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RESOURCE USE BY AMPHIPODA (CRUSTACEA:PERACARIDA) ON THE OUTER CONTINENTAL SHELF OF THE MIDDLE ATLANTIC BIGHT: IMPLICATIONS TO COMMUNITY STRUCTURE

A Thesis
Presented to
The Faculty of the School of Marine Science
The College of William and Mary

In Partial Fulfillment
Of the Requirements for the Degree of
Master of Arts

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by
Linda Carol Schaffner
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APPROVAL SHEET

This thesis is submitted in partial fulfillment of
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ABSTRACT

Benthic communities on the outer continental shelf of the Middle Atlantic Bight are characterized by abundant populations of amphipods in the families Ampeliscidae and Corophiidae. Members of these families occupy tubes at or near the sediment surface and, thus, potentially compete with each other for spatial and trophic resources. This study examines the spatial, temporal and trophic resource use of six numerically dominant species in these families as a means of assessing the relative importance of competition as a structuring force in outer shelf benthic communities.

Analysis of abundance data and the use of discriminant analysis to relate abundance to measured environmental parameters indicated that habitat partitioning was of major importance within the ampeliscid group. Spatial partitioning appeared to be of little importance within the corophiid group. Between group patterns suggest that only one species, the corophiid *Unciola irrorata*, was able to coexist in deep swales with the ampeliscid *Ampelisca agassizi*.

Seasonal abundance patterns were exhibited by all corophiids, but the high degree of temporal overlap in abundance suggests that this was not an important partitioning mechanism. Similarly, persistent abundances over time (*A. agassizi*) or variation in a non-seasonal manner suggests that temporal partitioning of resources was not important within the ampeliscid group.

Differences in body size which might facilitate differential spatial or trophic resource use among species were observed. These differences were most strongly pronounced in closely related species which frequently co-occured.

The use of trophic resources was indirectly assessed by comparing mouthpart morphologies and known feeding behaviors of each species. Quantitative morphological differences among species were evident which relate well to observed habitat preferences.

A complex set of physical and biological factors were found to govern the distribution and abundance of these species within the outer shelf zone. In outer shelf swale habitats the ampeliscid, *A. agassizi*, effectively excludes the other members of this family. This may be the result of the species superior abilities to utilize spatial or trophic resources. Outside of swale habitats the abundances of *Ampelisca vadorum* and *Byblis serrata* may be limited by the availability of trophic resources.

The corophiids show little evidence of resource partitioning, although some differences in microhabitat distribution may facilitate coexistence among the species in this family, as well as between families. Populations of these species may be held below the levels at which competitive interactions become important by benthic predators. The corophiids are known to comprise a major portion of the diet of benthic fishes on the outer shelf.

RESOURCE USE BY AMPHIPODA (CRUSTACEA:PERACARIDA) ON THE OUTER CONTINENTAL SHELF OF THE MIDDLE ATLANTIC BIGHT: IMPLICATIONS TO COMMUNITY STRUCTURE

INTRODUCTION

The ecology of the Middle Atlantic Bight continental shelf has not been intensively studied and most of the information available on shelf macrobenthic communities is descriptive in nature (Boesch 1972, 1979a, Boesch et. al. 1977, Maurer et. al. 1976, Pearce et. al. 1976, Wigley and Theroux 1976). Few studies have been directed towards an understanding of the dynamic ecological processes by which shelf communities are maintained (Boesch 1979a).

Analyses of composition and abundance data for macrobenthos on the entire outer shelf zone from New Jersey to Virginia by Boesch (1979a) indicate that polychaetous annelids and peracaridan crustaceans comprise the two most numerically important taxa. While the annelids exhibit high abundance across the shelf, the peracaridans reach maximum abundance on the outer shelf (50-100 m). A significant portion of the total peracaridan fauna on the outer shelf belongs to two amphipod families, Ampeliscidae and Corophiidae. Amphipods in these families occupy tubes at or near the sediment surface and thus potentially compete for space and trophic resources. Understanding the mechanisms which facilitate coexistence of species in these families would contribute greatly to understanding fundamental processes governing community structure on the outer continental shelf.

Elucidation of the factors which allow similar species to coexist in communities has been a major focus of ecological research for many years. Studies have sought both ecological and evolutionary answers to the question of why certain species coexist and others do not. Early interpretations were based heavily on the ecological niche concept. Grinnell's (1917) first adaptation of the term niche to describe the requirements and relative position within a community of a species was further clarified when Elton (1927) conceptualized the niche as "a species role within its community." The species role was defined primarily by its use of resources. Through the work of Gause (1934) and others (Hardin 1960) the niche concept became entwined with that of competition. The work of Hutchinson (1958) considerably strengthened this bond. He defined the "fundamental niche" of a species as an n-dimensional hyperspace encompassing the entire set of conditions under which a species can live and reproduce. The actual set of conditions in which the species lives defined the "realized niche." Hutchinson postulated competition to be the important distinguishing force responsible for the differences between fudamental and realized niche size. Most recent definitions of niche (Odum 1971, Krebs 1978, Pianka 1978) are based to some extent on Hutchinson's hyperspace model and the assumption that niches are shaped by competition. Thus, for many years competition, or more accurately, the mechanisms which reduce competitive interactions have been considered the primary structuring force in most communities.

In recent years, work by various marine ecologists (Connell 1975, Paine 1966, Dayton 1971, and Virnstein 1977) has provided evidence which seems to contradict this assumption. The studies by these authors have relied on the use of manipulative field experiments which alter species composition and predation pressure within given assemblages. Connell (1975) and Petersen (1979) have summarized much of the information available to show that in many cases predation is more important than competition in facilitating coexistence among species particularly in intertidal or shallow subtidal habitats.

When it has not been practical to delineate structuring mechanisms through the use of experimental techniques ecologists have often used an inferential approach (Schoener 1974, Connell 1975, and Pianka 1978). Ecologists using this method search for patterns in utilization of important resources such as space, food and time which suggest that species are avoiding extensive overlap in their use of resources and are thereby avoiding competitive intractions. Given an unlimited resource pool, species would be expected to differ in resource use in a random manner, therefore observable patterns must be cautiously considered. As a minimum, confirmation that these differences are non-random must be made before competition can be cited as the cause. A lack of departure from randomness would suggest the necessity for further assessment and quantification of the utilization of other resources. With evidence lacking for a competitive structure it becomes necessary to assess the potential role of predation.

Numerous terrestrial ecologists have studied the partitioning of resources by similar species in an attempt to understand community organization (see review in Schoener 1974) but fewer studies concerning resource partitioning and its implications have been attempted for marine organisms. Recent studies include work by Ivester (1975) and Whitlatch (1976). Both studies concentrate on resource utilization and partitioning among similar species and the ways in which this partitioning affects community structure and diversity. Additional studies focusing on resource use and partitioning among benthic invertebrates as a means of avoiding competitive interactions include Croker (1967), Dexter (1967), Peterson (1977) and Caine (1977).

This study was designed to consider the importance of competition as a structuring force in benthic peracaridan assemblages on the Middle Atlantic Bight outer continental shelf. The study is limited to an examination of spatial, temporal, and trophic resource use by six species in the families Ampeliscidae and Corophiidae. A lack of pressure towards competitive exclusion in both ecological and evolutionary time should result in random resource use and little evidence of resource partitioning among these species. Over-dispersion along potentially important resource axes will be interpreted as mechanisms which facilitate coexistence among potentially competing species. The possible role of predation as a structuring mechanism will be considered particularly when patterns of resource use are indistinct. Additionally, I will consider possible evolutionary and ecological processes which have enabled these species to attain dominant positions in the outer shelf macrobenthic community.

STUDY AREA:

The study area was a region of the outer continental shelf (approximately 50 to 100 m) of the Middle Atlantic Bight off New Jersey designated Area B in a larger study by Boesch (1979a). The location of this area and its position relative to other areas sampled by Boesch (1979a) is shown in Figure 1.

Most of the Middle Atlantic continental shelf is topographically complex as a result of both historic and more recent geological processes. Tiger Scarp (Figure 2) is a prominent feature of the eastern portion of Area B and is thought to be an erosional feature marking shoreline position during a major sea level stillstand during Holocene transgression (Boesch 1979b). Below the scarp a series of linear sand ridges trending roughly northeast to southwest further increases the topographic complexity. These major ridges on the outer New Jersey shelf have an average spacing of 6.1 km and a relief of 6.0 m from crest to swale (Duane et. al. 1972, Swift et. al. 1972). It is thought that these linear ridges were generated at the shoreface and later stranded by transgressing seas (Swift 1975, Swift et al. 1972). Contemporary hydrodynamic processes may be responsible for their further modification and maintenance (Duane et al. 1972, Swift et al. 1972, Stubblefield et al. 1975, Stubblefield and Swift 1976).

Figure 1. Stations sampled by Boesch (1979a). Stations utilized in this study (Area B) are enclosed in box.

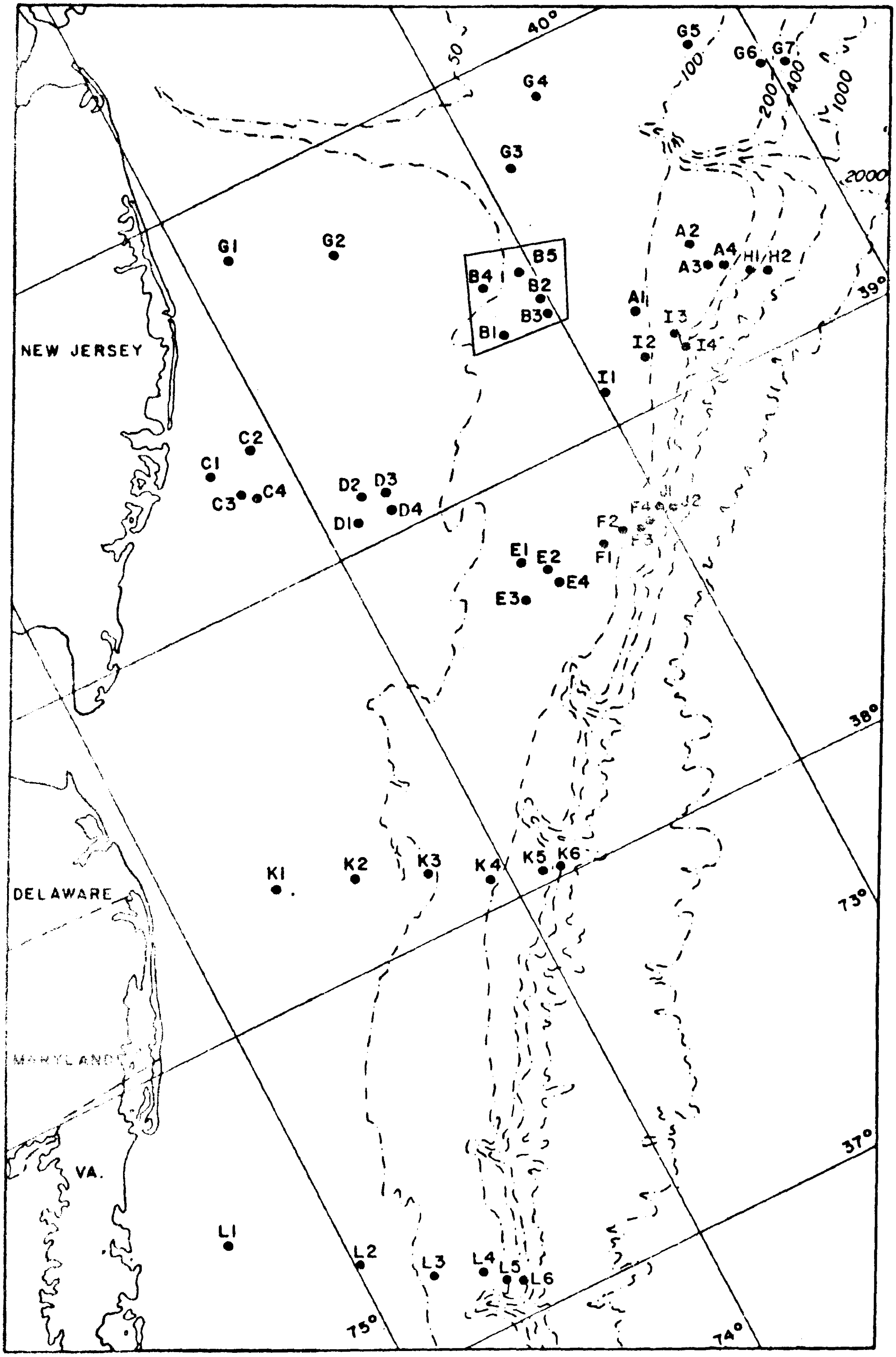
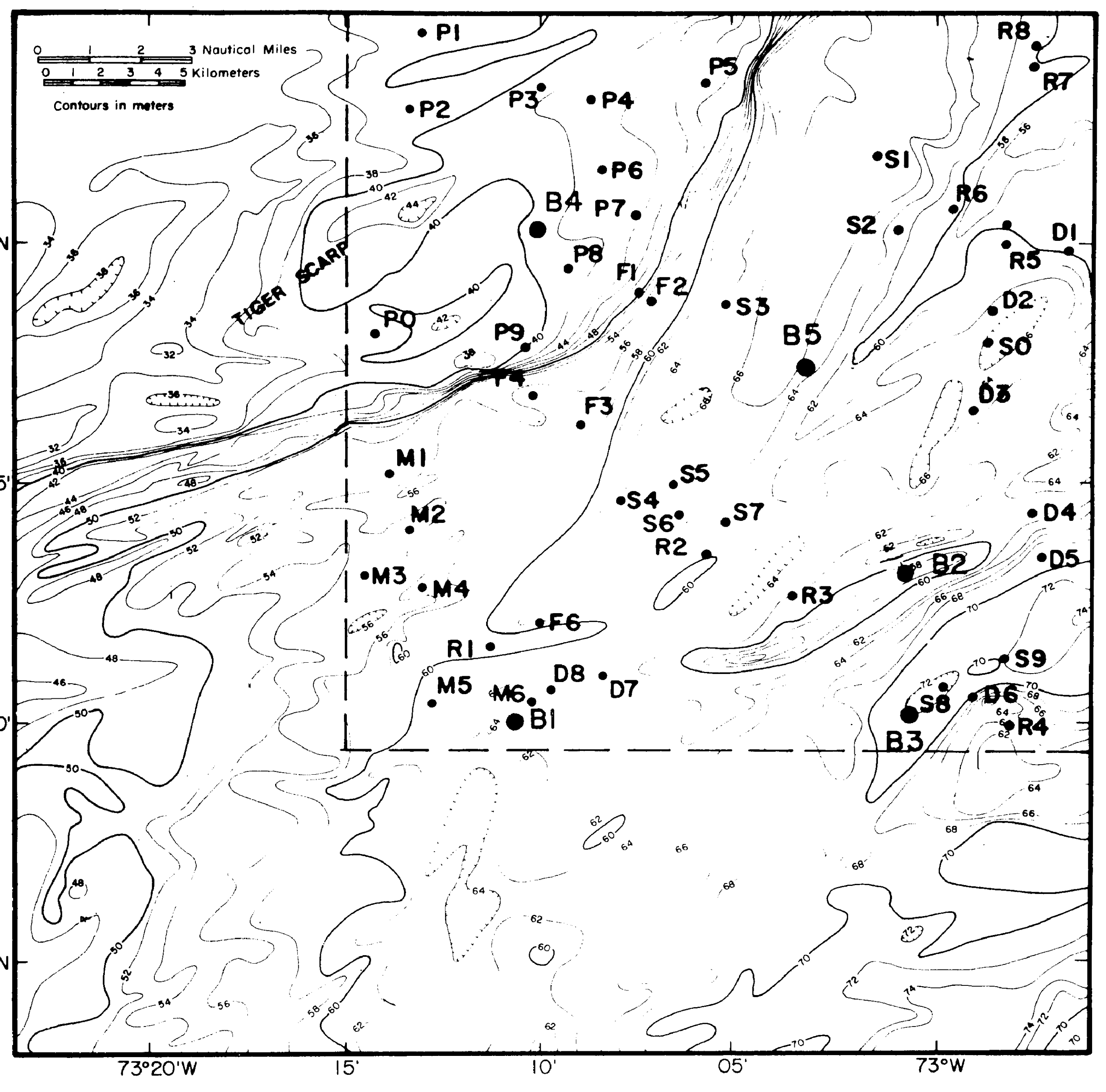

