this type feeders were Nemoura columbiana, N. haysii, Rithrogenia robusta, Epeorus deceptivus, and E. grandis. This, perhaps, is a mechanism to spearate niches among the herbivores. For the purposes of this study, however, both feeders were considered herbivores. The results of the analyses appear in Table 4. The raw data appear in the appendix (Appendix B).

Information on food of aquatic insects gained by examination of gut contents is somewhat scarce in the literature. Hynes (1971) has an extremely good literature review on the subject and is the source of the following information. Hynes (1941) and Chapman and Demory (1963) have reported a major constituent of the diet of nemourid stoneflies and some Trichoptera as being mosses. Hynes has found detritis in the gut of baetid mayflies. According to Lloyd (1921, Slack (1936) and Nielson (1942), dead leaves and water-soaked wood are common constituents of the diets of limnephilid caddisflies, the stonefly genus Pteronarcys (Muttkowski and Smith, 1929), and filipalpian stoneflies (Hynes, 1941). Work indicates that plant debris, mineral particles, diatom frustules, and leaf tissue serve as the main foodstuff in the diet of most aquatic insects (Bengtsson, 1924; Wissmeyer, 1926; Slack, 1936; Moon, 1939; Hynes, 1941, 1963; Jones, 1949, 1950; Brown, 1961; Warren et al, 1960; Chapman and Demory, 1963). Though many ephemeropteran species seem to be vegetarian (Derange, 1960), Muttkowski and Smith (1929), and Warren (1960) report Ephemerella doddsii as being "entirely carnivorous".

The results of the gut analyses appear in tabular form in Tables 10 and 11. The most common foodstuff found in the gut was organic material. They included Epeorus grandis which fed on 80-100% organic debris; E. deceptivus, 50-75%; and Baetis bicaudatus, 50-97%. All forms examined at site 2 contained some organic debris and seemed to vary their diets with diatoms, filamentous algae, and some sort of animal material. At both sites, dipteran of the family Tendipedidae served as a common source for animal material, with the Ephemeroptera, Trichoptera,

and Plecoptera following in frequency.

The Plecoptera as a group exhibited varied diets. Some were totally organic detritis feeders at site 5, but at site 2 the same species varied the diet with diatoms and filamentous algae. The diet of Peltaperla brevis included 50-90% organic material with filamentous algae and Tendipedidae larvae found occasionally. Arcynopteryx watertoni, found only at site 5, fed on organic debris (15-60%) diatoms (10-20%), and filamentous algae (1-5%), and up to 50% animal material. Animal material included unidentifiable pieces and parts of the orders Plecoptera, Ephemeroptera, Trichoptera, and Diptera (Tendipedidae). Often mouthparts, whole sclerites, and crania were all that remained in the gut making definitive identification difficult at best. The investigator found it necessary to illustrate these parts which were found to be the most persistent in the gut. These usually included the mandibles and maxillae, the crania, anal prolegs, and tarsal claws. Reference illustrations appear in Figures 8 - 15.

Arcynopteryx bradleyi, found only at site 2, eliminated organic debris from the diet, preferring animal material (90%) with some diatoms and filamentous algae present. A. watertoni fed to a much greater degree on vegetable matter, however A. bradleyi was found to contain trichoptera parts unlike A. watertoni which never evidenced these insect remnants. Further research is needed to determine feeding relationships and possible competition at the area of range overlap between the two species of Arcynopteryx. Because of the present state of the taxonomy of the aquatic insects of the area, the alloperlid stone-flies could not be identified to species. However, the data indicate that Alloperla (borealis fidelis complex) and the one sample of

Alloperla sp. at site 2 rely on diatoms, filamentous algae, pollen, and organic debris with some animal material (Tenidpedidae) present. The other alloperlids examined at site 5 fed on other Plecoptera. The last two species of stoneflies examined were members of the genus Isoperla. Isoperla ebria fed on diatoms (5-40%) and organic material (40%), mayflies (up to 60%), with filamentous algae and pollen appearing to be of secondary importance. The single sample of I. sordida contained only organic material.

With two exceptions, the Ephemeroptera were herbivores. The diet of Ephemerella doddsii consisted almost entirely of animal material with Tendipedidae (up to 90%) as the preferred prey. However, Ephemeroptera and Plecoptera nymphs were found in the gut occasionally and 5-60% organic material was found. Ephemerella coloradensis evidenced approximately 70% animal material in one gut sample, but concentrated on organic material (38-100%) and filamentous algae (10%). The other forms (i.e., Cinygmula sp., Rithrogenia robusta, Epeorus deceptivus, Epeorus grandis, Baetis bicaudatus) were found to contain entirely plant-based food (living or dead plant matter). Cinygmula sp. fed only on organic matter and in one instance 50% of the contents of one stomach consisted of diatoms. Rithrogenia robusta also fed on organic matter, but varied the diet with filamentous algae and pollen. Epeorus deceptivus and Epeorus grandis exhibited no preference for diatoms, but organic material appeared to compose 50-100% of the gut content. Baetis bicaudatus also preferred organic material (50-90%) but contained filamentous algae (up to 20%) and bryophyte material as well. At site 2, filamentous algae was fed upon with greater frequency at the lower site.

The Trichoptera examined were carnivores with little preference for feeding on vegetable matter. Only Parapsyche elsis, Arctopsyche grandis, and Rhyacophila accropedes exhibited a tendency to feed on vegetation. One sample of Parapsyche elsis was found to contain filamentous algae (2%). Arctopsyche grandis varied an otherwise carnivorous diet with diatoms and filamentous algae. Rhyacophila accropedes appeared to have a more general diet concentrating on organic debris (20-100%), diatoms (5%), and animal material (Plecoptera 80% in one sample, and Trichoptera 25% in another). Rhyacophila hyalinata appeared to be carnivorous (animal material provided 30% of one sample, as was Rhyacophila tucula. Samples of R. tucula contained up to 70% Plecoptera parts. Rhyacophila vaccua fed mostly on Ephemeroptera (80% in one sample) and the mouthparts of R. accropedes (50%) were found in another sample. Parapsyche elsis, though found to contain vegetation in one sample, fed mostly on Alloperla nymphs (60%), Baetis bicaudatus nymphs (25%), Hydropsychidae larva, unidentified Trichoptera (up to 80%), and some Tendipedidae larva. Epeorus sp., Rithrogenia robusta, Rhyacophila tucula were also found present in the gut of P. elsis. Rhyacophila accropedes at site 5 fed on organic detritis and animal material (up to 80%). At site 2, this insect varied its diet by feeding on diatoms, Plecoptera nymphs, and Trichoptera larvae as well as organic detritis.

Nearly all species examined contained mineral particles in the gut. It is possible that these particles aid in the grinding action of the midgut, thereby helping to reduce the mass of ingested material in preparation for digestion.

Table 4. Results of the gut analyses of aquatic insects from site 2.

	9/1 E. *Columbiana*(2)	9/1 A. *Lavsii* (3)	7/17 A. *wateri*[...](7)	7/9 A. *bradleyi*(8)	7/17	9/1	7/9 I. *ebria*(10)	7/25	9/1	7/25 I. *sordida* [illegible]	7/25 A. *boreali*[...]*s*(1)	9/1	9/1 *Alloperla* sp.(18)	7/9 *Cinygmula* sp.(20)	7/17	9/1	7/25 E. *robusta* (2?)	7/9 B. *bicaudatis* (24)	9/1	7/25 R. *angelita*(28)	9/1	7/9 R. *accropedes*(29)	7/25	9/2
Diatoms		2	20		+		40	5			1	+	5	40	10									
Cymbella		+			+		+	+						+										5
Ceratoneis							+							+										+
Navicula					+			+						+										+
Desmidaceae																								
Filamentous algae	40		5		+		10				1	10		10			5		20					
Oedogonium																								
Bryophyta																10			1					
Pollen			+				2	1			70													
Organic debris	60	98	10	10			48	40	2	50		90	95	50	90	50	5	100	60		100	20	100	65
Sand										50									2					5
Plant material														+		40	85							
Animal material				80	95	+														100				
Plecoptera																						80		
Isogenus																								
Alloperla																								
Isoperla																								
Brachyptera																								
Ephemeroptera				+				60																
Baetis																								
Epeorus																								
Rhithrogenia																								
Diptera																								
Tendipedidae			65	+	+	90					30													
Trichoptera																								25
Hydropsychidae					+	+																		
R. *accropedes*																								
R. *tucula*																								
Hydracharina						10																		

TABLE 10. GUT ANALYSES SITE 2

Table 5. Results of the gut analyses of aquatic insects from site 5.

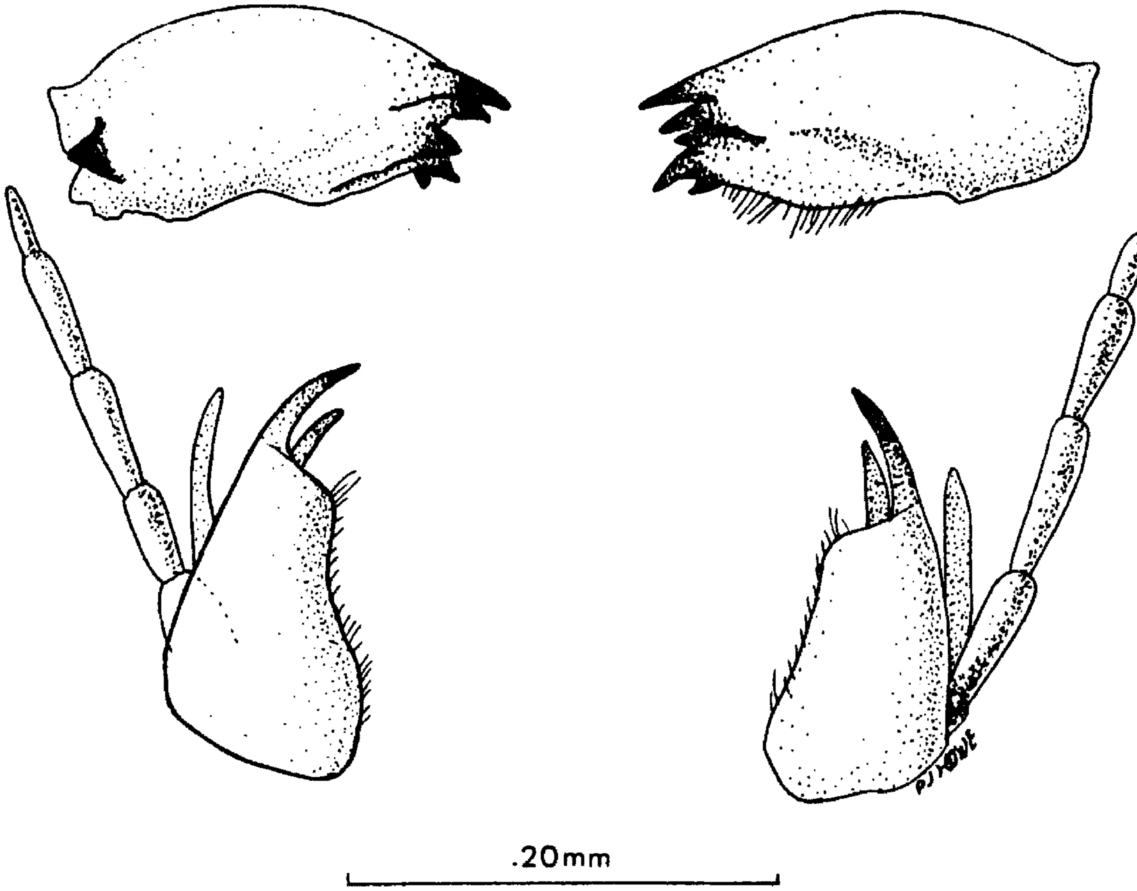
	9/1 L. columbiana	10/2	9/1 I. haysii(?)	10/2	4/24/73	4/24/73 Leuctra sp.	7/25 E. brevis( )	8/2	4/24/	7/25 A. water... (7)	8/2	9/1	10/2	4/24/73	9/1 Alloperla sp. A(17)	10/2 Alloperla sp.(18)	4/24/73	4/24/73 Ameletus sp.(19)	7/17 Cinygmula sp. (20)	7/25	?/2	4/24/73	7/17 R. robusta (21)	7/25	?/2	?	?/2	4/24/73	7/17 E. decepiens (22)	?/1	7/25 E. grandis(23)	10/2	4/24/73
Diatoms								+			10	+	20	5			1					50											
Cymbella													+																				
Cerataoneis											+		+																				
Navicula													+																				
Desmidiaceae													+																				
Filamentous algae									2	1	5		+											30				+					
Oedogonium																																	
Bryophyta																																	
Pollen															+									35									
Organic debris	50	100	100	100			50	+	90	60	60			15	30		5	90	15	15	15	50	20		95	20	10	100	50	75	90	80	100
Sand	50					1	50	+			+		30	30	30			10	85	85			80	35	5	80	90		50	25	10	20	
Plant material						99																											+
Animal material								+		40			10	50	40																		
Plecoptera												+		+	+	10095																	
Isogenus																																	
Alloperla																																	
Isoperla																																	
Brachyptera																																	
Ephemeroptera												+																					
Baetis														+																			
Epeorus																																	
Rithrogenia																																	
Diptera																																	
Tendipedidae									10		25		40		+																		
Trichoptera																																	
Hydropsychidae																																	
R. accropedes																																	
R. cucula																																	
Hydracharina																																	