NEW JERSEY
DELAWARE
MARYLAND
VA.
40°
39°
38°
37°
75°
74°
73°
50
100
200
400
1000
2000
G1
G2
G3
G4
G5
G6
G7
A1
A2
A3
A4
H1
H2
B1
B2
B3
B4
B5
I1
I2
I3
I4
C1
C2
C3
C4
D1
D2
D3
D4
E1
E2
E3
E4
F1
F2
F3
F4
J1
J2
K1
K2
K3
K4
K5
K6
L1
L2
L3
L4
L5
L6

Figure 2. Locations of quarterly sampled stations (B1-B5) and stations sampled on a stratified random basis in Area B. Letter prefixes for stratified random stations denote *a priori* habitat classifications as follows: P - plateau; R - ridge; F - shallow flank and flat; D - deep flank and flat; M - muddy flat; S - swale (Boesch 1979a).


0 1 2 3 Nautical Miles
0 1 2 3 4 5 Kilometers
Contours in meters
TIGER SCARP
P1
P2
P3
P4
P5
P6
P7
P8
P9
P0
B4
B5
B1
B2
B3
F1
F2
F3
F4
F6
S1
S2
S3
S4
S5
S6
S7
S8
S9
S0
R1
R2
R3
R4
R5
R6
R7
R8
D1
D2
D3
D4
D5
D6
D7
D8
M1
M2
M3
M4
M5
M6
39°30'N
25'
20'
39°15'N
73°20'W
15'
10'
05'
73°W

Stations within Area B were chosen as representative of the different sedimentary habitats which have been shown to be related to shelf topography. The stations represented the following habitats: B1 - deep flank; B2 - ridge; B3 - deep swale; B4 - terrace; B5 - shallow swale. During the course of the study an additional sampling program, as described below, was employed to obtain information on biota in areas similar to those sampled on a regular basis.

METHODS

Shipboard Procedure

Macrobenthos was sampled at five stations on a quarterly basis. Four of the stations, B1-B4, were sampled over a two year period beginning in November 1975 and ending in August 1977. Station B5 was sampled during the second year only (November 1976 - August 1977). During November 1977 fifty-three samples were collected in a portion of the study area based on a stratified random sampling scheme to test the hypothesis that macrobenthic species distribution and abundance was related to mesoscale topography. Based on *a priori* evidence concerning biota and sediment type from the first year's sampling and detailed bathymetric charts developed by the U.S. Geological Survey the area was divided into six habitat strata. Sampling positions within each stratum were determined by random selection of two Loran C coordinates. The positions of all stations sampled in Area B are shown in Figure 2.

Smith-MacIntyre grab samples (0.1 m^2) were collected at each station (6 replicate grab samples were collected at each quarterly station, 1 sample was collected at each of the stratified random stations). A Benthos-Edgerton camera and strobe fitted onto the grab frame were used to take photographs of the sediment surface just prior to the time the grab made contact.

Following the removal of cores for sediment analyses the remaining contents of the grab were emptied into buckets and placed in specially constructed elutriation stands. Light bodied organisms and fine sediments were elutriated out of the buckets with running seawater. This overflow was trapped on 0.5 mm mesh Nitex screen at the base of the elutriator. The screen and trapped organisms were placed into a cloth bag while the remaining sediment was sieved through a larger surface area screen of the same mesh size. The second screen along with any remaining organisms and sediment was placed in a large cloth bag. Both bags were labeled and secured at the open ends. The bags were placed in isotonic $MgCl_2$ to anesthetize the enclosed organisms. After approximately 30 minutes the bags were transferred to 30 gallon drums containing 10% buffered Formalin with Rose Bengal as a vital stain.

Due to the fragile nature of amphipods and their susceptability to loss of appendages it was necessary to collect additional specimens in which care would be taken to maintain specimens suitable for examination of functional morphology. Three additional replicates were collected using the Smith-MacIntyre grab at each of the quarterly stations during August-September of 1977. These samples were placed in buckets and gently elutriated into small 0.5 mm mesh bottom boxes. Minimum water pressure was employed in an attempt to keep the amphipods intact. Animals from the screen were placed in jars containing isotonic $MgCl_2$. After 30 minutes the $MgCl_2$ was drained off and replaced by 70% ethanol. No attempt was made to retrieve amphipods which may have remained in the sediment following elutriation.

Laboratory Procedures

In the laboratory regularly collected samples were first soaked for several hours in fresh water. The "light" fractions were sorted to major taxa with the aid of a binocular dissecting microscope. "Heavy" fractions were spread out in pans and examined for stained organisms with the naked eye. The organisms from both fractions were combined by taxa and stored in 70% ethanol. Organisms were identifed and counted for each replicate. Following this, replicates of amphipod species from a single station for a single sampling date were lumped together by species for storage purposes. Amphipods from samples collected for morphological studies were sorted to species and stored in 70% ethanol.

The six species of amphipods chosen for this study, the ampeliscids, *Ampelisca agassizi*, *Ampelisca vadorum*, *Byblis serrata*, and the corophiids, *Unciola irrorata*, *Unciola inermis*, and *Erichthonius rubricornis*, were removed from quarterly samples collected during the second year only and separated into approximately 0.25 mm size classes with the aid of a micrometer in the ocular of a binocular dissecting microscope. Because replicate samples had been previously combined it was necessary in some cases (large sample size) to reduce the number of specimens to be measured for that sample. This was accomplished using standard techniques for splitting zooplankton samples. Entire samples were placed in the splitting apparatus and divided in half. This procedure was repeated on successive half-samples until a split containing approximately 100 specimens was obtained. Preliminary splitting tests indicated that this procedure produced size class distributions which were not significantly different from the original unsplit population (Mann-Whitney U statistic). Length was measured on extended specimens from the tip of the rostrum (if present) to the end of the telson. As a result of difficulty encountered in determining the specific identification of juvenile Unciola ($\leq$ 3 mm) the organisms were measured as a separate group. Length-frequency histograms and mean size information were tabulated for each species for each season and station.

Sediment Analyses

All sediment and organic carbon samples were processed by procedures described in Boesch (1979b).

Grain size parameters calculated for each sample included:

a) gravel, sand, silt and clay fraction percentages
b) the median, mean, standard deviation, skewness and kurtosis using the graphic measures of Folk (1968)

Scanning Electron Microscopy

Whole specimens, portions of specimens and individual mouthparts of specimens were used in analyses of functional morphology. Organisms were placed in small mesh containers and dehydrated through an increasing concentration series of ethanol (70, 80, 90, 100%) for approximately 1/2 hour at each step. In some cases mouthparts of fully dehydrated specimens were dissected and individually air dried. Whole specimens and large portions of specimens were transferred through two changes of 100% acetone. These specimens were dried in a Polaron Critical Point Dryer using carbon dioxide at high pressure (1200 p.s.i.) and temperature (40°C). The dried specimens were mounted on carrying stubs using a specially prepared mounting medium (see Appendix A). All specimens were coated with a thin film of gold-palladium using a vacuum evaporation coater. An AMR 1000 Scanning Electron Microscope was used to observe and record specimen images at various accelerating voltages. Micrographs were produced using Kodak Graphic Arts Film (4127) processed according to the manufacturer's directions.

Data Analysis - Spatial Patterns

Preliminary examination of amphipod distribution within the study area indicated that abundance could not be related to any single environmental gradient. The data were, therefore, analyzed from a multivariate approach.

Normal classification was used to group collections from the 53 stratified random stations and the November 1976 quarterly collections (mean abundances) on the basis of abundance of the six species in those samples. In actuality, seven taxa were considered in the classification since juvenile *Unciola* were considered separately.

Log-transformed ($\log_{10}$ x+1) species counts were used to calculate Bray-Curtis similarity measures for each pair of stations. This measure can be expressed as:

$$S_{jk} = 1 - \frac{\sum_i \left| x_{ji} - x_{ki} \right|}{\sum_i (x_{ji} + x_{ki})}$$

where S_{jk} is the similarity between stations j and k; x_{ji} is the abundance of the ith taxon for station j; and x_{ki} the abundance of the ith taxon for station k. Both group-average and flexible sorting strategies were used to cluster the stations (Clifford and Stephenson 1975, Boesch 1977). The cluster intensity coefficient in the flexible sorting strategy was set at -0.25 which effects moderately intense clustering (Boesch 1977). Some stations at which low abundances of amphipods were sampled showed low similarities to other groups. Based on sediment data and *a priori* evidence suggesting a sometimes patchy distribution of the amphipod fauna some of these samples were reallocated on the basis of the proportional abundance of each species in the sample.

The magnitude of contribution of each species to faunal definition of the groups in which it occurred was estimated by comparing geometric mean abundances within each group of stations and through the use of the F-statistic as an indicator of the among-groups to within-groups variation (log-transformed abundances) (Green and Vascotto 1978). Species which are primarily limited to one habitat group and show little spatial heterogeneity in this optimal habitat will have the highest F-ratios, while those species exhibiting low affinities with any particular habitat and/or exhibiting a high degree of small scale spatial variability will have low F-ratios.

Multiple discriminant analysis (Rao 1952, Cooley and Lohnes 1962) was used to elucidate the abiotic factors most strongly related to the differences between habitat groups and therefore to differences in species abundances within the study area. Multiple discriminant analysis (MDA) is a procedure which maximizes the ratio of among-groups sums of squares to the within-groups sums of squares (Cooley and Lohnes 1971). It starts with a data set consisting of n measurements on m parameters. Each of these n measurements is associated with one of g groups. The data set is reduced to n measurements on k new parameters. These k parameters are orthogonal, additive functions (discriminant functions) of the original m parameters (Green 1971). The technique simplifies the modeling and analysis of among-group differences by producing a reduced-rank model of group distribution in multivariate space. In the reduction from m to k dimensions any parameters that are highly correlated, invariant or irrelevant to group separation are combined or eliminated (Green 1971). Several statistical assumptions which must be met in order to validly utilize MDA are outlined in Green (1971). These inlcude:

1) the ability to define mutually exclusive groups on an *a priori* basis.

2) The original m parameters must be normally distributed. This assumption is likely to be fairly well satisfied by most

random sampling programs. Additionally, the _k_ new dimensions are more likely to be normally distributed as a consequence of the Central Limit Theorem (Cooley and Lohnes 1962).

3) The postulated orthogonal discriminant functions must be linear functions of the original correlated parameters. Transformations may be used to increase linearity and improve normality.

4) Groups must exhibit homogeneity of variances and covariances. Statistical tests of groups separation are based on this assumption.

The last assumption is unlikely to be satisfied with most ecological data, particularly if group membership is a function of species abundance and composition. Taking this into account Green (1971) notes that if a) the overall chi-square test of departure from randomness is highly significant, b) the discriminant function coefficients are ecologically interpretable and c) there are obvious group separations on each discriminant function it should "be reasonable to conclude that the differences are greater than would be produced by drawing random samples from a multivariate swarm."

Temporal Patterns

Abundance data from quarterly stations were used to determine if a) the six species exhibited strong seasonal trends in abundance which could lessen competitive interactions on other resource axes such as spatial and trophic and b) to assess the extent of temporal overlap. A one-way ANOVA comparing variation among sampling dates with inter-replicate variability at a given station was computed for each species (Boesch 1979a, unpublished). The F-ratio of among-group/within-group variance was used as an estimate of temporal vs. spatial variance. A highly significant F-ratio indicates a strong temporally varying component in population abundance. Patterns of temporal variation in abundance from one year to the next were compared for each species using Kendall's Coefficient of Concordance (Siegel 1956). The ranks of seasonal densities were tested using all quarterly sampled stations within the study area. The average abundance rank for each species for each season was also calculated. This average rank was computed by first ranking seasonal abundances within a sampling year for a given species at each station. The ranks for each season were then summed and divided by the number of stations considered ([4 stations x 2 years] + [1 station x 1 year] = 9). Maximum abundances are ranked 1, minimum abundances are ranked 4. Thus, average abundances range between 1 and 4. Finally, graphical analysis of data was used to assess extent of temporal overlap.

Body Size

Mean body size was calculated for each species at each station and season during the second year from length-frequency data. Ratios of body sizes for certain species pairs were obtained by first calculating the ratio of body size for the pair for each season at the stations being considered and then averaging these four ratios to obtain a single value. This value was used to assess the possibility that displaced size facilitated coexistence of species with, otherwise, similar resource requirements.

RESULTS

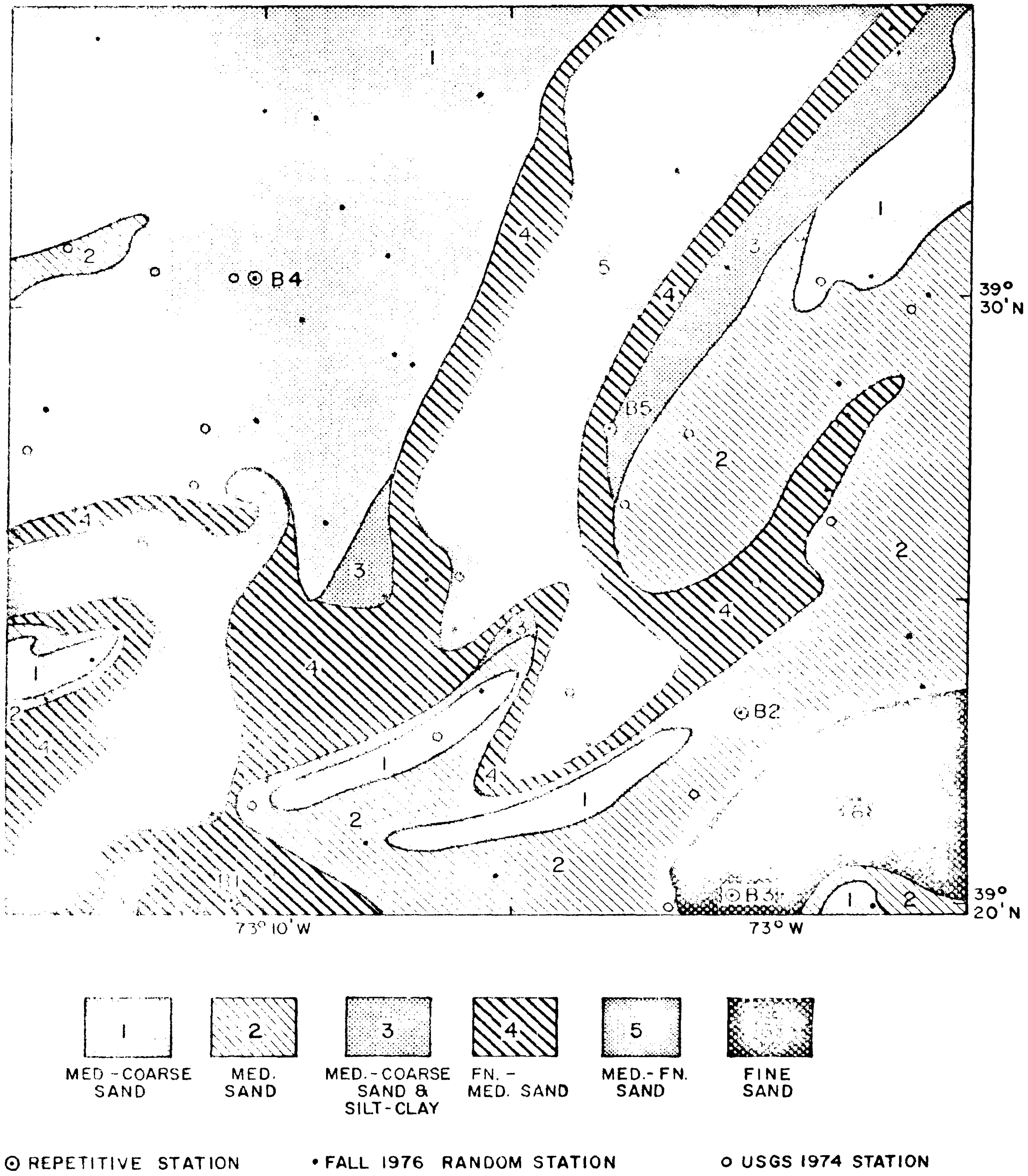
Physical Characteristics of the Study Area

Measured environmental parameters for both quarterly and stratified random samples are presented in Appendix B. Letter prefixes for stratified random samples refer to a priori habitat classifications as indicated at end of Appendix B. Based on these data and on an analysis of the distribution of all macrobenthic taxa Boesch (1979b) identified six sediment regimes within the study area (Figure 3).

The stations sampled on the terrace atop the Tiger Scarp (Figure 2), including the quarterly sampled station B4, are characterized by coarse-skewed medium sands containing low organic carbon and silt-clay concentrations. Inferred sediment mobility (frequency of surficial sediment movement) is fairly high in this shallow (<52 m) area.

With increased depth to the east of the scarp, sediments grade from fine-skewed medium sand on flanks to medium-fine sands in a broad swale (≃ 66 m) referred to as the shallow swale. Associated with this swale are numerous patches, found primarily at flank edges, of mixed sediment which contain up to 6% silt and clay. These areas apparently represent erosional windows in which underlying Holocene clay deposits have been exposed and mixed with surficial sands. The quarterly sampled station B5 was located at a transition zone between swale and eroded flank habitats. This was reflected in the temporally varying sediment characteristics found at this station.

Figure 3. Distribution of sediment types in a portion of Area B (from Boesch 1979b).


B4
B5
B2
B3
39° 30' N
39° 20' N
73° 10' W
73° W
1 MED - COARSE SAND
2 MED. SAND
3 MED.- COARSE SAND & SILT-CLAY
4 FN. - MED. SAND
5 MED.- FN. SAND
FINE SAND
⊙ REPETITIVE STATION
• FALL 1976 RANDOM STATION
○ USGS 1974 STATION

A number of ridges covered by coarse-skewed medium sands traverse the study area. These are located at greater depths than the terrace to the west and are probably subjected to slightly less frequent sediment disturbances. Within the study area these ridges grade into medium sand flanks as depth increases.

The deepest portion of the study area (> 70 m) is covered by fine sands with up to 8% silt and clay content. This deep swale constitutes a relatively quiescent environment subjected only to infrequent bottom disturbance as a result of winter storm activity (Butman et al. 1979).

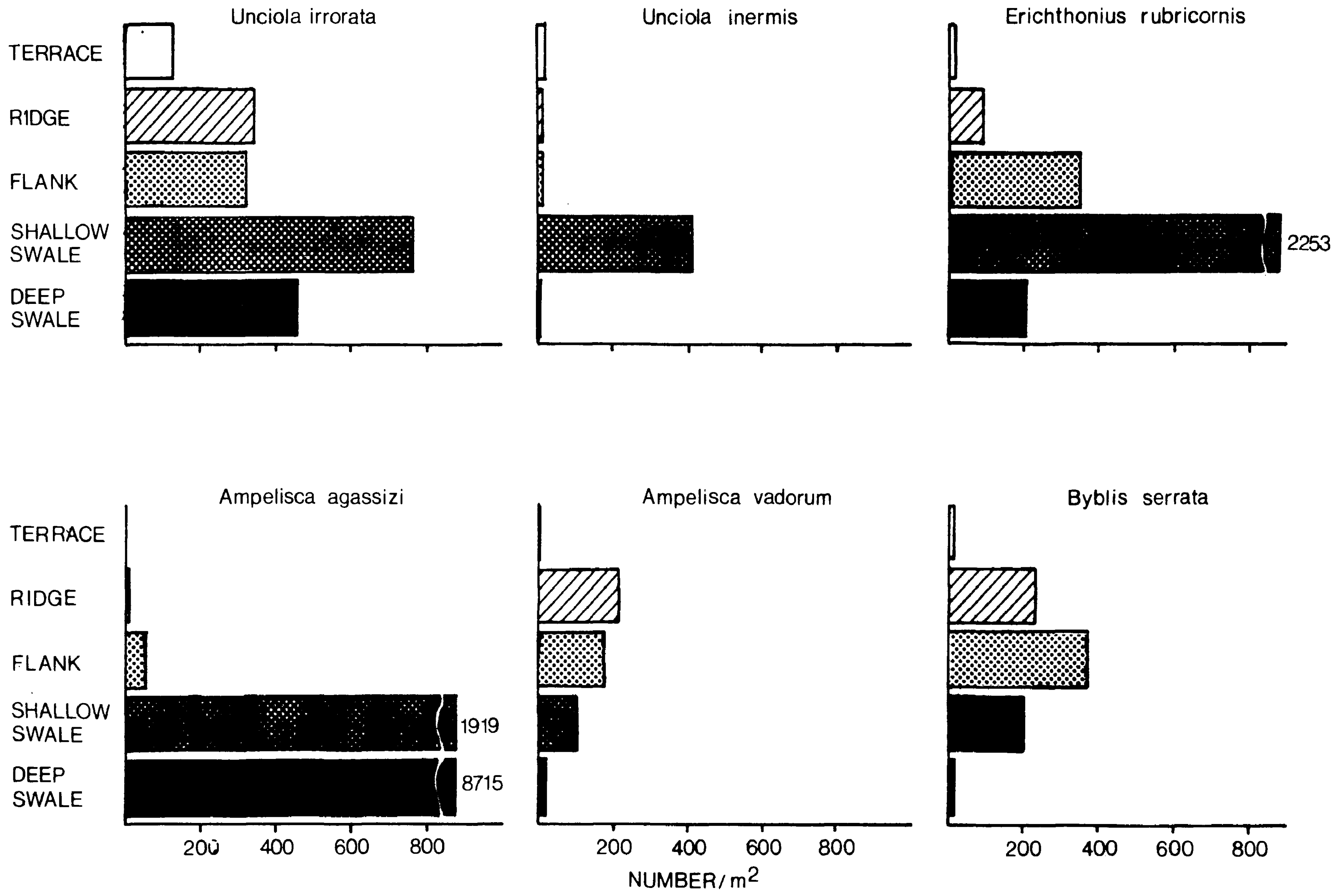
Spatial Patterns in Species Distribution

Abundances of species collected in each sample are listed in Appendix C. Grand mean (mean of quarterly means) abundance values for each species at quarterly sampled stations are presented in Figure 4. These data provide preliminary evidence suggesting habitat partitioning by some of the species within the study area.

The corophiid *Unciola irrorata*, found throughout the study area, is common over much of the Middle Atlantic shelf (Boesch 1979a). It reached maximum abundance at the shallow swale station. The species was also abundant in ridge, flank and deep swale habitats.

In marked contrast to its congener *U. irrorata*, *U. inermis* was relatively rare within the study area. It was present in large numbers at station B5, particularly when collections at this station

Figure 4. Grand mean (mean of quarterly means) abundances of the six species considered in this study in each habitat type represented by quarterly sampled stations. Stations represent habitats as follows: B1 - flank; B2 - ridge; B3 - deep swale; B4 - terrace; B5 - shallow swale.


Unciola irrorata
Unciola inermis
Erichthonius rubricornis
Ampelisca agassizi
Ampelisca vadorum
Byblis serrata
TERRACE
RIDGE
FLANK
SHALLOW SWALE
DEEP SWALE
2253
1919
8715
200
400
600
800
NUMBER/m2

included poorly sorted coarser sediments characteristic of eroded flanks. It was also occasionally found in high densities on the terrace.

Erichthonius rubricornis was found throughout most of the study area although its distribution was less even than that of *U. irrorata*. The species was most abundant at the shallow swale station B5.

The ampeliscids *Ampelisca vadorum* and *Byblis serrata* were found primarily in the intermediate (ridge and flank) habitat types. *A. vadorum* was most abundant at the ridge station, B2. *B. serrata* exhibited greatest abundance at the flank station, B1.

Ampelisca agassizi reached extremely high densities at the deep swale station, B3. These abundance values reflect an approximate density of one individual/cm^2. Abundance levels were lowered in the shallow swale, but remained equal to or greater than the abundances of the other species.

Based on these data there appears to be little evidence suggesting habitat partitioning within the corophiid group. All three species reached maximum abundances at the shallow swale station. Conversely, some tendency towards spatial segregation is suggested for the ampeliscides with *A. agassizi* concentrated in the deeper, finer sediment portions of the study area and both *A. vadorum* and *B. serrata* concentrated in the intermediate habitats.