TABLE 11. GUT ANALYSES SITE 5

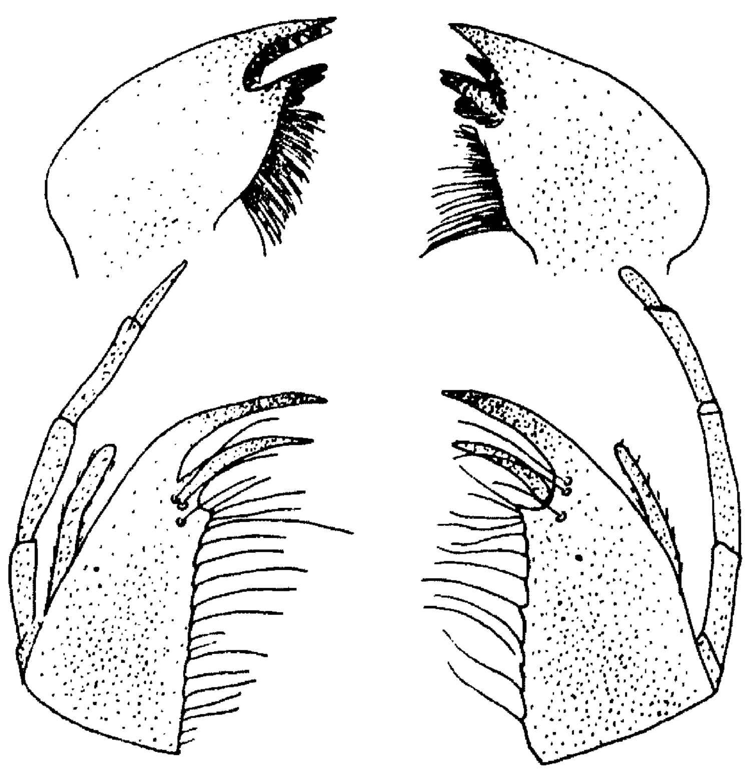
	B. bicaudatis(24)						E. doddsii(				E. coloradensis([illegible])				[illegible]hyalinata(30)	R. [illegible]ucula(31)		[illegible]			[illegible]						[illegible] occidentalis(40)	[illegible]acopula(nude)([illegible]7)		[illegible] acroredes(29)		[illegible] ramulis(35)
	7/17	7/25	[illegible]/2	[illegible]/1	[illegible]0/2	4/24/73	7/17	7/25	[illegible]/2	[illegible]/2	[illegible]/17	/2	[illegible]/1	[illegible]/24/73	7/2[illegible]	7/25	[illegible]/1	[illegible]	[illegible]	[illegible]	7/17	[illegible]	[illegible]	[illegible]/1	[illegible]0/2	[illegible]/24/73	[illegible]/24/73	5/2	[illegible]/1	10/2	[illegible]/24/73	4/24/73
Diatoms											2																					1
Cymbella																																
Ceratoneis																																
Navicula																																
Desmidaceae																																
Filamentous algae						1					10	+													2							1
Cedogonium													30																			
Bryophyta																																
Pollen																																
Organic debris	50	50	30	35	75	97	5	5		40	33	50		1[illegible]0	70		30	50	3[illegible]	20									100		20	
Sand	50	50	20	15	25		5	5		60	50	50																		95		
Plant material			+			2																										
Animal material								90	+				70		30				[illegible]			100			98					5	80	98
Plecoptera																+	70				+			10	+		+				+	
Isogenus																																+
Alloperla									+												60											
Isoperla																																
Brachyptera																																
Ephemeroptera								+					+							20												
Baetis									+												25											
Epeorus									+													+										
Rithrogenia																						+										
Diptera																																
Tendipedidae							90	+	+												15	+			+							
Trichoptera																						+		80							+	+
Hydropsychidae																								10								
R. acroredes																		50														
R. [illegible]ucula																							100									
Hydracharina																																

Table 11. (cont.) [illegible]

Fig. 1. Nymphal mouthparts, ventral view, of mandibles and maxillae of Arcynopteryx bradleyi, A. watertoni.



Arcynopteryx bradleyi



Arcynopteryx watertoni

Fig. 2. Nymphal mouthparts, ventral view, of mandibles and maxillae of *Nemoura haysii*, *N. columbiana*, and *N. cataractae*.

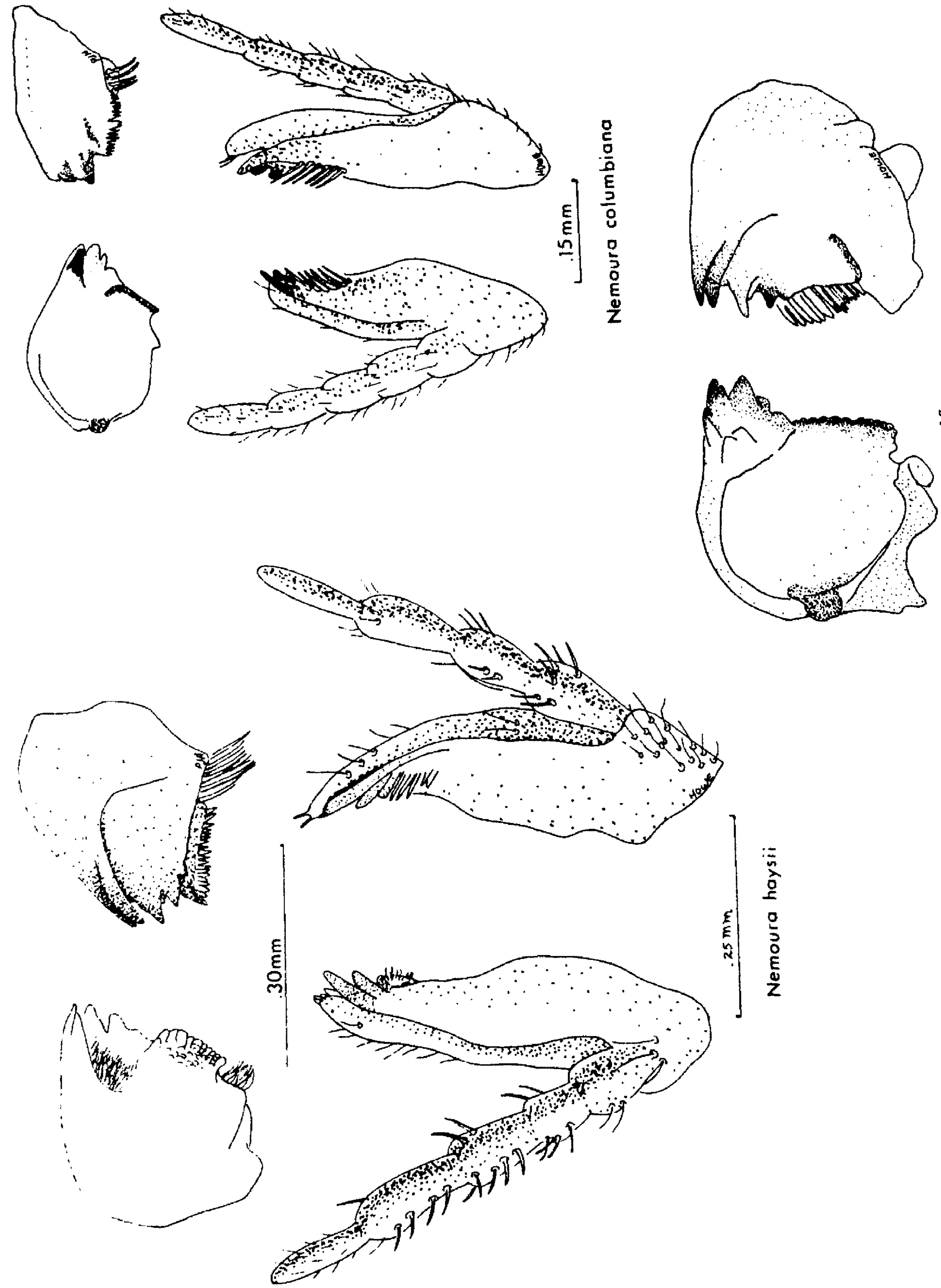
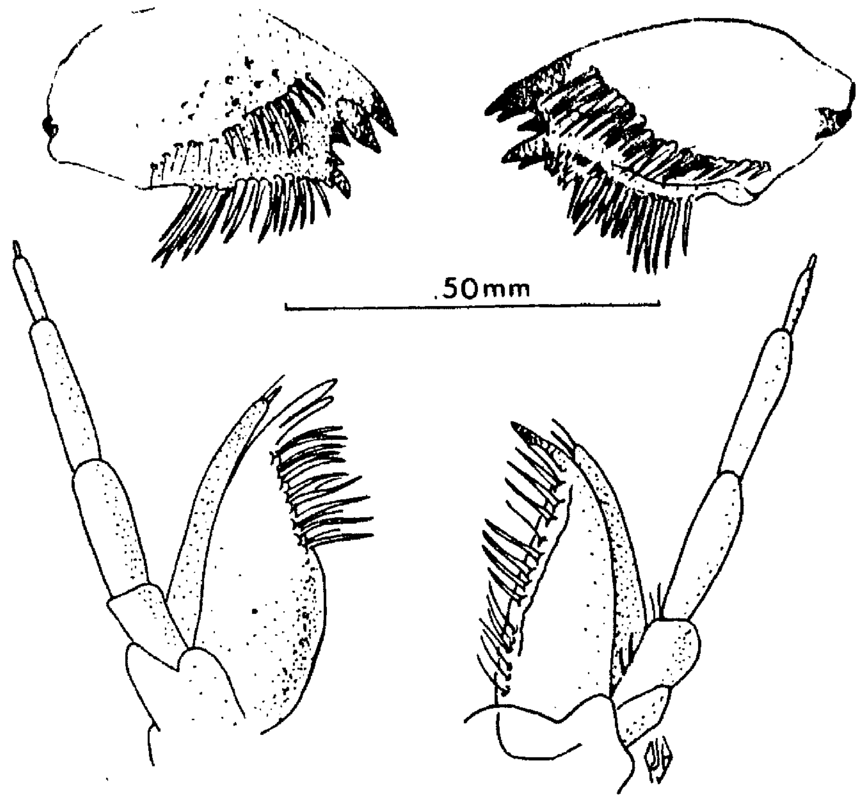
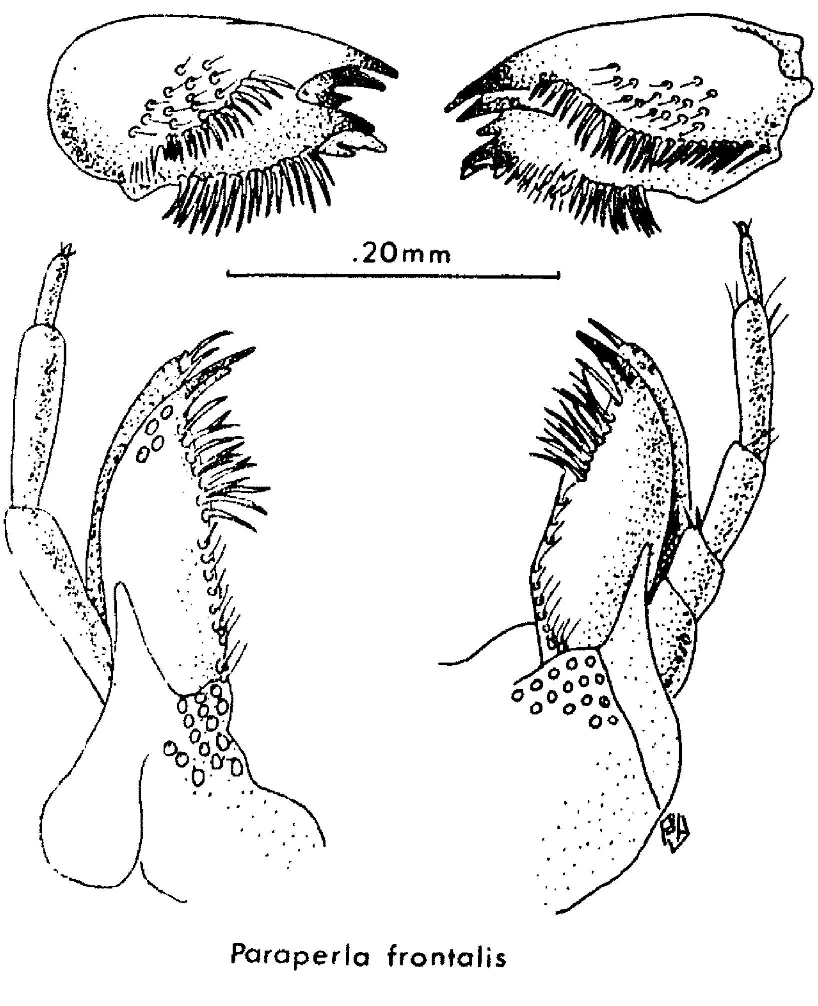

.15mm
Nemoura columbiana
.15mm
Nemoura cataractae
30mm
.25 mm
Nemoura haysii

Fig. 3. Nymphal mouthparts, ventral view, of mandibles and maxillae of <u>Alloperla</u> (Borealis-fidelis), <u>Paraperla frontalis</u>.