Classification and Multiple Discriminant Analysis

Patterns of species distributions were further resolved using species abundance data and abiotic parameters measured at the 53 stratified random stations.

The cluster groups formed as a result of the group-average technique seemed over-divided relative to the number of species considered in the data set. The flexible sorting strategy provided a smaller number of groups which appeared more adequately descriptive. This dendrogram is presented in Figure 5. Station D8 was dropped from the analysis since none of the species considered were present at the station. Cluster groups are labeled I-VI. Stations which were reallocated based on examination of proportional species abundance are marked by an asterisk.

The relative contribution of each species to site group definition or conversely, the relative ability to define a set of stations within a group by the particular species present at those stations was estimated using the F-ratio of among-groups to within-groups variations in abundance. Table 1 presents the F-ratio for each species as well as the geometric mean abundance and 95% confidence intervals (transformed) for each species in each group.

Group II stations clearly represent the conditions most conducive to high densities of _A. vadorum_. _B. serrata_ was most abundant at the station in Group III, but was also fairly common at the stations in Groups II and V. Groups V and VI were characterized by high

Figure 5. Dendrogram resulting from normal classification of stratified random stations. Stations which were reallocated are denoted by asterisks.

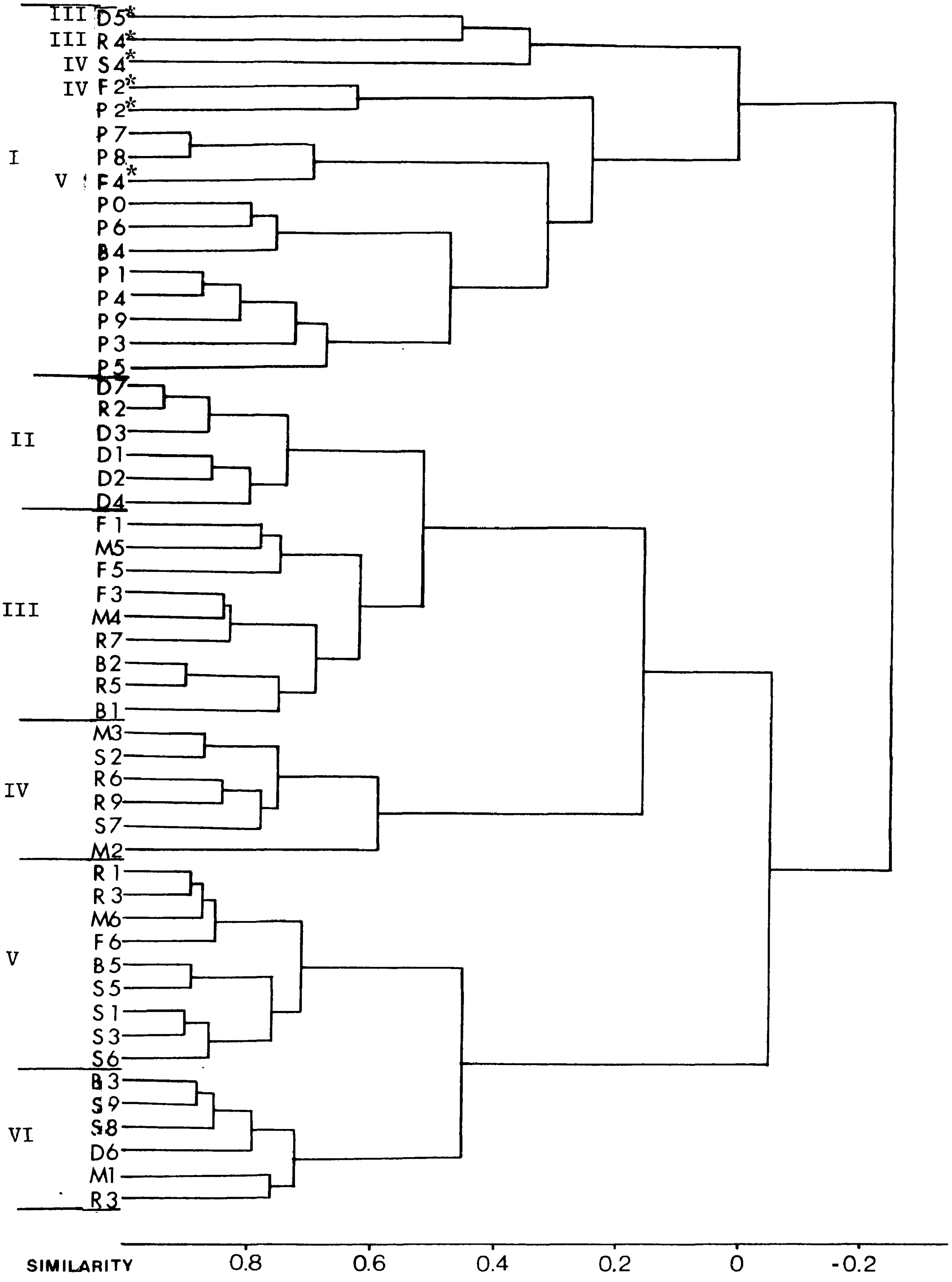

III D5*
III R4*
IV S4*
IV F2*
P2*
P7
I
P8
V F4*
P0
P6
B4
P1
P4
P9
P3
P5
D7
R2
II
D3
D1
D2
D4
F1
M5
F5
F3
III
M4
R7
B2
R5
B1
M3
S2
R6
IV
R9
S7
M2
R1
R3
M6
F6
V
B5
S5
S1
S3
S6
B3
S9
S8
VI
D6
M1
R3
SIMILARITY
0.8
0.6
0.4
0.2
0
-0.2

Table 1. F-ratios and geometric mean abundances (number of individuals/.1 m^2) with 95% confidence limits for each species at each site group. ** indicates that the F-ratio is significant at 0.01 level (5,46 d.f.).

		Geometric mean abundance (95% C.L.)					
Species	F-ratio	I	II	III	IV	V	IV
Byblis serrata	14.98**	0.39 (0.00,0.96)	11.44 (4.32,30.30)	29.19 (15.46,55.12)	5.24 (0.00,24.26)	9.97 (4.71,21.08)	1.22 (0.00,4.03)
Ampelisca vadorum	10.42**	0.00	22.80 (11.97,40.97)	2.28 (0.00,6.50)	2.17 (0.00,7.96)	3.05 (1.05,6.97)	1.88 (0.00,6.03)
Ampelisca agassizi	56.40**	0.00	0.00	1.05 (0.00,1.63)	0.66 (0.00,2.96)	68.90 (28.20,170.60)	273.74 (91.07,822.91)
Erichthonius rubricornis	9.48**	0.00	5.39 (0.53,15.09)	7.22 (2.56,18.01)	3.08 (0.00,11.96)	35.00 (20.18,60.69)	1.95 (0.00,3.86)
Unciola irrorata	3.21**	11.19 (7.94,15.64)	6.49 (2.62,14.50)	18.79 (7.63,44.31)	32.54 (13.63,77.72)	26.00 (16.71,40.46)	17.09 (10.51,27.77)
Unciola inermis	22.03**	0.45 (0.00,1.64)	0.86 (0.00,2.51)	1.69 (1.16,2.45)	62.76 (38.69,101.78)	1.90 (0.00,4.99)	0.90 (0.00,3.25)

abundances of _A. agassizi_. _U. inermis_ was found in high abundances only at the stations in Group IV. _E. rubricornis_ was most abundant at the stations in Group V. _U. irrorata_ had a low F-ratio. This species was not characteristic of any particular group of stations although it reached maximum abundances in Groups IV and V.

Analysis of environmental differences among groups which might account for the observed patterns in distribution and abundance of the six species was accomplished using multiple discriminant analysis. Measured abiotic parameters used in the analysis included depth, percent gravel, percent coarse sand, percent medium sand, percent fine sand, percent silt and clay, total organic carbon content (mg/g) and sediment sorting coefficient (ϕ). All percentage sediment components were transformed ($\arcsin\sqrt{p}$) to minimize non-linearity and improve normality. The raw data are summarized in Table 2 which shows the untransformed mean values for each abiotic parameter for each group as well as the species most strongly associated with that set of stations.

The overall chi-squared test of significance of among-group differences was highly significant [$X^2 = 172.53$, 40 df]. This value is likely to be biased as a result of heterogeneity in within-groups variance-covariance matrices. Using the criteria outlined by Green (1971) it was decided that only the first two axes should be considered. Table 3 summarizes the results for the first two discriminant functions which together account for 93% of the among-group variance.

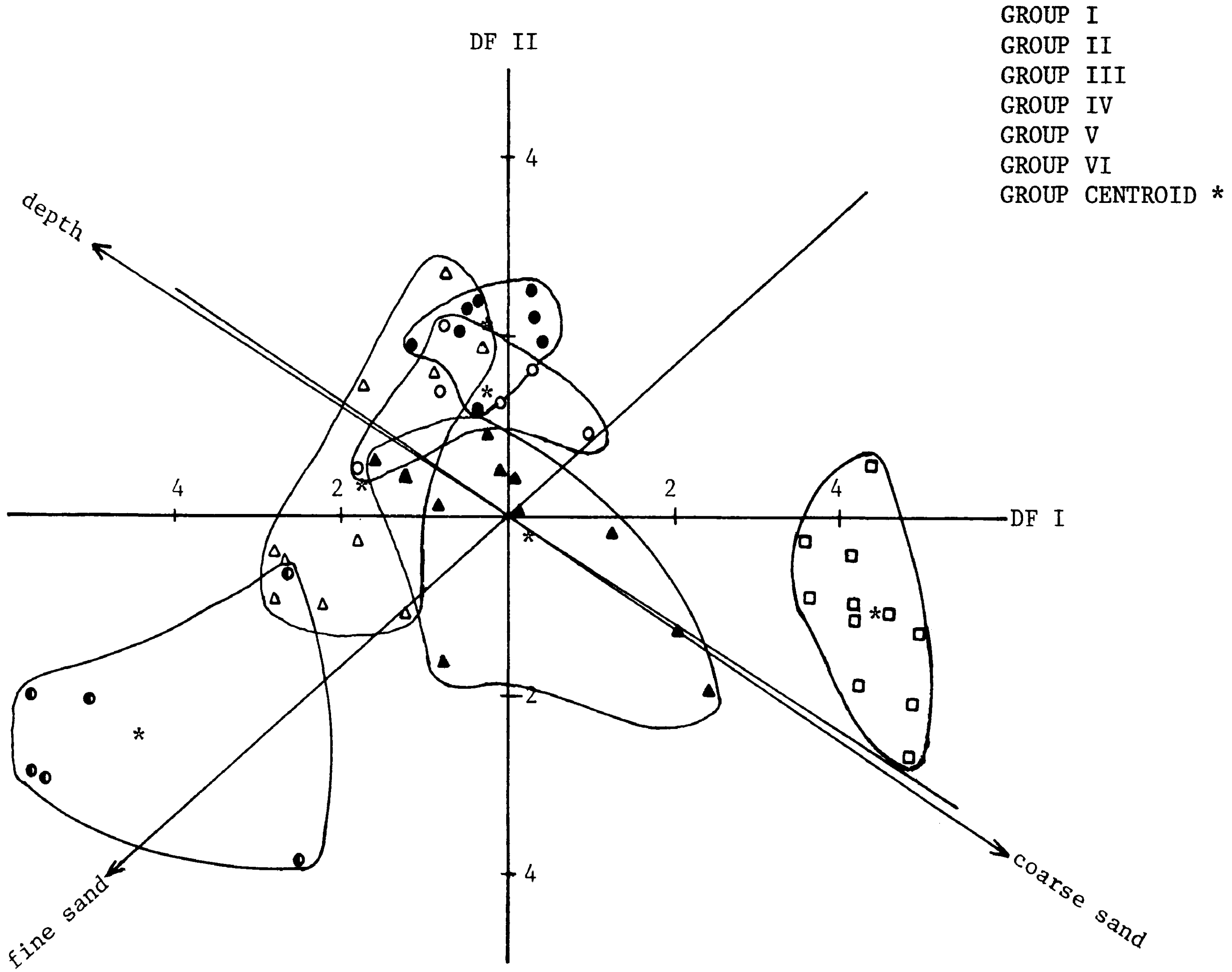
Table 2. Untransformed mean values of abiotic parameters for each group. The species most strongly associated with each group are indicated.

Group/ Principal Species	# of stations in Group	Depth(m)	% Gravel	% Coarse Sand	% Medium Sand	% Fine Sand	% Silt+Clay	(mg/g) Organic C	Sorting Coeff.(ϕ)
I none	11	43.6	4.98	29.21	60.69	4.94	0.19	0.36	0.64
II *A. vadorum* *B. serrata*	8	64.5	3.94	16.10	68.94	10.49	0.55	0.91	0.56
III *B. serrata* *U. irrorata*	11	60.0	3.22	22.23	54.38	18.21	1.62	0.64	0.67
IV *U. inermis* *U. irrorata*	6	63.1	12.15	21.63	49.82	13.40	3.35	0.97	0.89
V *E. rubricornis* *A. agassizi* *U. irrorata*	10	64.2	2.77	5.93	51.78	35.30	3.84	1.22	0.48
VI *A. agassizi*	6	69.8	2.82	3.05	27.31	60.75	4.95	1.71	0.53

Table 3. Discriminant function coefficients for each parameter utilized in the discriminant analysis. Percent of among-group variance accounted for by DFI and DFII is also indicated.

	DISCRIMINANT FUNCTION	
	I	II
% of among-groups variance:	74.15	19.25
PARAMETERS:		
DEPTH (m)	-0.867	0.058
GRAVEL (%)	-0.077	0.436
COARSE SAND (%)	-0.082	-0.979
MEDIUM SAND (%)	0.155	0.381
FINE SAND (%)	-0.630	-1.040
SILT + CLAY (%)	0.119	0.217
SORTING COEFFICIENT (ϕ)	0.160	-0.102
ORGANIC CARBON (mg/g)	0.008	0.279

Figure 6. Orientation of _a priori_ identified site groups in discriminant space. Vectors indicating the relative orientation of important sediment parameters contributing to among-groups variance were plotted using correlations of original parameters with discriminant functions I and II.


GROUP I
GROUP II
GROUP III
GROUP IV
GROUP V
GROUP VI
GROUP CENTROID *
DF II
DF I
4
2
2
4
4
2
4
depth
coarse sand
fine sand

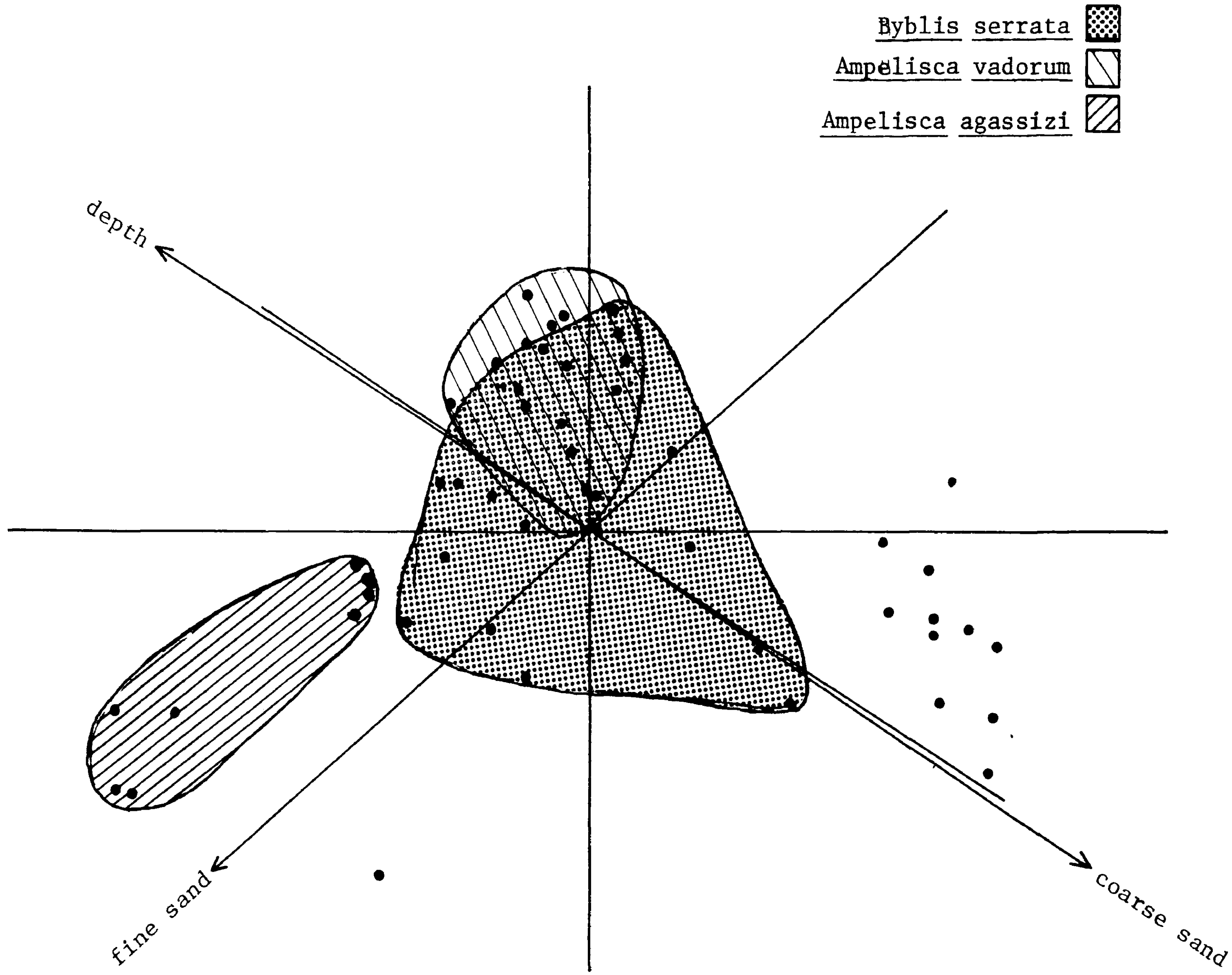
The orientation of groups in discriminant space is shown in Figure 6. Pooled within-groups correlations between discriminating variables and discriminant functions were used to label vectors indicating the relative orientation of the most important parameters contributing to among-group separation on the first two discriminant functions.

Discriminant function (DF) I is related to changes in both depth and fine sand content in sediments. Deep stations with sediments consisting of much fine sand have the highest negative scores on this axis. Shallow stations with little fine sand have the highest positive scores. DF II separates medium sand habitats from the more extreme habitat types.

Direct consideration of species abundance patterns in discriminant space was made by first standardizing all abundance values for a particular species by its maximum value and then plotting these in discriminant space. In Figures 7 and 8 the encircled areas include all those stations at which a species reached abundances $\geq$25% of their maximum. Standardizing abundance values by the geometric mean produced nearly identical results. Due to the great overlap between members of different families each family is presented separately.

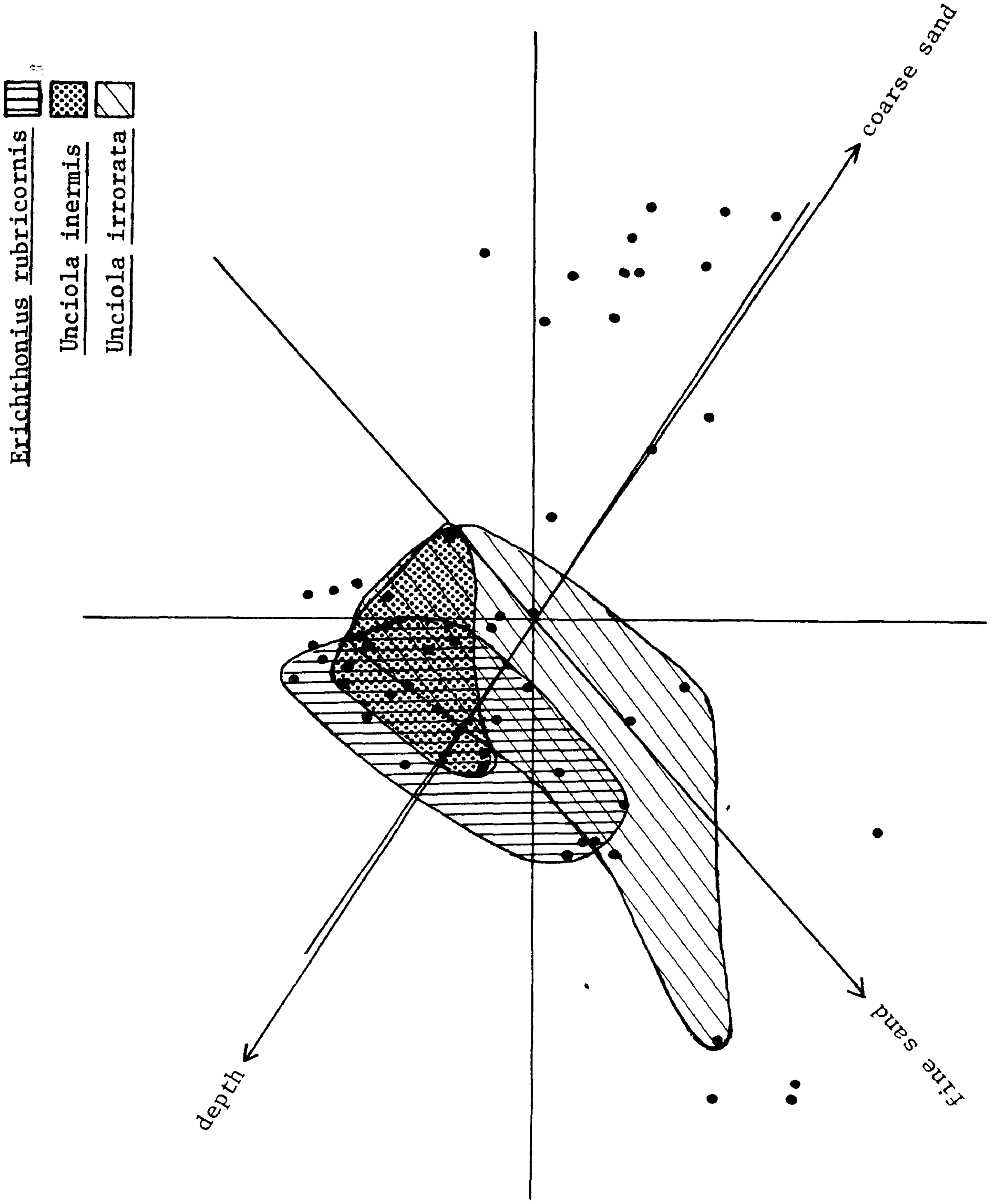
There is a clear separation of A. agassizi from the other ampeliscids in discriminant space (Figure 7). The orientation of the line of separation suggests the importance of factors related to

Figure 7. Standardized abundances of *Ampelisca agassizi*, *Ampelisca vadorum* and *Byblis serrata* in discriminant space. Shaded areas enclose all points at which abundance was ≥ 25% of maximum sampled for each species.



Byblis serrata ▩
Ampelisca vadorum ▧
Ampelisca agassizi ▨
depth
coarse sand
fine sand

Figure 8. Standardized abundances of _Unciola irrorata_, _Unciola inermis_ and _Erichthonius rubricornis_ in disrciminant space. Shaded areas enclose all points at which abundance was ≥ 25% of maximum sampled for each species.


Erichthonius rubricornis
Unciola inermis
Unciola irrorata
coarse sand
fine sand
depth

sediment fine sand content. The distributions of *A. vadorum* and *B. serrata* are poorly separated. *B. serrata* is distributed in shallow coarse habitats as well as in the more intermediate portions of discriminant space.

Within the corophiid family the distribution of *U. inermis* is completely overlapped by the distribution of the other two species (Figure 8). The relative orientation of the areas occupied by *E. rubricornis* and *U. irrorata* suggest a possible trend towards segregation.

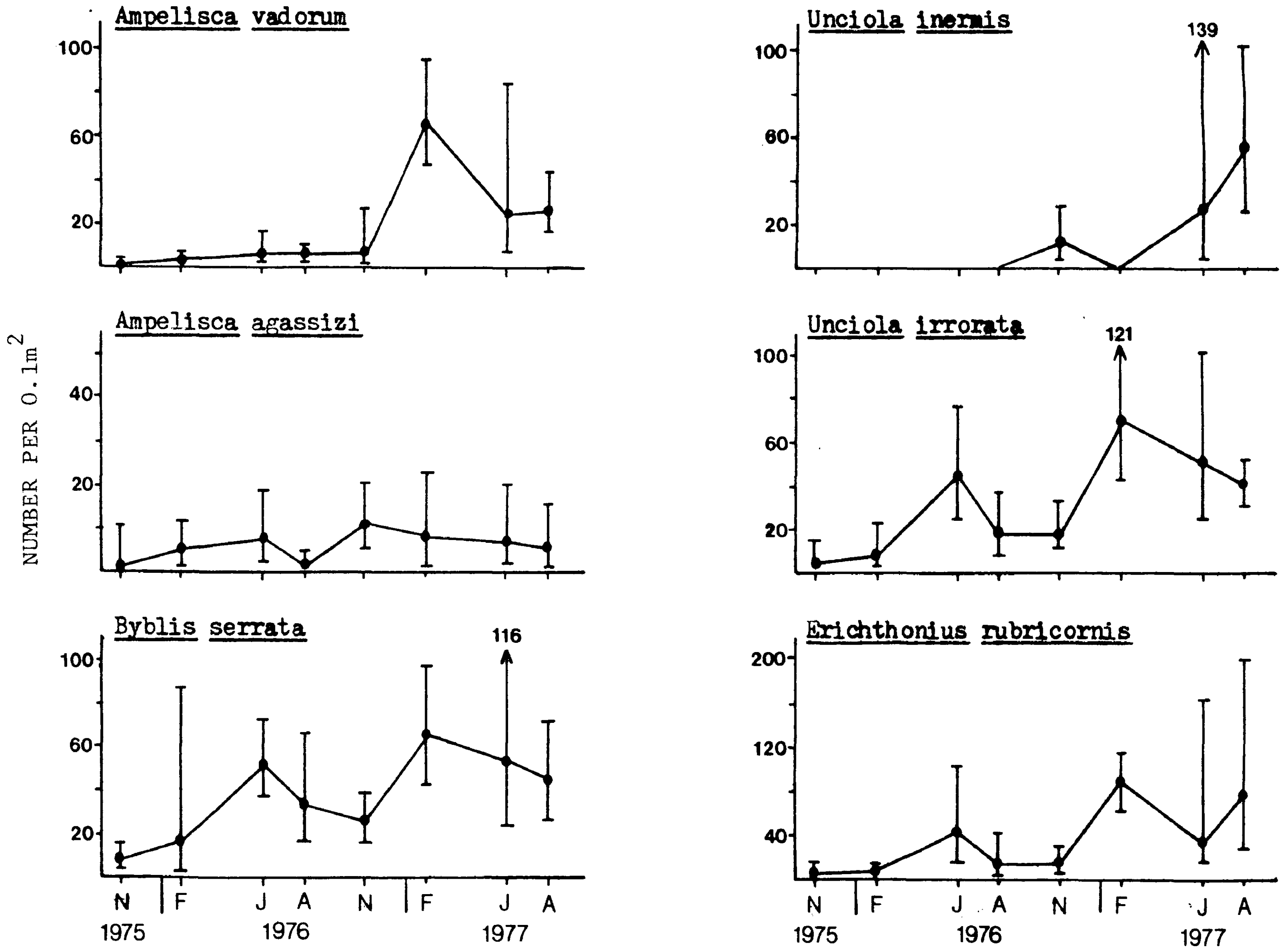
The only apparent cross-family pattern of spatial segregation concerns the absence of all species except *A. agassizi* and *U. irrorata* from the deepest, finest grained portions of the study area.