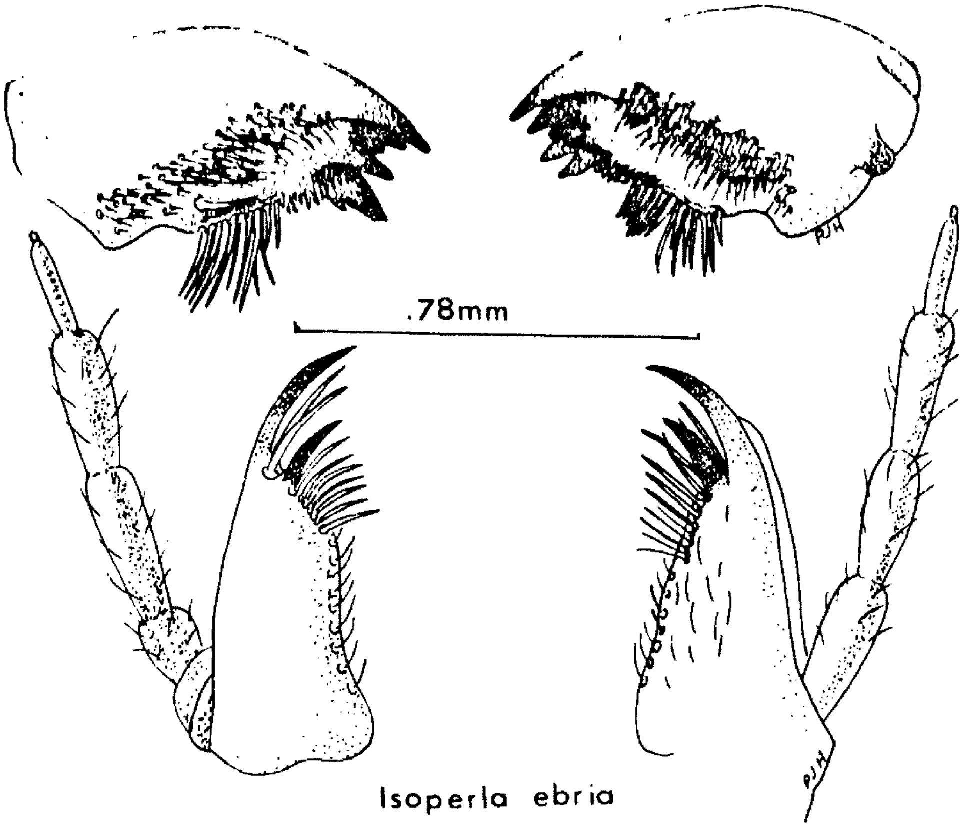


Alloperla borealis-fidelis

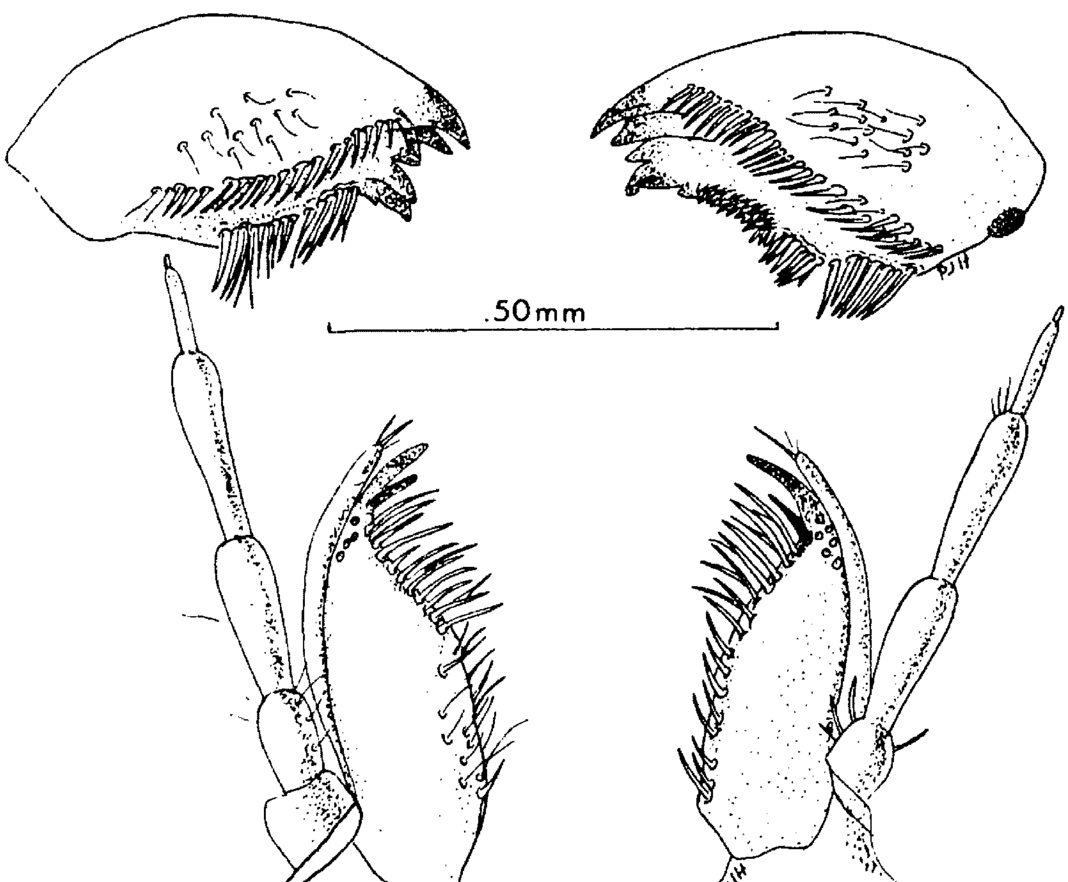


Paraperla frontalis

Fig. 4. Nymphal mouthparts, ventral view, of mandibles and maxillae of _Isoperla_ _ebria_, _I_. _sordida_.

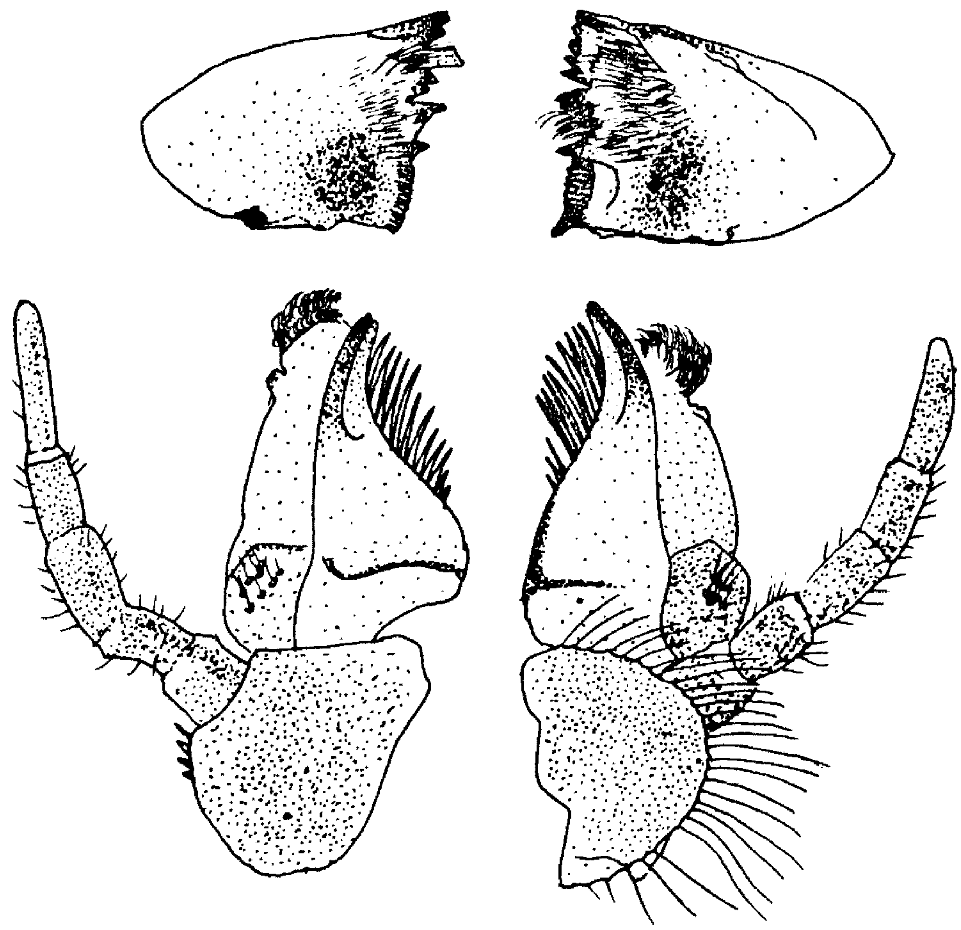


Isoperla ebria



Isoperla sordida

Fig. 5. Nymphal mouthparts, ventral view, of mandibles and maxillae of *Peltaperla brevis*.



Peltaperla brevis

Fig. 6. Larval mouthparts, and anal proleg of the genus *Rhyacophila* (Trichoptera), (a) *R. accropedes*, (b) *R. angelita*, *R. tucula*, (d) *R. hyalinata*, (e) *R. vaccua*, (f) *R. verrula*.