Temporal Patterns in Abundance

Temporal patterns in abundance for each species at each quarterly-sampled station are plotted in Figures 9-13. Table 4 summarizes the results of the statistical tests designed to determine if there were significant seasonal trends in species abundances. F-ratios, which were significant for all species at most stations, were generally higher for corophiid family members.

The results of the Kendall's test of concordance were markedly different for species in the two families. All corophiids exhibited strongly significant ($p < 0.01$) seasonal trends in abundance. The ampeliscids either remained relatively persistent over time (*A.*

Figure 9. Temporal patterns in abundance exhibited by each species at Station B1 (flank) from November 1975 to August 1977.



NUMBER PER 0.1m^2
Ampelisca vadorum
100
60
20
Ampelisca agassizi
40
20
Byblis serrata
116
100
60
20
N
F
J
A
N
F
J
A
1975
1976
1977
Unciola inermis
139
100
60
20
Unciola irrorata
121
100
60
20
Erichthonius rubricornis
200
120
40
N
F
J
A
N
F
J
A
1975
1976
1977

Figure 10. Temporal patterns in abundance exhibited by each species at Station B2 (ridge) from November 1975 to August 1977.

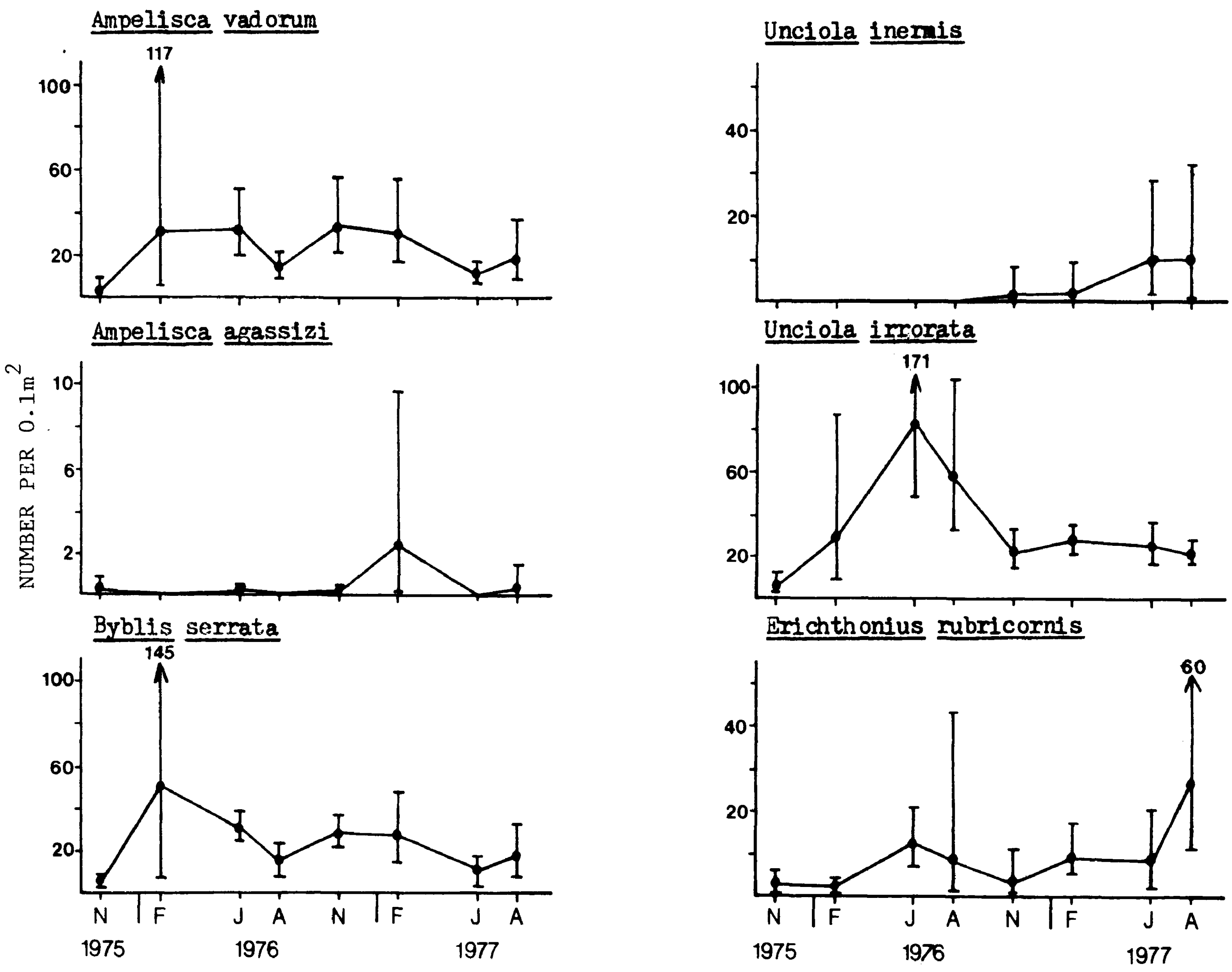

Ampelisca vadorum
117
100
60
20
Ampelisca agassizi
NUMBER PER 0.1m^2
10
6
2
Byblis serrata
145
100
60
20
N
F
J
A
N
F
J
A
1975
1976
1977
Unciola inermis
40
20
Unciola irrorata
171
100
60
20
Erichthonius rubricornis
60
40
20
N
F
J
A
N
F
J
A
1975
1976
1977

Figure 11. Temporal patterns in abundance exhibited by each species at Station B3 (deep swale) from November 1975 to August 1977.

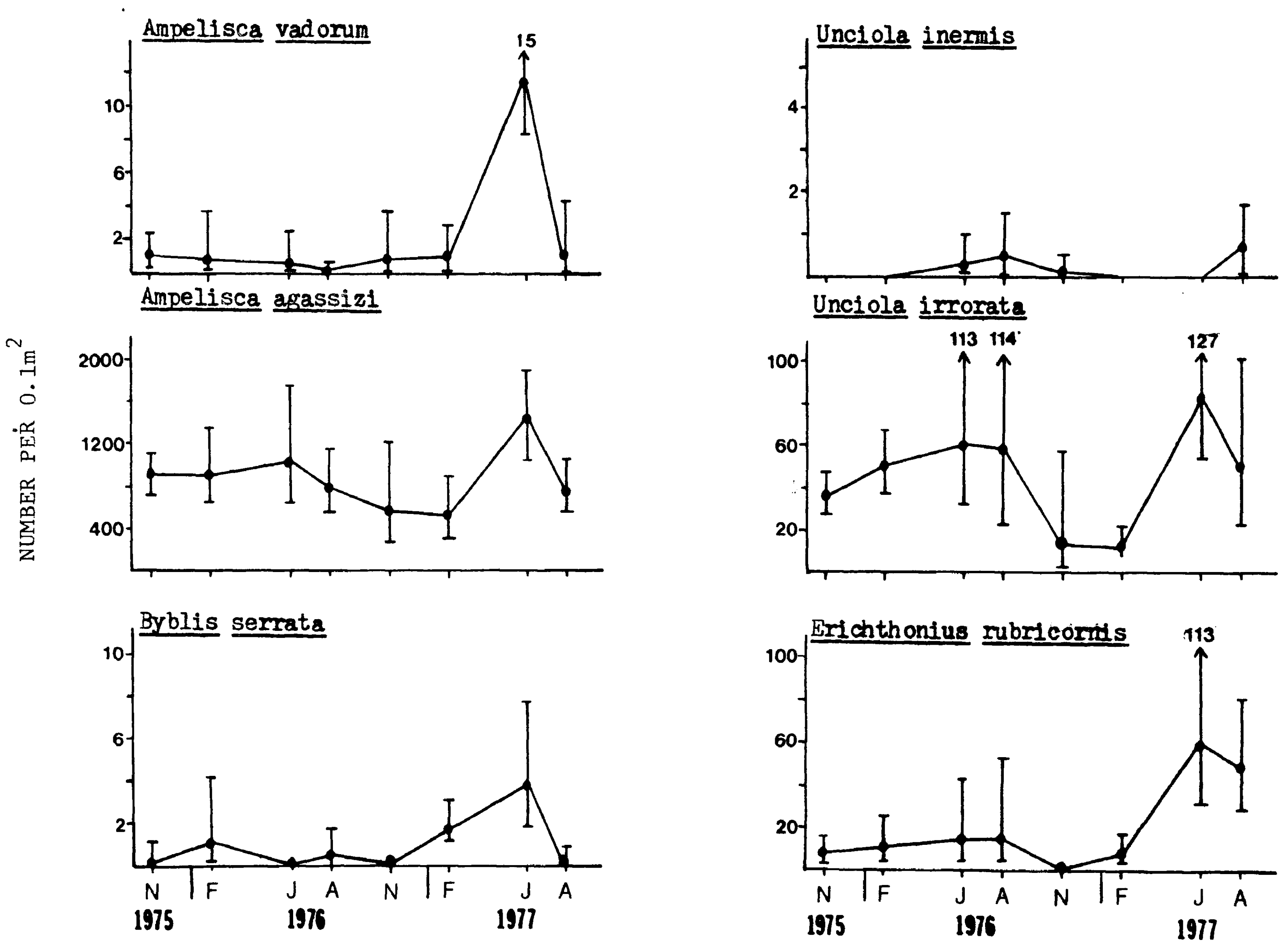

NUMBER PER 0.1m²
Ampelisca vadorum
15
10
6
2
Ampelisca agassizi
2000
1200
400
Byblis serrata
10
6
2
N
F
J
A
N
F
J
A
1975
1976
1977
Unciola inermis
4
2
Unciola irrorata
113
114
127
100
60
20
Erichthonius rubricornis
113
100
60
20
N
F
J
A
N
F
J
A
1975
1976
1977

Figure 12. Temporal patterns in abundance exhibited by each species at Station B4 (terrace) from November 1975 to August 1977.

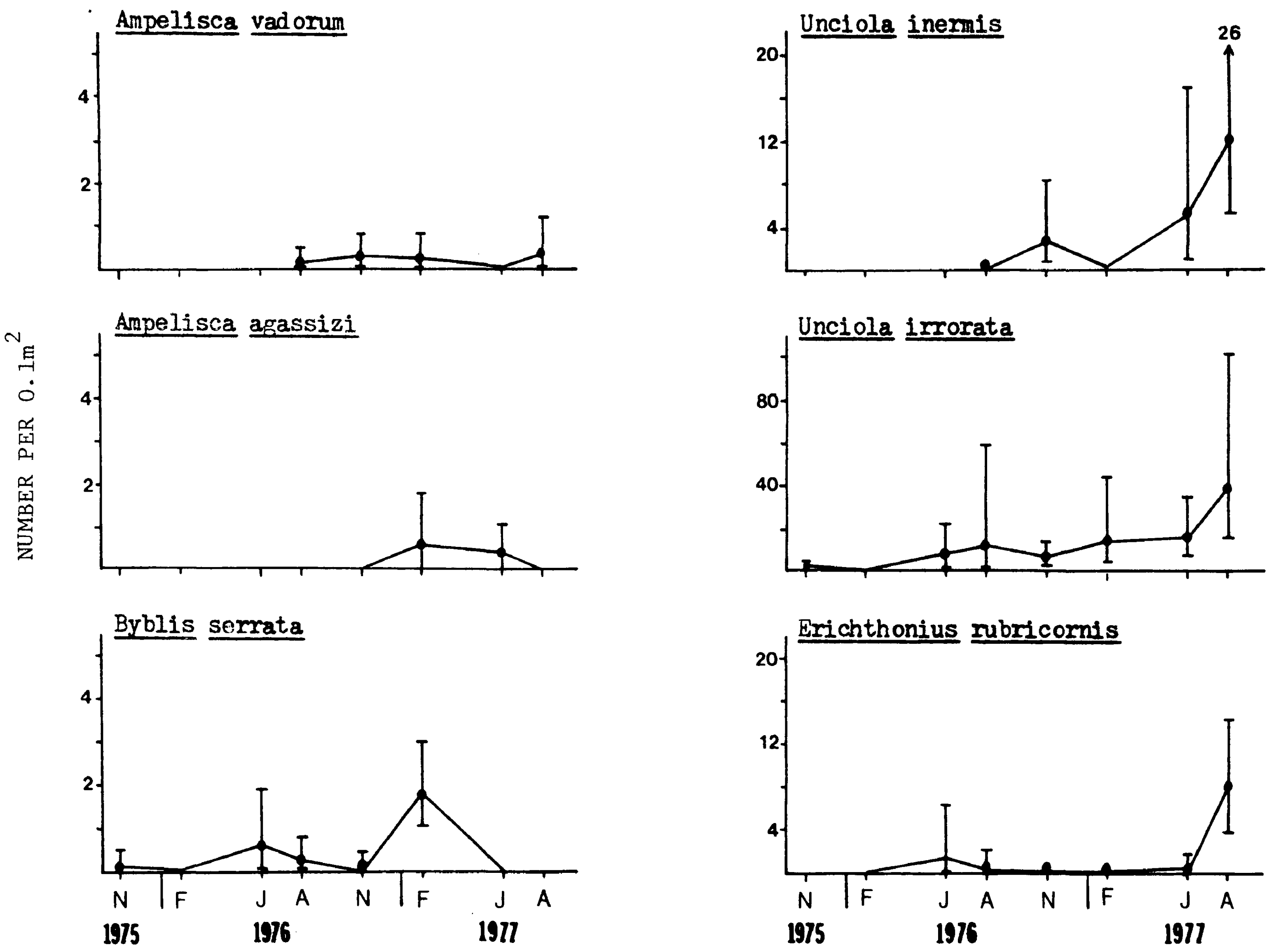

NUMBER PER 0.1m2
Ampelisca vadorum
Ampelisca agassizi
Byblis serrata
Unciola inermis
Unciola irrorata
Erichthonius rubricornis
26
4
2
20
12
80
40
N
F
J
A
1975
1976
1977

Figure 13. Temporal patterns in abundance exhibited by each species at Station B5 (shallow swale) from November 1976 to August 1977.