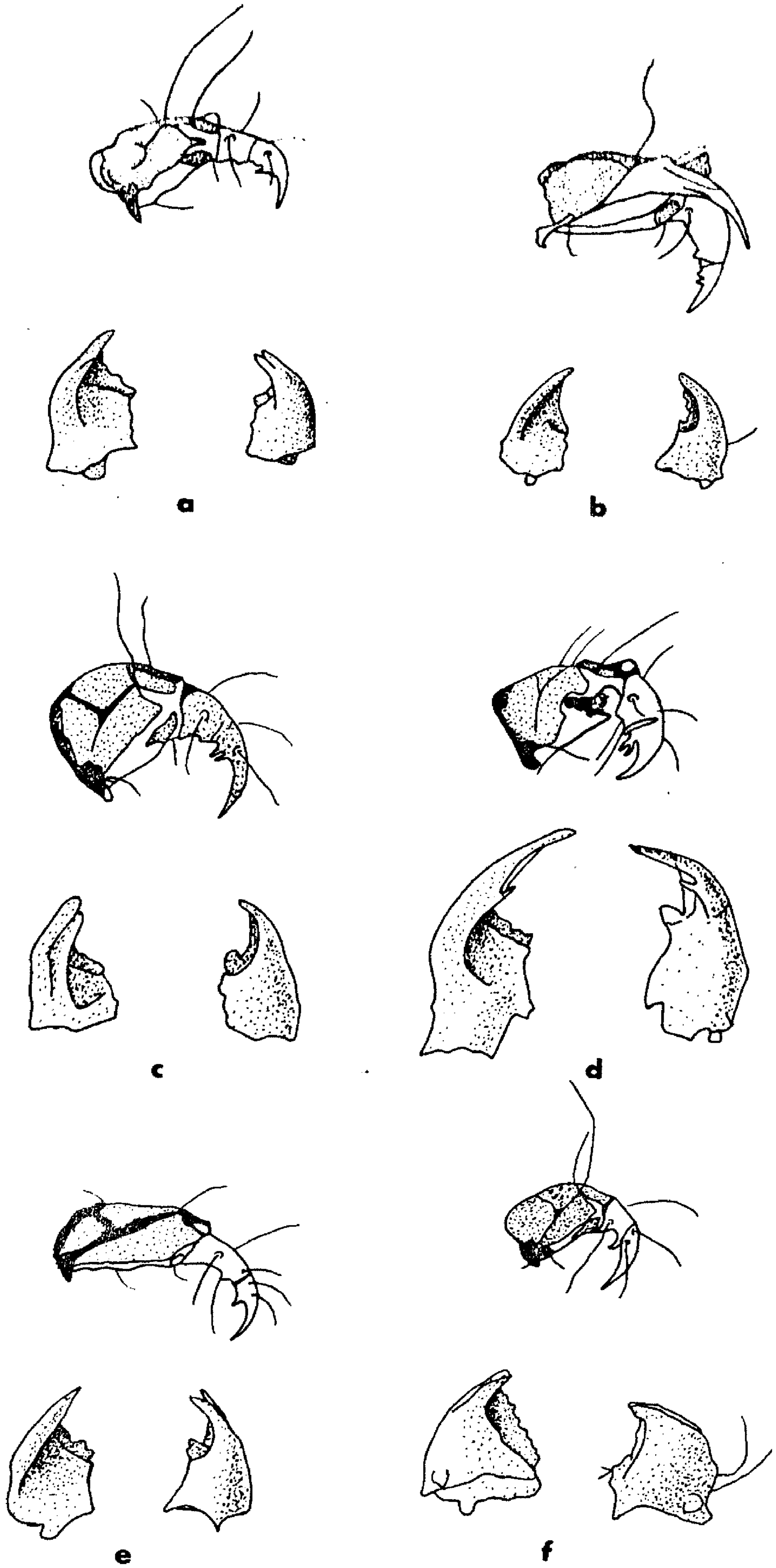

a
b
c
d
e
f

Fig. 7. Nymphal mouthparts of members of the Ephemeroptera found in Wilbur Creek: (a) Ephemerella doddsii, ventral view of mandibles; maxillae; (b) Baetis bicaudatus, ventral view of mandibles; (c) Ephemerella coloradensis, ventral view of mandibles,maxillae; (d) Epeorus deceptivus, ventral view of mandibles; (d)Rithrogenia robusta, ventral view of mandibles.

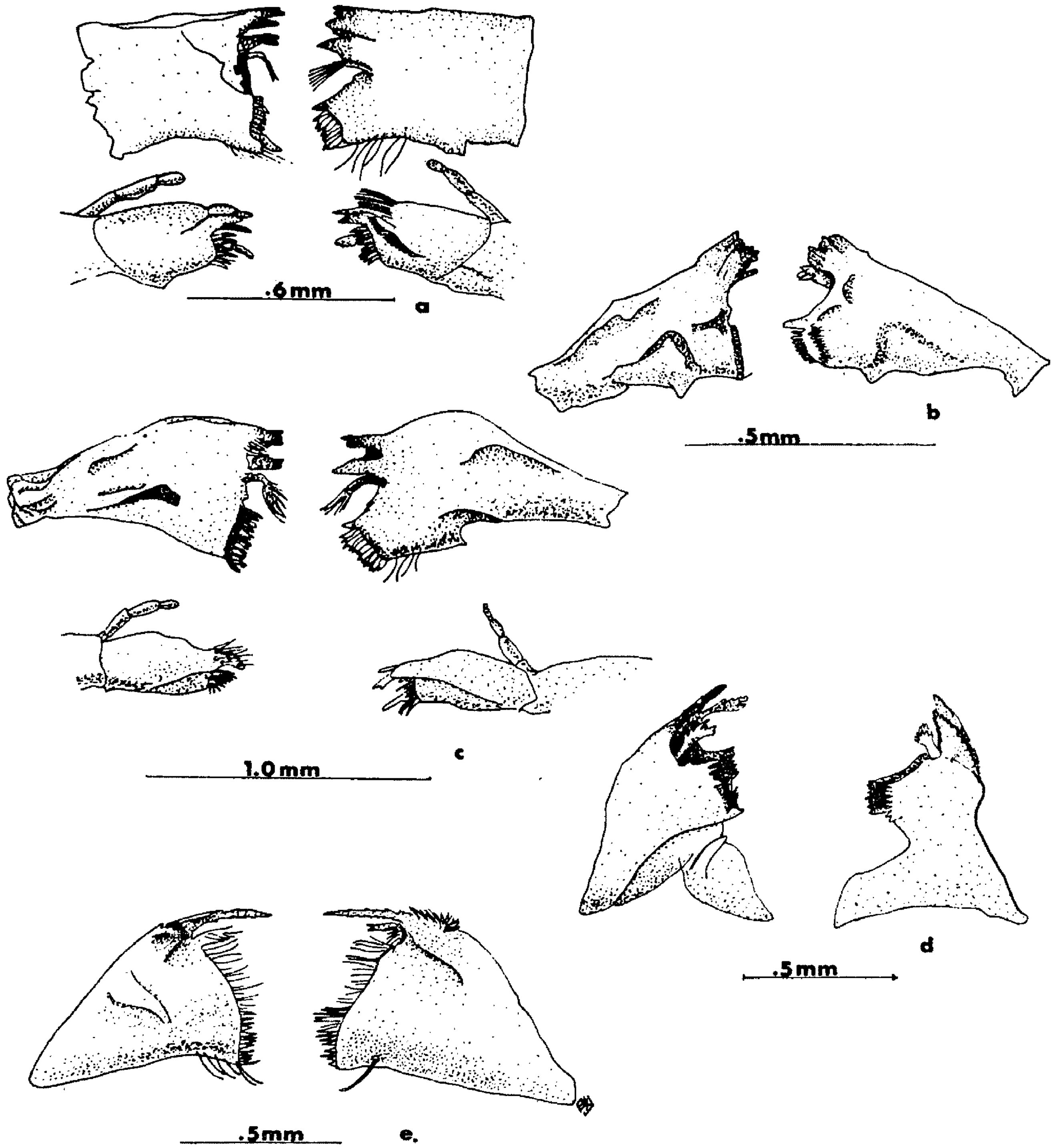
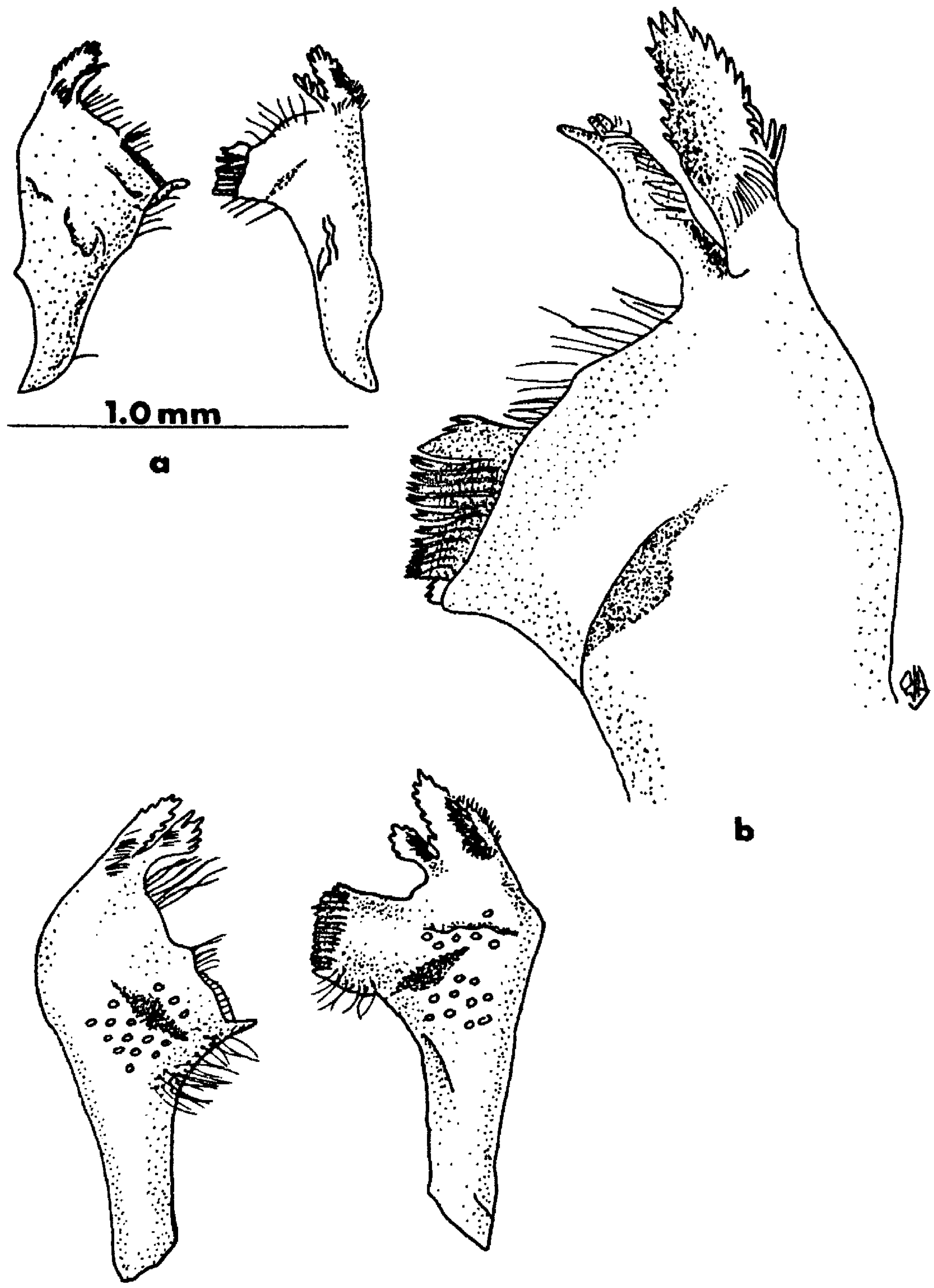

.6mm
a
b
.5mm
1.0mm
c
d
.5mm
.5mm
e.

Fig. 8. Nymphal mouthparts of Ephemeroptera found in Wilbur creek: (a) *Cinygmula* sp., mandibles, ventral view; (b) *Cinygmula* sp. left mandible enlarged to show arrangement of combs on the medial surface.(c) *Epeorus grandis*, mandibles, ventral view.


1.0 mm
a
b
c

Statistical

The values for the phi coefficient ranged between 0.000 and 1.000. A value of 1.000 indicated that the two species were found together 100% of the time, and a value of 0.000 that the species were never found together. Each species was given a number for identification purposes. The phi coefficient was calculated by computer using the program appearing in Appendix A. This program clusters the similar coefficients in the data output. From these data it was relatively simple to construct dendrograms to display associations among the insects. Groups of insects occurring together at any given level of association were termed aggregations. Tables 5 - 9 display the aggregations that occurred per site. These tables display the numerical aggregations among the insects and were drawn directly from the computer printout of the phi coefficients in numerical order from 0.000 to 1.000. In addition, for each cluster that occurred, the species within each cluster were also printed in order. For example, if a cluster of twelve pairs should occur at the .612 level of association, the computer would print those pairs in order as they occurred in the matrix (i.e., 1 and 3, 1 and 4, 1 and 5, 2 and 16, 2 and 36, 4 and 27, 12 and 16, 13 and 18, 14 and 16, 25 and 26, 30 and 36, 30 and 37).