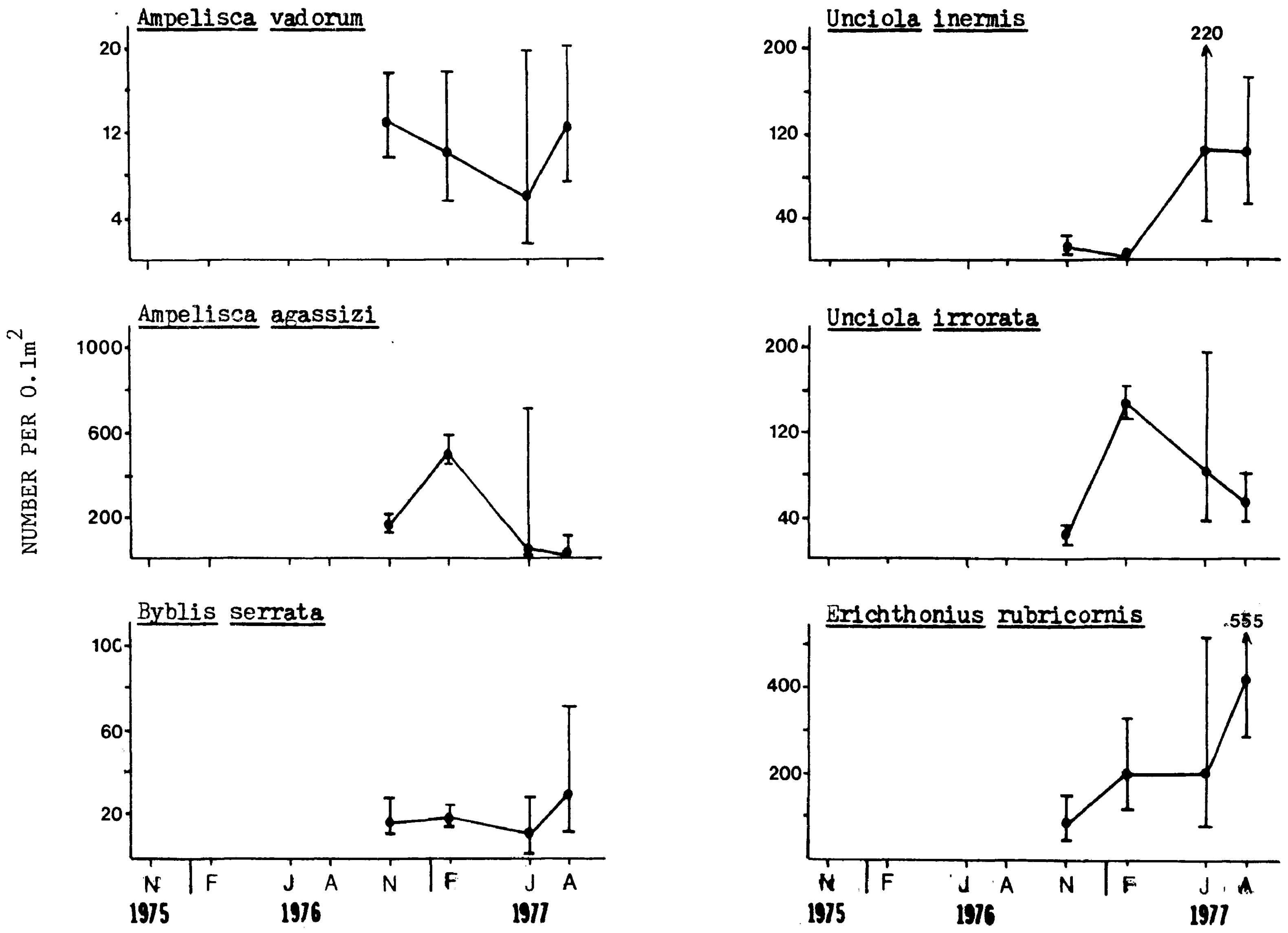

NUMBER PER 0.1m^2
Ampelisca vadorum
20
12
4
Ampelisca agassizi
1000
600
200
Byblis serrata
10C
60
20
N
F
J
A
N
F
J
A
1975
1976
1977
Unciola inermis
220
200
120
40
Unciola irrorata
200
120
40
Erichthonius rubricornis
555
400
200
N
F
J
A
N
F
J
A
1975
1976
1977

Table 4. Results of statistical analyses of temporal variability.

Species	Temporal Variation Within Stations (F-Ratio)	Kendall coefficient of Concordance: W	Average Seasonal Rank F	W	Sp	Su	Season of Maximum Abundance
Ampelisca vadorum	B1-14.38**, B2-5.46*, B3-6.91**, B4-1.37, B5-1.55	n.s.	2.61	2.50	2.67	2.22	
Ampelisca agassizi	B1-2.12, B2-5.59**, B3-3.86** B4-4.11**, B5-5.06**	n.s.	2.47	2.25	1.97	3.31	
Byblis serrata	B1-4.84**, B2-8.45**, B3-7.46** B4-1.30, B5-2.19	n.s.	3.00	2.00	2.50	2.50	
Unciola inermis	B1-17.32**, B2-4.44**, B3-2.99* B4-20.05**, B5-35.01**	**	2.92	3.83	2.00	1.25	summer
Unciola irrorata	B1-10.86**, B2-12.02**, B3-5.41** B4-9.72**, B5-18.33**	**	3.67	2.56	1.56	2.23	spring
Erichthonius rubricornis	B1-7.54**, B2-4.75**, B3-12.59** B4-10.81**, B5-6.64**	**	3.72	2.94	1.78	1.56	spring-summer

*significant at 0.05
**significant at 0.01
Stations B1 - B4 (7,40 d.f.), Station B5 (3,20 d.f.)

agassizi) or did not vary in a strongly seasonal manner. The seasons during which the corophiids achieved maximum abundances are noted in Table 4 along with average abundance ranks computed for each species for each season.

E. rubricornis was most abundant during spring and summer. U. irrorata, also frequently exhibiting maximum abundances during the spring, occasionally peaked during the winter particularly during the second study year. Both of these species were least abundant during the fall. Although low abundances of U. inermis at most stations within the study area made it more difficult to analyze the species abundance patterns, the data suggest a trend toward maximum abundances during late spring and summer, with lowest abundances occurring during winter months. Spatial overlap of U. inermis with its congener U. irrorata might be lessened by these offset peaks in high population densities. This would also be true for the spatially co-occurring E. rubricornis and U. irrorata populations.

Patterns of temporal segregation are less apparent among the ampeliscids although slight shifts in peak abundance are suggested by the average rank of seasonal densities. A. vadorum and B. serrata which broadly overlap spatially have the most strongly displaced maximum abundances in this group. B. serrata is the only species which was not most abundant during the spring and summer sampling periods.

Size distribution

Length-frequency data were tabulated for each species at each station sampled during the second sampling year (Appendix D). Exceptions to this were those sampling dates when only a few individuals of a given species were collected. These individuals were not measured and this is noted in the figures where appropriate. The data were originally recorded in ≈0.25 mm units but have been regrouped into 1 mm size classes for statistical reasons (Sokal and Rohlf 1969) and for ease and clarity of presentation.

The difficulty associated with identifying juvenile Unciola (< 3 mm) to species posed numerous problems. During the course of the study it was discovered that specimens as small as 2 mm could be positively identified. Time constraints prevented a total re-enumeration of juveniles. Only the juveniles at stations B4 and B5 have been re-examined since these stations represented the important habitats in the study area for U. inermis. Even at these stations juveniles < 2 mm could not be considered in the length-frequency histograms.

Mean body length data are presented in Table 5. The exclusion of juvenile Unciola (< 2mm) from consideration results in a bias towards larger sized individuals and a slight displacement of average body length for Unciola irrorata and U. inermis. Caution must, therefore, be observed since the data for these species are not directly comparable with the data for the other species considered in the study. Clear differences in body size, particularly among closely

Table 5. Mean body lengths (mm) of each species at each station and season sampled during the second sampling year.

Species	Station	B1				B2				B3				B4				B5			
	Season	F	W	Sp	Su	F	W	Sp	Su	F	W	Sp	Su	F	W	Sp	Su	F	W	Sp	Su
Byblis serrata		7.4	3.7	5.6	6.6	6.6	4.3	6.3	6.8	-	4.3	4.0	-	-	-	-	-	6.4	4.2	5.7	5.7
Ampelisca vadorum		3.9	2.8	4.2	4.6	3.6	3.5	4.3	4.9	4.3	2.4	3.5	-	-	-	-	-	3.8	3.5	4.2	4.4
Ampelisca agassizi		4.6	3.7	3.7	4.2	-	-	-	-	4.5	3.4	4.5	4.5	-	-	-	-	3.2	4.4	5.0	5.2
Erichthonius rubricornis		3.4	4.3	4.2	3.9	3.5	4.3	5.0	4.6	4.9	5.0	4.4	3.9	-	-	-	-	3.4	5.1	4.1	3.9
Unciola irrorata		6.8	4.7	6.2	6.3	6.3	5.2	6.4	4.7	5.4	5.0	5.4	5.0	4.8	3.9	4.8	4.2	3.6	3.4	5.2	7.4
Unciola inermis		7.2	-	5.6	6.1	7.5	-	3.5	4.2	-	-	-	5.2	8.1	8.5	4.5	3.6	7.0	2.7	4.5	7.3

related spatially co-occurring species, are evident. B. serrata always had a mean body length greater than that of A. vadorum. These species differ in size by an average factor of 1.5 at the stations where they are most abundant and commonly co-occur (i.e. B1, B2, B5). The ratio of body lengths of the pairs A. agassizi - B. serrata and A. agassizi - A. vadorum, which tend to co-occur only at the fringes of their population distributions, are lower (1.4 at stations B1, B5 and 1.2 at stations B1, B3, B5 for each pair respectively). The congeners U. irrorata and U. inermis had an average size quotient of 1.4 where they co-occurred (Stations B4, B5). Although the data does not include the smallest individuals the difference is apparently real. The length-frequency data from station B5, particularly during the spring and summer suggest that size differences between species are maintained by offset modal peaks rather than one species ultimately attaining a greater size. Comparisons of E. rubricornis with U. irrorata and U. inermis cannot be made because of the problem with juveniles, but the length-frequency histograms and personal observations suggest that E. rubricornis is generally smaller than the other two species. Similarly, cross family comparisons between Unciola spp. and ampeliscids cannot be made. Length ratios between E. rubricornis and the ampeliscids are variable. E. rubricornis and A. agassizi have nearly the same mean size (ratio = 1, stations B1, B3, B5) A. vadorum and E. rubricornis differ by a factor of 1.2 (stations B1, B2, B5) while B. serrata and E. rubricornis differ by a factor of 1.5 (stations B1, B2, B5).

Functional Morphology of Feeding Appendages

For the purpoes of this study the morphology of four feeding appendages is considered. These include the maxilliped, first and second maxillae and mandible. A view of the buccal region of *Ampelisca agassizi* is presented in Figure 14 as a general guide to the arrangement of feeding appendages in Gammaridea. Scanning electron micrographs of individual mouthparts for each species are presented in Figures 15-32. Although the morphology of each mouthpart conforms to basic gammaridean plans as outlined by Barnard (1969) quantitative differences are evident among species.

The maxillipeds of *Unciola irrorata* and *Unciola inermis* (Figures 15, 18) are stout in comparison with those of the other species. The palps are moderately setose. The inner margin of the outer plates of both species are armed with stout, flattened spines which become more elongate apically. These spines are flanked by a row of short setae along the inner margin.

The maxilliped of *Erichthonius rubricornis* (Figure 21) is less stout. The palp is more heavily stose than in the *Unciola* spp.. The medial spines of the outer plate are slender. These spines are flanked by pectinate setae.