The phi coefficients can be read from the aggregation tables. Although these tables were designed to display aggregations, the phi coefficient of any pair of species above the .250 level can be easily read. The table relates from the bottom row of digits beginning at the 1.000 level. When no associations occurred at the 1.000 level, then the graph is read from the next level up as all numbers relate from the bottom number of the highest level of association. All numbers relate

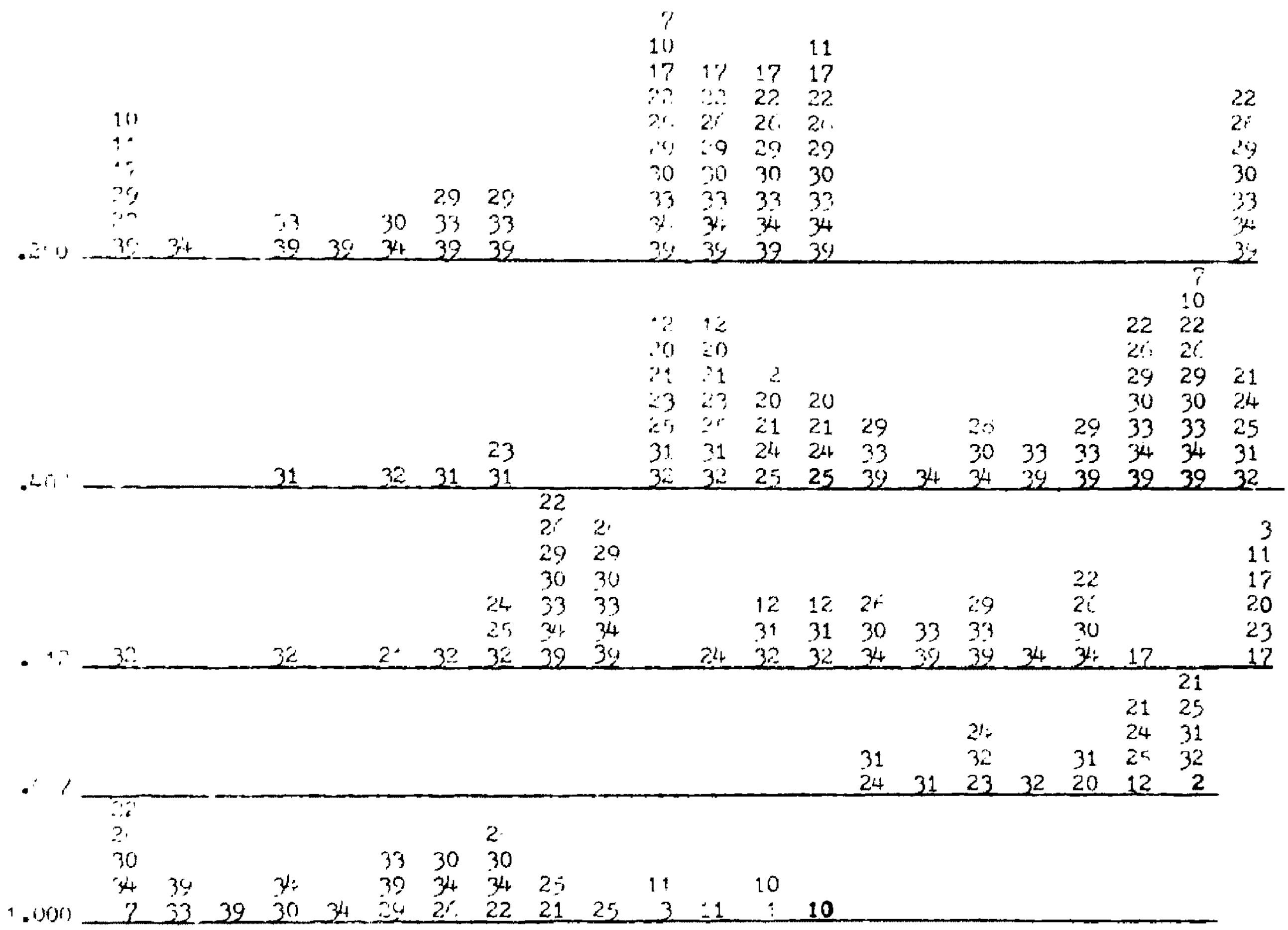
Table 6. Table of phi coefficients showing aggregations of species at site 2. For specific identification see Table 12.

.250					13		13	13			9 10 11 21	21			6 9 10 11 13 21	
.408			29	29	20 29 36 37	29 36 37	29 36 37	20 29 36 37	9 10 11 21	21	7 24 28 29 36 37	24 28 29 36 37	9 10 11 21 29	9 10 11 13 21	8 20 29 36 37	
.612					24 28	24 28	24 28	24 28	13 29	29	8 20	20	3 6 13	29	7 24 28	29
.667			37 36	37 36					24 28	24 28			36 37 2	7	3	
1.000	37 36	37	28 24	20 28	21 11	21	11 21 10	10 11 21 9	20 8	20	13 6	13				

AGGREGATIONS
SITE NUMBER 2

TABLE 6

Table 7. Table of phi coefficients showing aggregations of species at site 3. For specific identification see Table 12



Site Number 3 - [illegible]

[illegible] 7

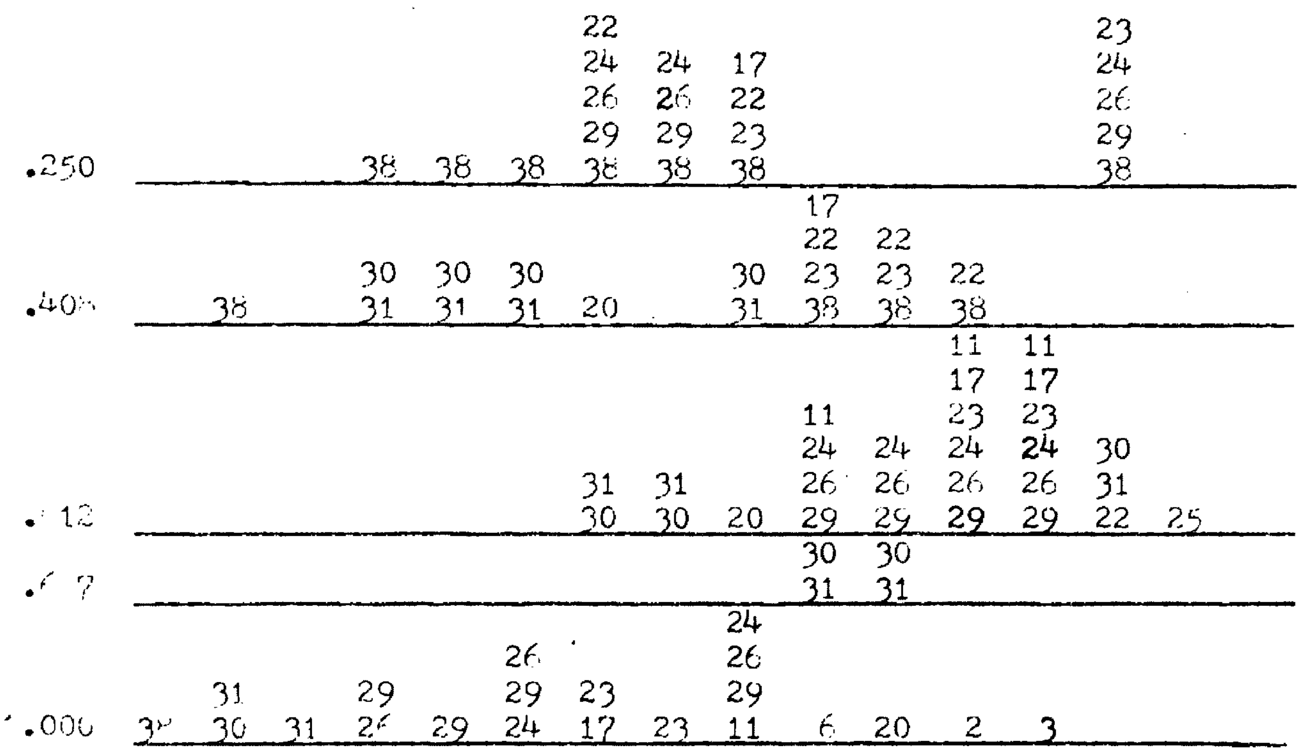
Table 8. **Table of phi coefficients showing aggregations of species at site 4.** For specific identification see Table 12

.250	31 27 26 22 7 32 34 37 38	7 22 26 27 31 32 34 37 38												38	37 38	37 38	31 37 38	31 37 38	32 34 37 38	31 37 38	31 37 38	7 22 26 27 31 32 34 37 38
.408	6 20 21 23 24 25 29	6 20 21 23 25 24 2	31 38 26 27 32 34 37	31 32 34 37	26 27 32 34 37	31 38	31 38	22 26 27 31 32 34 38	31 37	31 37	7 22 26 27 31 32 34 38		31 32 34				29 30	29 30		24 29 30	24 29 30	6 20 21 23 24 25 29
.612	5 17 30	5 17 30		38	31 38	26 27 32 34 37	22 26 27 32 34 37	37	22 26 27 32 34 38	7 22 26 27 32 34 38	37	38	37 38 29	37	34	32	27	26	31	23 25 22	20 21 23 25 7	30 5 17 30 3
.667			30 25	30	25 24	24 30 23	24 30 20	21 24 17	21	17 6	6 21 24 5											
1.000	2 1	2																				

Site Number 4 - AGGREGATIONS

TABLE 8

Table 9. Table of phi coefficients showing aggregations of species at site 5
For specific identification see Table 12



AGGREGATIONS
Site Number 5

TABLE 9

Table 10. Table of phi coefficients showing aggregations of species at site 6. For specific identification see Table 12

Level																				
.250				27 29 32 39	39			27 29 32 39	13 22 27 29 34 39	34 39									32 34 39	29 32 34 39
.408	29 34 39	34 39	29 34 39	24 25 30 31 35	35	27 32 39	27 32 39	20 24 25 30 31 35 13	16 20 21 23 26		13 22 27 34 39	34 39	13 22 27 29 34		27 39 32	29 32 39	22 29 32 34	27 29 39	31 35	30 35
.612	27 32	32	27 32	23 26		22 29 34	34	16 21 23 26	24 25 30 31 35	35	9 29 32	32	9 32 39 29 34	39	34 39	22 27 34	27 39	9 13 22 32 34	30 29	31 27
.667	26		26			20 24 25 31 35	24 25 31 35				20 21 26		16 21 23		31 30 26	30 35 21	23 30 20	20 7		
1.000	25 31 24	31	25	34 22	34	23 16	23	22 34 13	32 9	32	30 3	30	35 2	35						

Site Number 6 - AGGREGATIONS

TABLE 10

only to the numbers in that column and not in adjacent rows. For example, at site 2, the species relating level .667 to species 8 are numbers (species) 24 and 28. For species 7 at the .667 level, in which there are no correlations at the 1.000 level, one should read the numbers up from the highest level of association. Species No. 29 will correlate at the .612 level with species 7 only. Species nos. 21, 13, 11, 10, and 9 all correlate with species 7, but at the .408 level. They do not indicate correlation with each other. These tables eliminate the necessity of working with long lists of numbers.

Dendrograms

All dendrograms were constructed from the highest level of association. Usually a number of pairs appeared at the 1.000 level. At site 4, however, only species 1 and 2 appeared at the 1.000 level, as opposed to site 6 which exhibited sixteen pairs of species associating at the 1.000 level. It should be noted that all of these pairs did not necessarily associate with each other (i.e., ⟨24, 21, 25⟩ associated together, and ⟨22, 34, 16, 23, and 13⟩ associated together). The species in each group (aggregation) associated with members of that particular group (aggregation) but the two major aggregations associated with each other only at the .667 level of association.

The associations become less and less significant as one approaches 0.000. In this study the .250 level was used as a cutoff point. Beyond this point, the associations approach insignificance. From the aggregation tables, dendrograms were constructed and the results appear in Figures 9 - 13. Each site was found to exhibit particular aggregations.

Site 2 (Fig. 9) exhibited five small groups associating at the 1.000 level. They were: ⟨36, 37⟩ , ⟨24, 28⟩ , ⟨11,21,10,9⟩ , ⟨8,20⟩,

⟨6, 13⟩. They then formed a complex with species 2 (<u>Nemoura haysii</u>) at the .667 level, and with ⟨7, 3, 29⟩ at the .612 level.

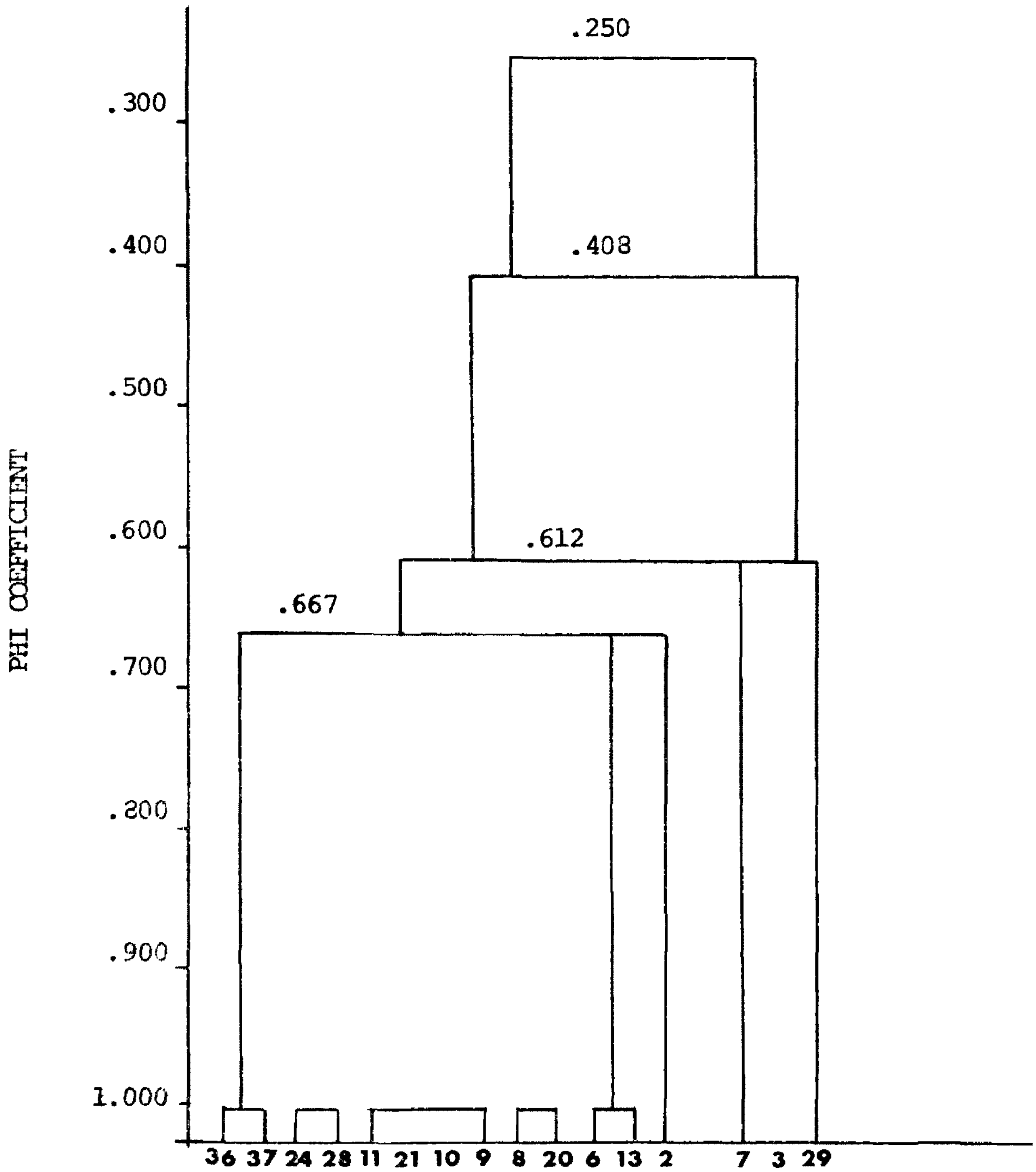
Site 3 (Fig. 10) was found to contain two specific complexes. One aggregation occurred at the 1.000 level and included the species: ⟨7, 33, 39, 30, 34, 29, 26, 22⟩. One smaller aggregation, ⟨21, 25⟩ , associated with the following complex at the .667 level: ⟨24, 31, 23, 32, 20, 12, 2, 17⟩ , forming the second of the two specific complexes.

Site 4 (Fig. 11) evidenced two major specific complexes. ⟨1, 2⟩ associated at the 1.000 level, attached to a larger complex in itself occurring at the .667 level. Specifically this complex is composed of the following aggregation: ⟨25, 30, 24, 23, 20, 17, 21, 6, 5⟩ . The second complex occurred at the .612 level and is composed of the aggregation ⟨38, 29, 37, 34, 32, 27, 26, 31, 22, 7, 3⟩.

Site 5 (Fig. 12) appeared to form no major specific complexes. However, at least four aggregations occurred at the 1.000 level. They included ⟨30, 31⟩, ⟨26, 29, 24, 17, 23, 11⟩ , ⟨6, 20⟩ ,⟨2, 3⟩ . All associated with each other at the .667 level.

Site 6 (Fig. 13) presented an interesting development in that the aggregations occurred at a relatively low level and appeared to form rather distinct complexes. Five aggregations occurred at the 1.000 level:⟨24, 31, 25⟩ ,⟨22, 34, 16, 29, 13⟩ ,⟨4, 32⟩ ,⟨3, 30⟩,⟨2, 35⟩. The first two associated together at the .667 level and the latter three also at the .667 level. Association between the two groups occurred only at the .250 level, which is relatively insignificant. Another complex at the .667 level was formed by two little aggregations: ⟨26, 21⟩ and⟨20, 7⟩which then associated with⟨39,29,27⟩at the .612 level.

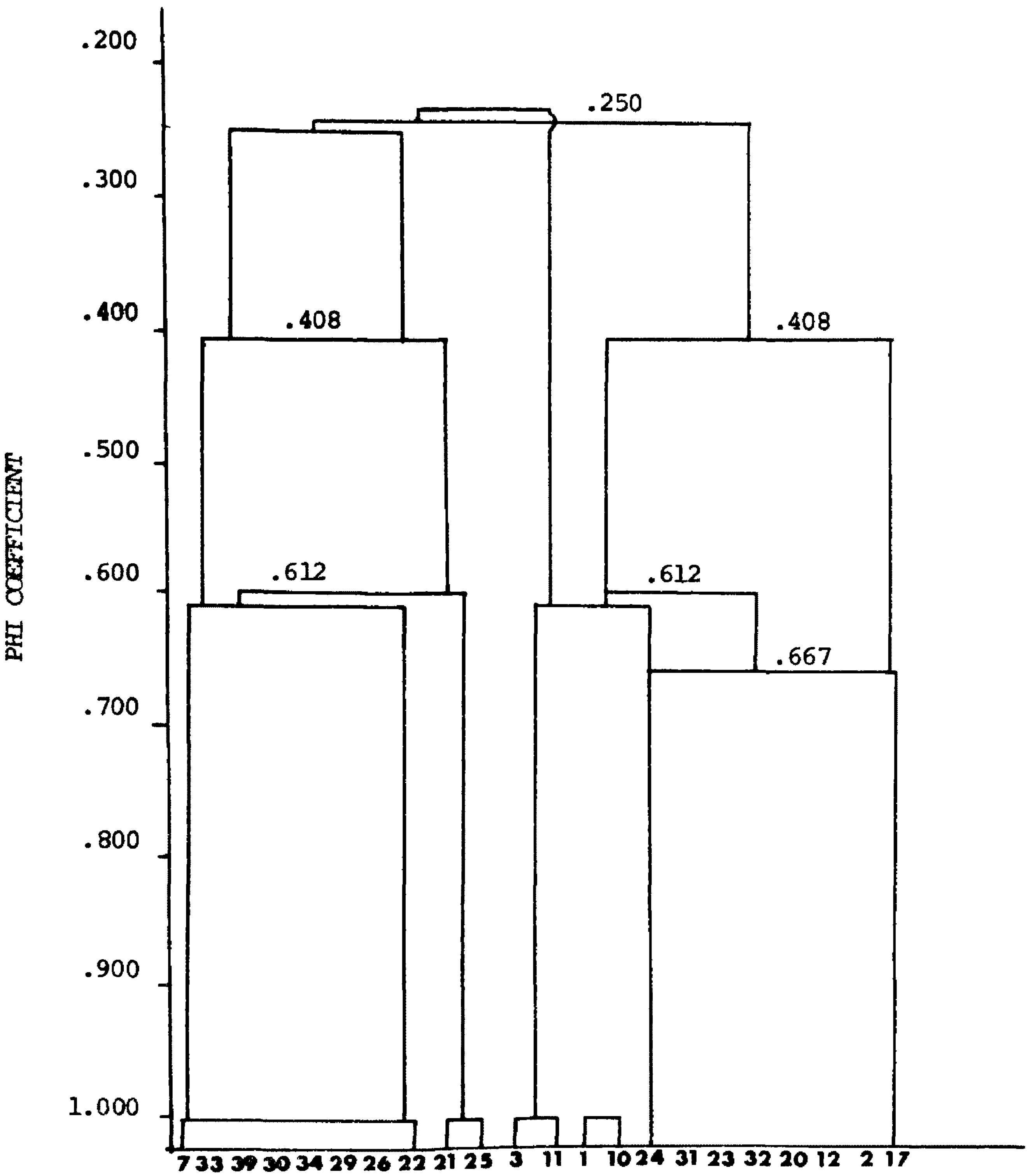
Fig. 9. Dendrogram showing specific occurrence among aquatic insects at site 2.
For specific identification see Table 12



SPECIFIC OCCURRENCE

SITE 2

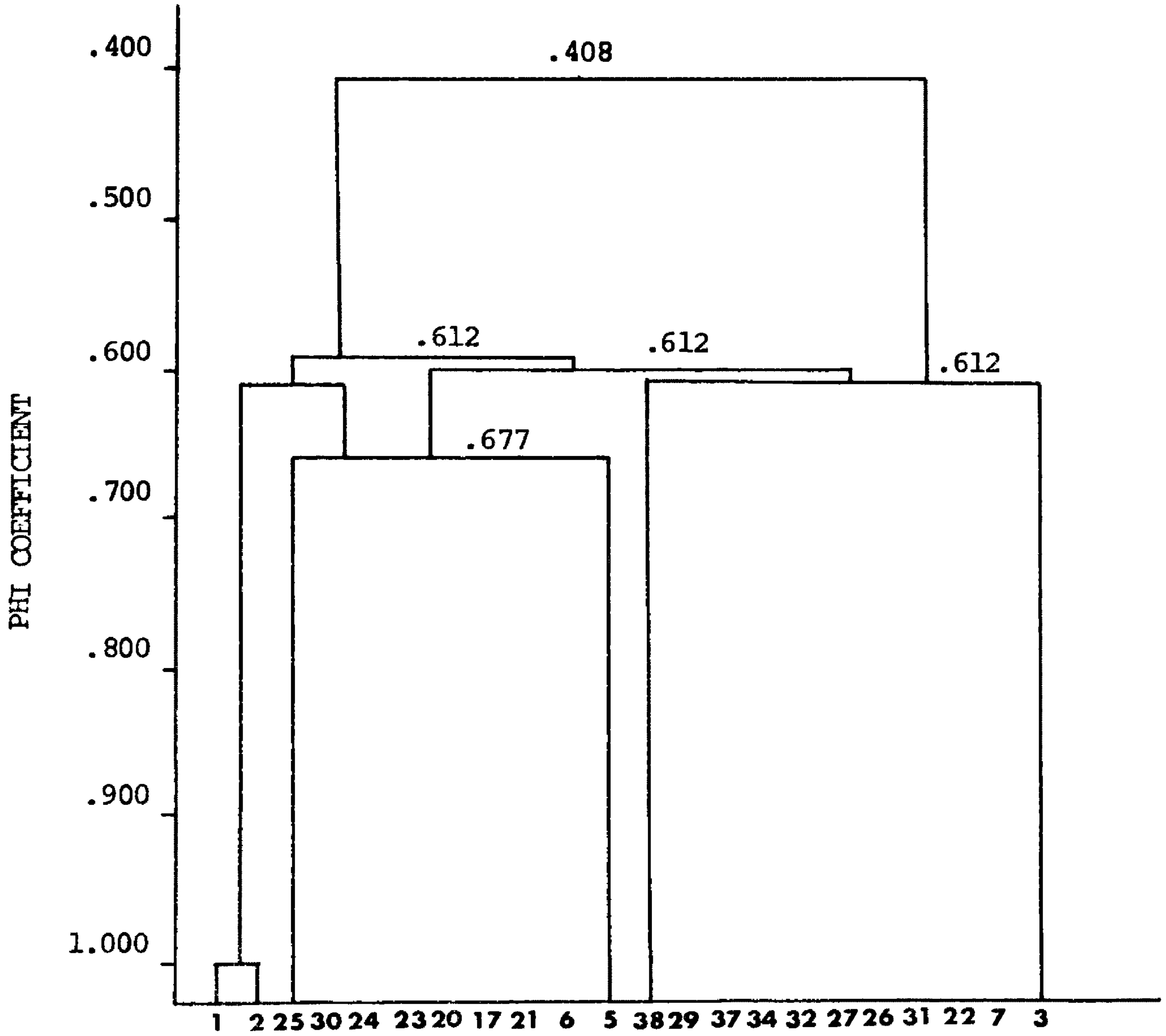
Fig. 10. Dendrogram showing specific occurrence among aquatic insects at site
For specific identification see Table 12



SPECIFIC OCCURRENCE

SITE 3

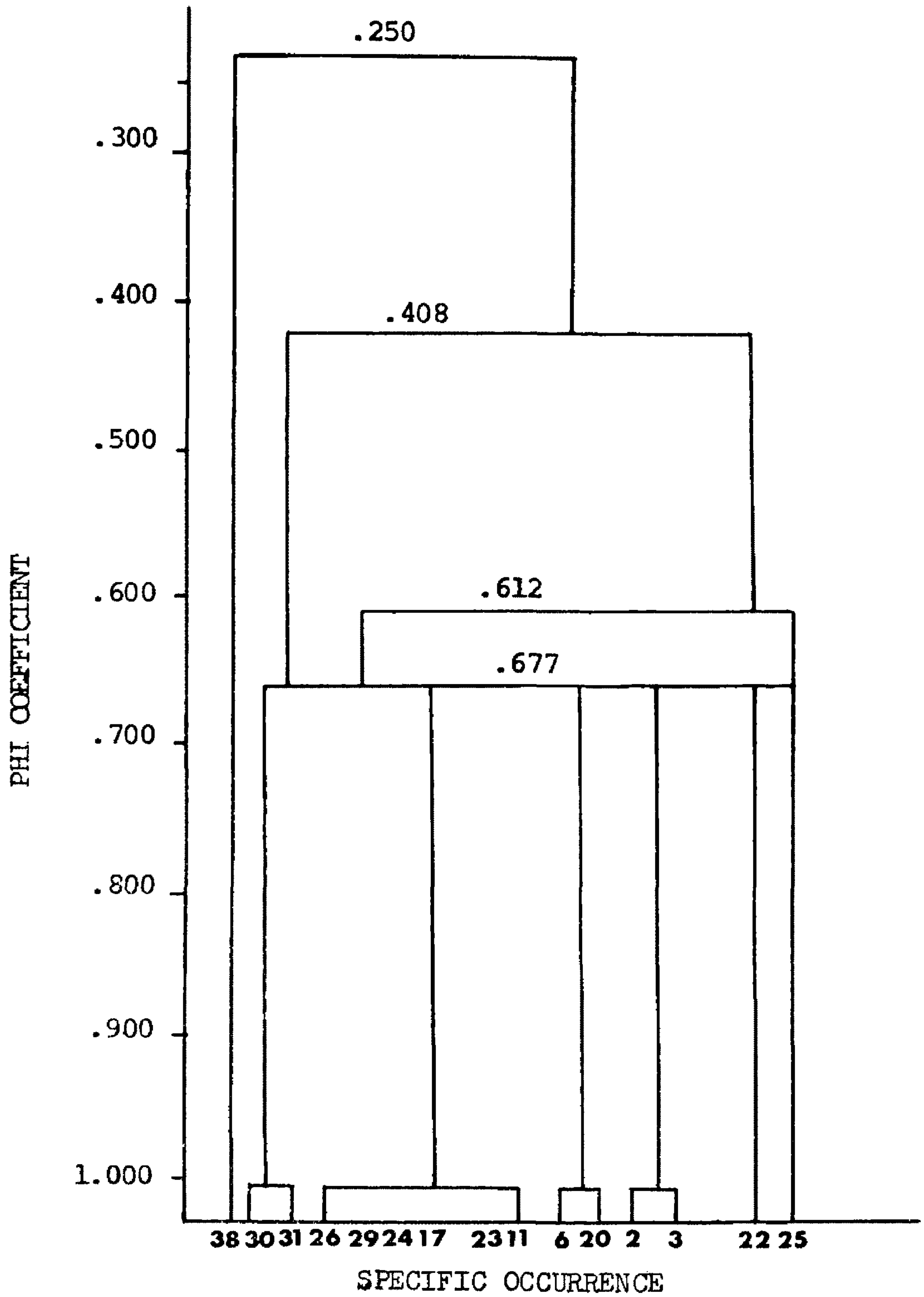
Fig. 11. Dendrogram showing specific occurrence among aquatic insects at site
For specific identification see Table 12



SPECIFIC OCCURRENCE

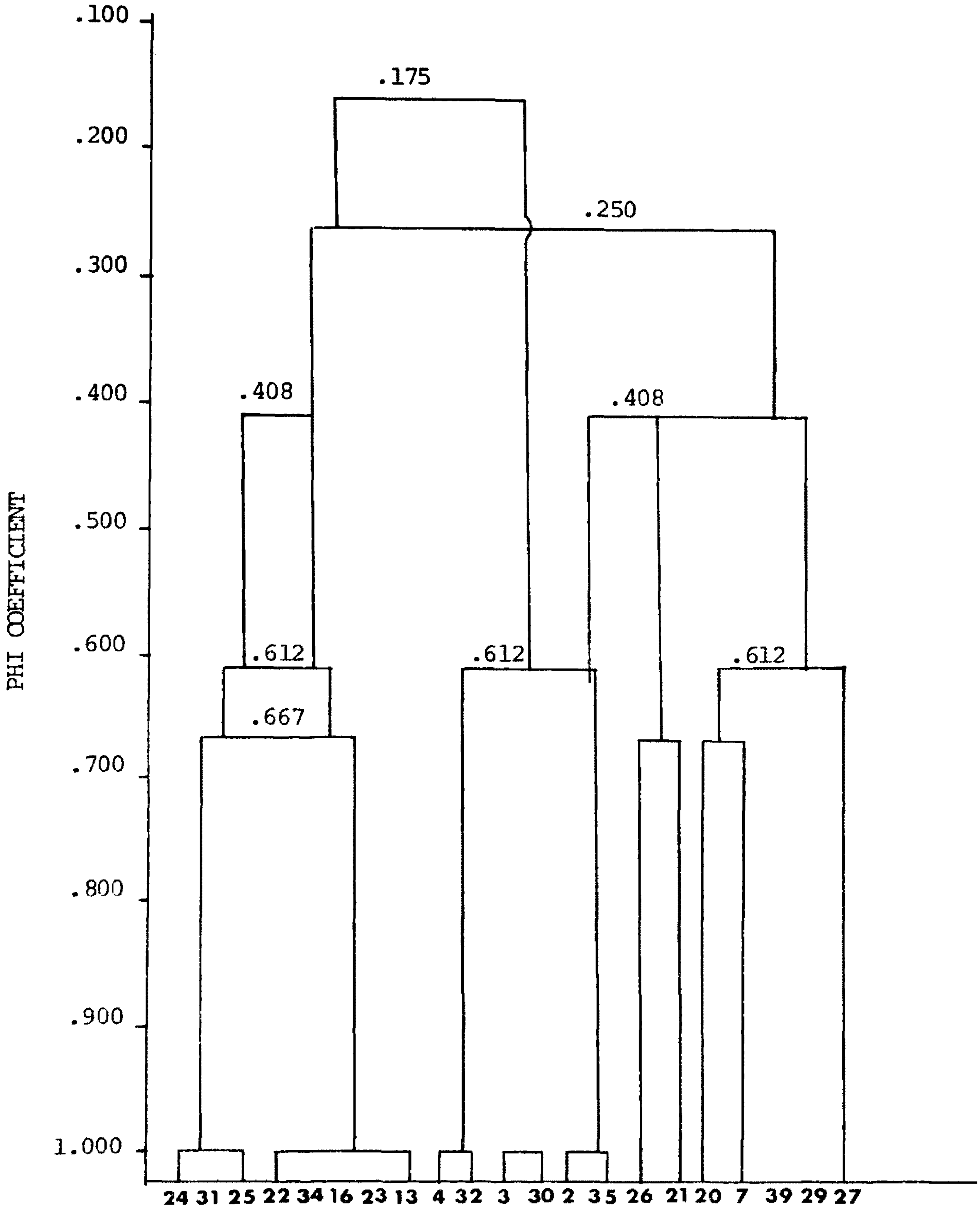
SITE 4

Fig. 12. Dendrogram showing specific occurrence among aquatic insects at site 5.
For specific identification see Table 12


.250
.300
.400
.408
.500
.600
.612
.677
.700
.800
.900
1.000
PHI COEFFICIENT
38 30 31 26 29 24 17 23 11 6 20 2 3 22 25
SPECIFIC OCCURRENCE

SITE 5

Fig. 13. Dendrogram showing specific occurrence among aquatic insects at site 6.
For specific identification see Table 12



.100
.200
.300
.400
.500
.600
.700
.800
.900
1.000
PHI COEFFICIENT
.175
.250
.408
.408
.612
.612
.612
.667
24 31 25 22 34 16 23 13 4 32 3 30 2 35 26 21 20 7 39 29 27
SPECIFIC OCCURRENCE

SITE 6

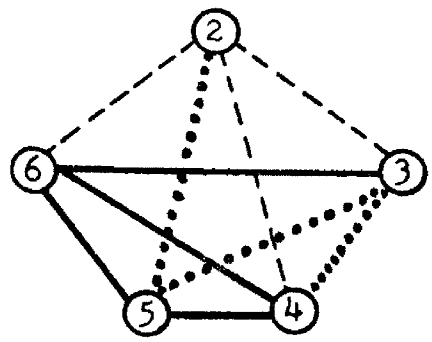
Similarity Coefficient (S)

The results of the S calculations appear in Figure 6a. The results indicate greatest similarity occurred between sites 4, 5, and 6, with site 3 being intermediate and site 2 most dissimilar (Figure 6b). The dendrogram drawn from the S coefficients indicates that each site associates most closely with its adjacent sites, resulting in the stairstep pattern seen in Figure 7.

Fig. 14. (a) calculated values of the similarity (S) index.
(b) Diagram showing those sites most similar, least similar, and those of intermediate similarity.

SITE 2	(S)
2x3	.5116
2x4	.5238
2x5	.6195
2x6	.5121
3x4	.6863
3x5	.6863
3x6	.7500
4x5	.8400
4x6	.7600
5x6	.7234

A.



——— Sites most similar (high coefficient)

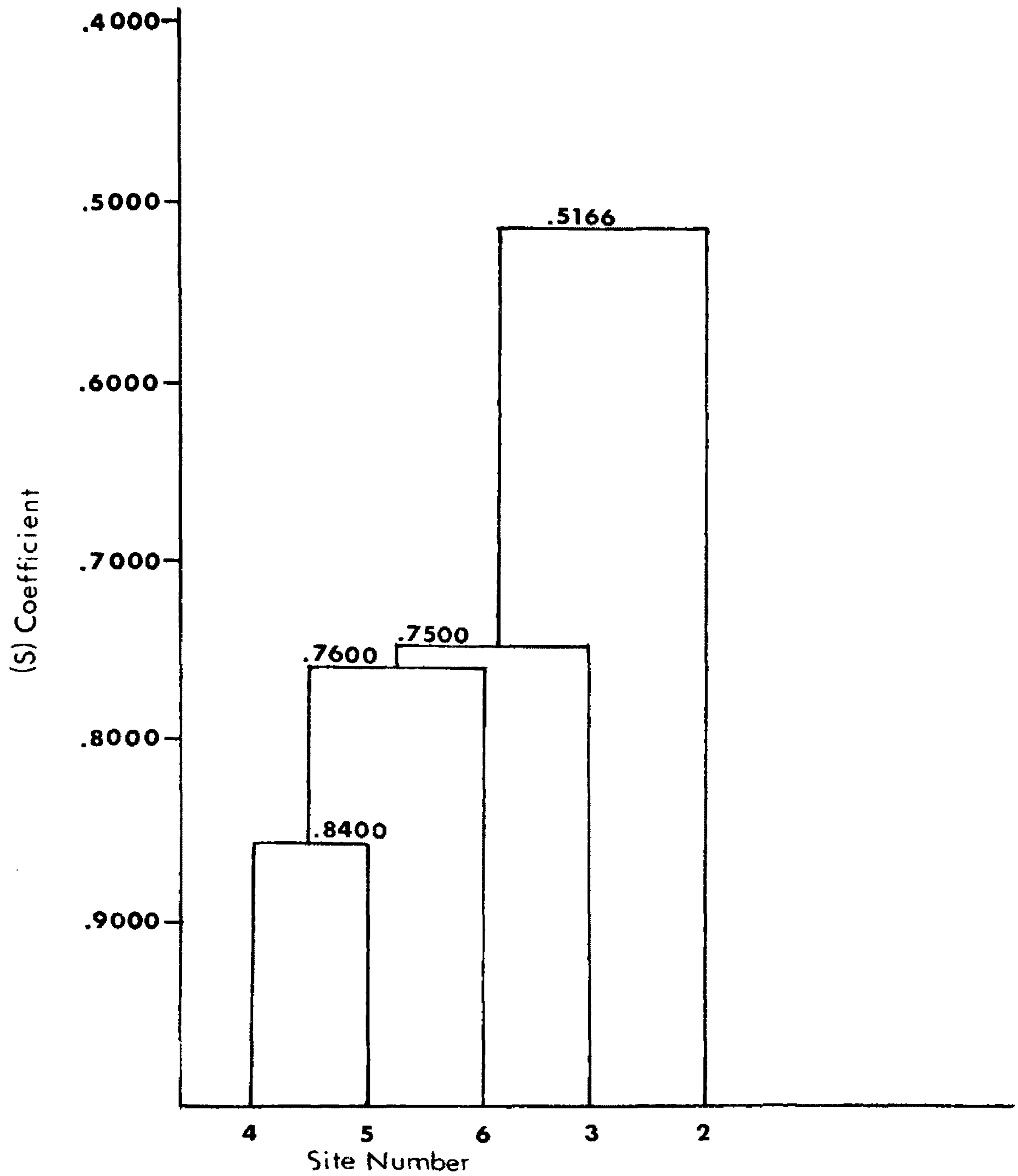
••••••• Sites intermediate

- - - - Sites most dissimilar (low coefficient)

B.

Figure 14.

Fig. 15. Graph displaying the (S) index in dendrogram form.


.4000
.5000
.6000
.7000
.8000
.9000
(S) Coefficient
.5166
.7500
.7600
.8400
4
5
6
3
2
Site Number

DISCUSSION

Barring alteration by man, certain elements of the stream (i.e., substrage composition, water temperature, sgream length, and water chemistry) will remain constant. Other factors such as width, depth, and flow patterns may fluctuate as often as the yearly snow runoff. The abiotic elements of the system dictate the patterns that the biotic elements assume. The results of this investigation indicate that particular aggregations occur among the species of the aquatic insects. From taxonomic and statistical data we were able to define the specific occurrence in the stream during the summer and fall months. From these data it seems probably that one could predict the species structure to be similar under similar abiotic conditions. Gut analyses allowed definition of food sources which were utilized in the stream, as well as relatively precise definition of the food specificity of individual species. A general idea was also obtained of the specific composition of trophic levels existing in the stream. From these data we also gained some idea of the niche relations. Individual insect niches were described at given points in time and were found to fluctuate geographically. Because algae, particularly the diatoms, exhibit substrate preference, (Prescott, 1967), adherence to a particular food source by an insect may indicate substrate specificity. Using both statistical and dietary data, changes were detected in the specific complex as a result of natural changes in the environment. Because there is little opportunity for chemical or biological aging of the

water in alpine situations, the primary productivity or ability of the system to support biomass is at its lowest at the headwaters. Therefore it appears that a progressive change in association and specific occurrence occurs as a relfection of substrate change and gradual increase in primary productivity as one progresses away from the headwaters. Changes in niches are relfected by shifting substrate at the lower sites 3 and 4 which removed or altered existing niches. Natural changes which occurred in the community structure reflected gradient change from headwaters to the valley floor. The substrate, most primitive at the upper site, exhibited sheets of argellitic bedrock, with a few boulders and rocks, but little or no rubble present.

The most evolved or eroded substrate occurs the farthest distance from the headwaters at site 5. A definitive community gradient occurs in response to this substrate gradient in Wilbur Creek. The most primitive community occurs at the outlet of the lake and the most advanced at the site just above the campground (site 5). The diets of the species in the outlet community are of a generalized nature (refer to Tables 10 and 11). The most common food sources are organic debris, dilamentous algae, diatoms, and animal material. The species at this level utilize a wider variety of food sources per species. At this point, the primary productivity of the stream is very low, and niche specialization least developed. The increase in species diversity and apparent trend toward a specialized diet indicate an increase in the primary productivity of the stream. The insects at the lower site were found to exhibit a more specialized diet than the same species at the headwaters. The downstream community exhibited a more diverse species-complex. *Nemoura columbiana* and *N. haysii* at the outlet site were found to feed on

diatoms, filamentous algae, and organic debris, whereas the diet at lower site 5 consisted entirely of organic debris. The alloperlid stoneflies at the outfall community subsisted mainly on organic debris, pollen, filamentous algae, and some animal material. At the lower site 5, the alloperlids fed on organic debris, and to a much greater extent on animal material, particularly the Plecoptera.

Among the mayflies, Cinygmula sp., in the outlet community fed on diatoms, filamentous algae, and bryophytes. At the lower site, they exhibited a diet limited to organic debris. Baetis bicaudatus at the upper site subsisted mainly on organic debris, dilamentous algae, and some bryophyte material. At the lower site, stomachs were found to contain only organic debris. Rhyacophila accropedes at the upper site fed mainly on organic debris, some animal material (Trichoptera and Plecoptera), and some diatoms. At the lower site, the diet consisted of organic debris, and to a much greater extent animal material, but no diatom material was found.

Patterns of specific occurrence revealed that the upper site supported a total of seventeen species, while the lower site 5 contained twenty-five species. Twelve species were common to both sites. The species found to be common to both sites (Table 11) included herbivores, carnivores, and omnivores and seemed to serve as a "core" community, and was found persistently at all sites. The upper site, simpler in structure, contained three species that did not occur in the lower section. They were Arcynopteryx bradleyi, Isogenus aestivalis, and Rhyacophila angelita. This site exhibited a community dominated by stoneflies with over 50% of the insect species belonging to the order Plecoptera. There was a lack of mayflies, particularly the carnivorous

forms Ephemerella coloradensis and Ameletus sp. It is possible that these forms replaced either Arcynopteryx bradleyi or Isogenus aestivalis as carnivores. Among the herbivores, Epeorus deceptivus, Epeorus grandis, and Ephemerella coloradensis appeared at site 3 and were persistent from there on downstream. These added herbivores may reflect an increase in the primary productivity below the outlet of the lake. Often members of primitive communities (Table 11) are pioneer forms, unable to compete in more productive situations. It is suggested, therefore, that A. bradleyi, I. aestivalis, and R. angelita in this stream are pioneer forms, only found in the most primitive of the running water communities. The ability of the system to handle an increased number of herbivores and increased number of carnivores was indicated by an increase in the number of Trichopteran species: Rhyacophila hyalinata, R. tucula, R. vaccua, Parapsyche elsis, and Arctopsyche grandis. The data indicate that community structure is a direct function of substrate evolution and corresponding development of the primary productivity.

SUMMARY

In June, 1972, a study was undertaken to discover and describe the community structure and gradient among the benthic aquatic insects in Wilbur Creek in the Many Glacier Valley of Glacier national Park, Montana.

The stream was sampled with a hand screen during the summer of 1972 and once the following spring.

A total of forty species were identified and their occurrence was tabulated. The probability of occurrence of any given species with any other species was calculated by using the correlation coefficient phi. The calculated values were then displayed in dendrograms by using the unweighted pair group method to show specific occurrence among the species.

Gut samples were analyzed to discover biological associations. A substrate gradient exists in Wilbur Creek. The least developed occurred at the headwaters. At least three insect taxa, Arcynopteryx bradleyi, (Plecoptera), Isogenus aestivalis (Plecoptera), and Rhyacophila angelita (Trichoptera) are pioneer forms, as they were found only at the headwater site. An increase in primary productivity in the downstream sites was accompanied by an increase in the number of herbivores, a corresponding rise in the number of predators, and shift in diet from general to specific.

It is suggested therefore that community structure is a direct function of substrate evolution and a corresponding development of primary productivity.

Table 11. Table showing species specific to sites 2 and 5, species common to both, and the trophic levels of the species involved.

Site 2		"Core Community"		Site 5	
Arcynopteryx bradleyi	c-o	*Nemoura columbiana*	h	*Alloperla* sg. A	–
Isoganus aestivalis	–	*Nemoura haysii*	h	*Ameletus* sp.	c-o
Rhyacophila angelita	c-o	*Peltaperla brevis*	c-o	*Epeorus deceptivus*	h
		Arcynopteryx watertoni	c-o	*Epeorus grandis*	h
		Isoperla ebria	c	*Ephemerella coloradensis*	h
		Isoperla sordida	h	*Rhyacophila hyalinata*	c-o
		Alloperla sg.	–	*Rhyacophila tucula*	c
		Cinygmula sp.	h	*Rhyacophila vaccua*	c-o
		Rithrogenia robusta	h	*Parapsyche elsis*	c
		Baetis bicaudatus	h	*Arctopsyche grandis*	c
		Rhyacophilla accropedes	c-o		
		Limnephilidae	–		

c= Carnivore

h= Herbivore

o= Omnivore

c-o= Carnivorous omnivore

Note: A level of c-o was assigned to an animal whose gut was found to contain a greater percent of animal than plant material. This distinguished it from an animal whose gut contained plant material and much organic detritis. Ordinarily the latter would also be considered an omnivore.

Table 11.

Table 12. Trophic levels of aquatic insects occurring in Wilbur creek.

TAXON	7/17	8/2	9/1	10/2		7/17	8/2	9/1	10/2	4/27
(1) Nemoura cataractae										
(2) Nemoura columbiana			h					h	h	
(3) Nemoura haysii			h					h	h	
(4) Capnia spenceri										
(5) Leuctra sp.										
(6) Peltaperla brevis										h
(7) Arcenopteryx watertoni	c-o					h	c-o			o
(8) Arcenopteryx bradleyi	c-o		c			o	c-o	c-o	c-o	c-o
(9) Isogenus aestivalis										
(10) Isoperla ebria	c									
(11) Isoperla sordida	h									
(12) Kathroperla perdita										
(13) Alloperla sg.										
(14) Alloperla sg. Suwallia										
(15) Alloperla sg. Pallidua										
(16) Alloperla sg. Borealis-fidelis	o		h							
(17) Alloperla g. A										
(18) Alloperla sp.			[illegible]					o		
(19) Ameletus similor										c-o
(20) Cinygmula sp.	h		h			h	h			h
(21) Rithrogenia robusta	h					h	h	h	h	h
(22) Epeorus deceptivus						h		h		
(23) Epeorus grandis						h			h	h
(24) Baetis bicaudatis						h	h		h	h
(25) Ephemerella doddsii						c	c			
(26) Ephemerella coloradensis						h	h	o		h
(27) Rhyacophila (undetermined)							c	o		
(28) Rhyacophila angelita	c		o							
(29) Rhyacophila accropedes	o	c-o							c	c-o
(30) Rhyacophila hyalinata						c-c				
(31) Rhyacophila tucula						c				
(32) Rhyacophila vaccua						c-o	c	c	c	c-c
(33) Rhyacophila verrula										
(34) Parapsyche elsis				c		c	c	c		c
(35) Arctopsyche grandis										
(36) LEPIDOSTOMATIDAE										
(37) LIMNEPHILIDAE										
(38) GLOSSOSOMATIDAE										
(39) BRACHYCENTRIDAE										
(40) Brachyptera occidentalis										

h= herbivore
c= carnivore
o= omnivore

TABLE 12 TROPHIC LEVELS

APPENDIX A

SPECIES NUMBER SITES: FORMAT CARD FOR DATA

1 2 3 4 5 6

0000000000000000000000000000000000000000000000000000000

11111111111111111111111111111111111111111111111111111

222222222222222222222222222222

3333333333333333333333333

Column 1 - 4 Species number

Sites:
2 - Col 4-9
3 - col 10-14
4 - col 15-19
5 - col 20-24
6 - col 25-29

At each site five collumns were used:
Column one, July sample 7/17.
Column two, July sample 7/25.
Column three, August sample 8/4.
Column four, September sample 9/1.
Column five, October sample 10/2.

```
      REAL X(39,40)
      INTEGER ROW(1000)
      INTEGER COL(1000)
      REAL    SORT(1000)
      INTEGER OCC(40,25)
      KIN=2
      KOUT = 3
      WRITE (KOUT,3)
      READ (KIN,2)  M,N
  2   FORMAT(2I2)
      READ (KIN,1) ((OCC(I,J),J=1,25), I=1,40)
  1   FORMAT(4X,25I1)
      DO 10 I=1,39
      K=I+1
      DO 10 J=K,40
      A=0
      B=0
      C=0
      D=0
      DO 11 L=M,N
      IF (OCC(I,L)-OCC(J,L)) 12,13,12
 13   IF (OCC(I,L))  15,15,16
 15   D=D+1
      GO TO 11
 16   A=A+1
      GO TO 11
 12   IF (OCC(I,L))  17,17,18
 17   B=B+1
      GO TO 11
 18   C=C+1
 11   CONTINUE
      SQ=((A+B)*(C+D)*(A+C)*(B+D)
      IF (SQ .NE. 0) GO TO 19
      PHI=0
      GO TO 10
 19   PHI=ABS(B*C-A*D)/SQRT(SQ)
      X(I,J)=PHI
 10   CONTINUE
  3   FORMAT(1H1, 'SPECIES BEING COMPARED'  9X '  PHI ')
      M=1
      DO 101 I=1,39
      DO 101 J=1,40
      IF(I.GE.J)GO TO 101
      IF (X(I,J).EQ.0) GO TO 101
      SORT(M)=X(I,J)
      ROW(M)=I
      COL(M)=J
      M=M+1
101   CONTINUE
      J=M-2
 99   J=J-1
```

```
      DO 1Ø2 K=1,J
      Y1=SORT(K)
      Y2=SORT(K+1)
      IF(Y1.LE.Y2)GO TO 1Ø2
      SORT(K)=Y2
      SORT(K+1)=Y1
      Y1=ROW(K)
      ROW(K)=ROW(K+1)
      ROW(K+1)=Y1
      Y2=COL(K)
      COL(K)=COL(K+1)
      COL(K+1)=Y2
102   CONTINUE
      IF(J.GT.1)GO TO 99
      WRITE (KOUT,31)  (ROW(I),COL(I),SORT(I),I=1,M-1)
31    FORMAT(1H,5X,I2,'  AND    'I2,16X,F5.3)
      CALL EXIT
      END
```