The maxillipeds of all three ampeliscids (Figure 24, 27, 30) are more heavily setose than in the corophiids. In *Byblis serrata* (Figure 30) the setae on the palps are, in some cases, barbed. The medial margin of the outer plate is lined with spines similar to those observed in *E. rubricornis*, (Figure 21) whereas in both of the *Ampelisca* (Figures 24, 27) spp. these spines are somewhat longer. From the bases of the maxillipeds of *Ampelisca vadorum* and *Ampelisca agassizi* project numerous, long plumose setae. In *A. agassizi* these setae mesh into a basket-like structure (Figure 14).

The second maxillae (Figures 16a, 19a, 22a, 25a, 28a, 31a) are similar in all species although they tend to be slimmer in the ampeliscids. The setae along the inner margin of the inner plate are long and plumose in most of the species. In *E. rubricornis* (Figure 22a) these setae are pectinate rather than plumose.

The general morphology of the first maxilae (Figures 16b, 19b, 22b, 25b, 28b, 31b) are also similar among species. The inner plate is reduced and has one or two plumose setae at its distal end, except in *E. rubricornis* (Figure 22b) where three to four plumose setae are present along the inner margin. The outer plate bears heavy spines at its terminus. These spines are mainly bifurcate in *U. irrorata*, multipointed in *U. inermis*, moderately serrate in *E. rubricornis*, and strongly serrated in the ampeliscids. The spines and setae borne at the terminus of the palp are similar in all species. Only *E. rubricornis* and *A. agassizi* have a band of very fine hair setae on the outer margin of the outer plate.

The mandibles of *U. irrorata* and *U. inermis* (Figures 17 and 20) have heavy, robust tooth-like incisors, a lacinia mobilis, two accessory spines, and large triturative molars. *E. rubricornis* (Figure

Figure 14. Lateral view of the buccal region of Ampelisca agassizi. Feeding appendages are labeled as follows: a-maxilliped; b-maxilla 2; c-maxilla 1; d-lower lip; e-mandible;f-upper lip. X 90.

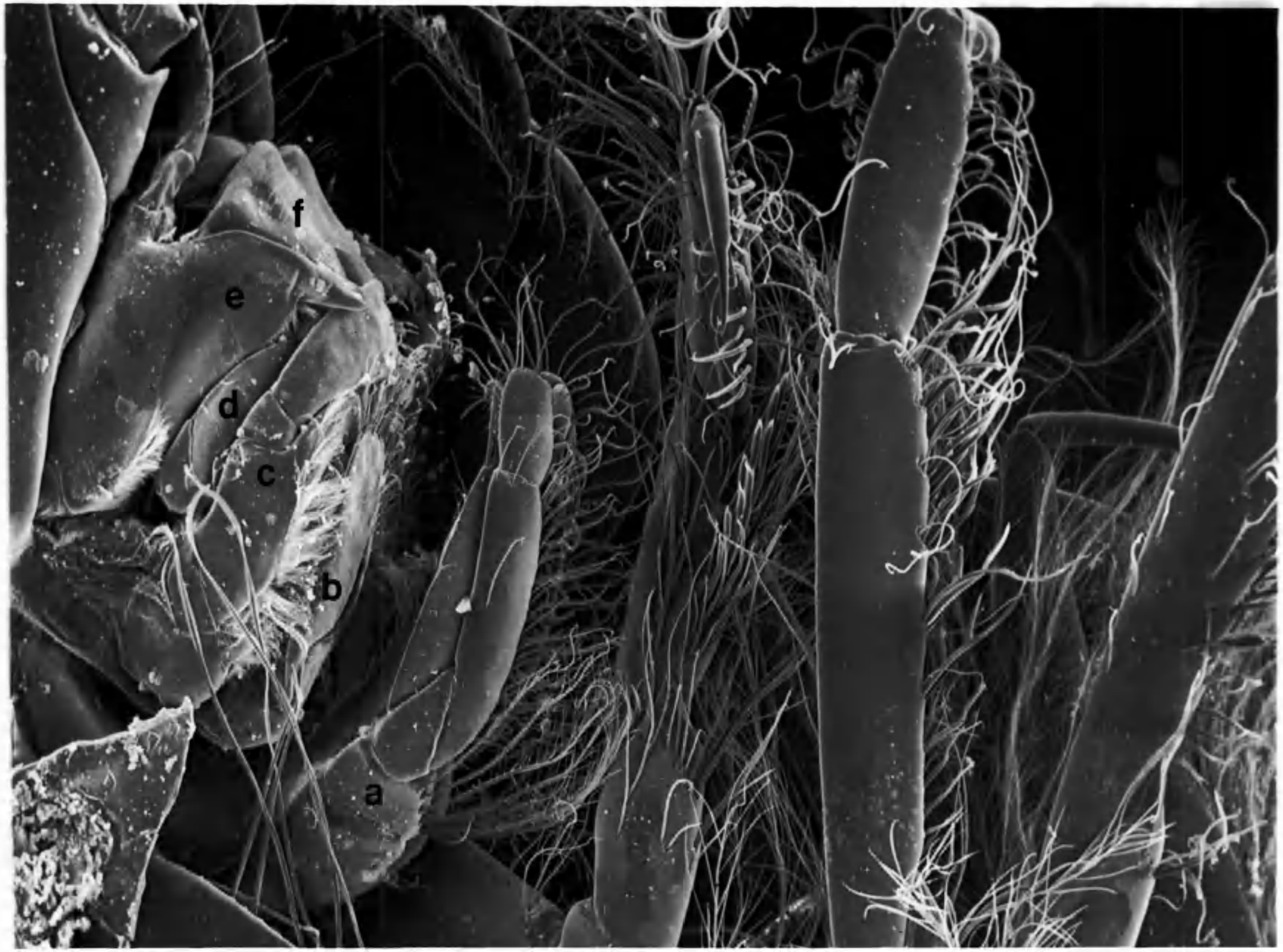

f
e
d
c
b
a

Figure 15. Maxilliped of *Unciola irrorata*. a-outer plate; b- outer plate palp. X 160.

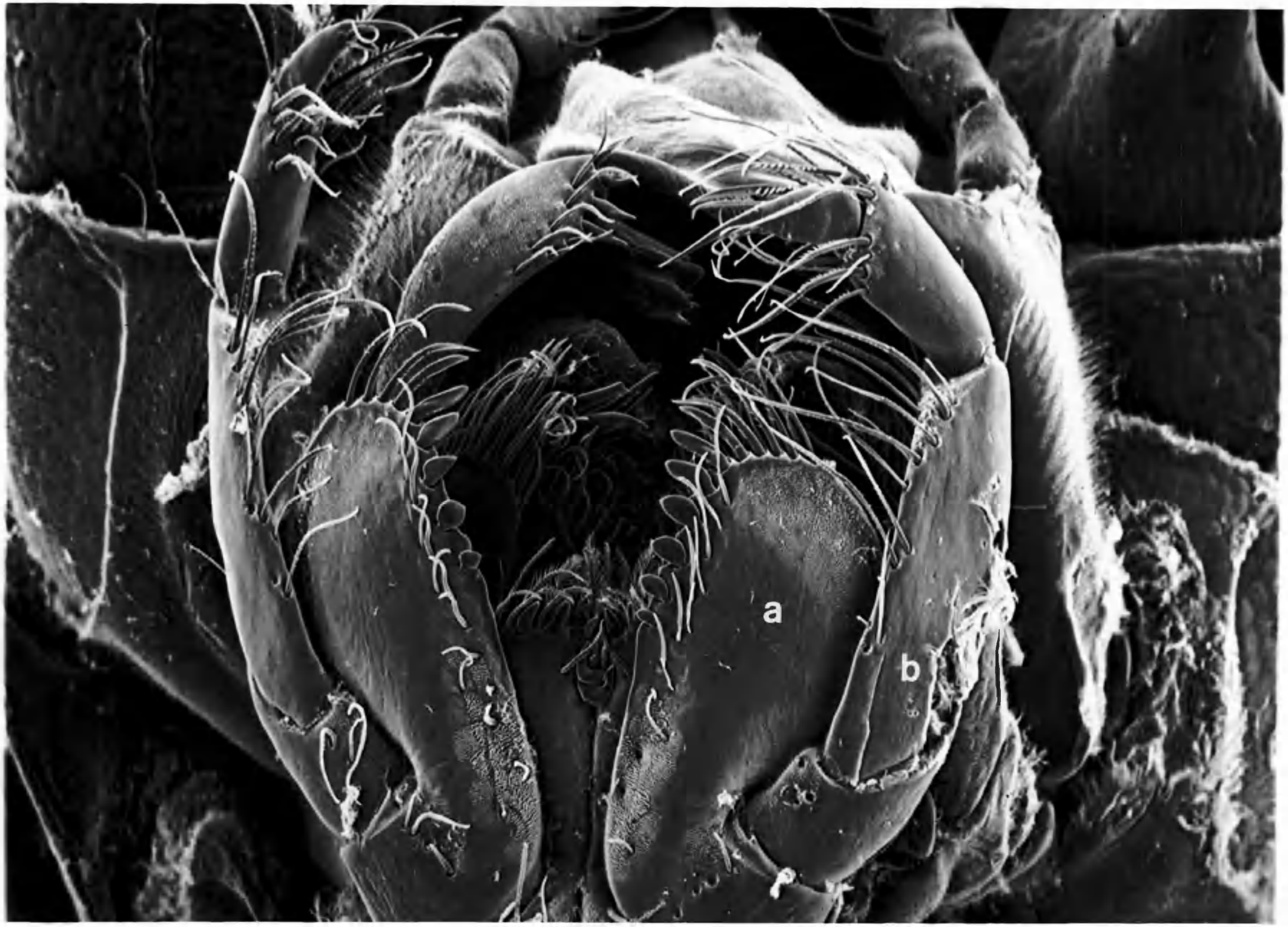

a
b

Figure 16.a. Maxilla 2 of <u>Unciola</u> <u>irrorata</u>. X 220.

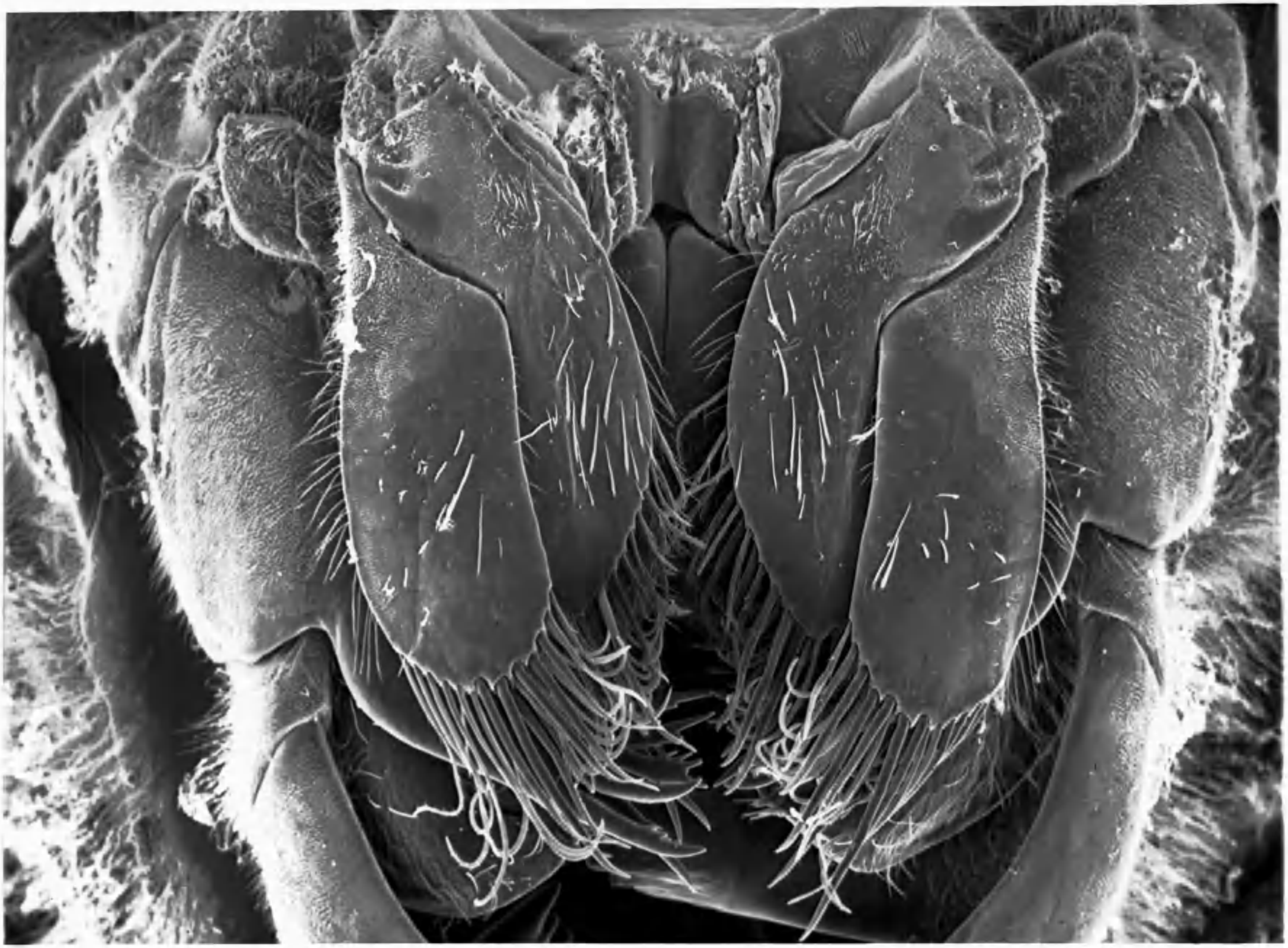


Figure 16.b. Maxilla 1 of *Unciola irrorata*. a-outer plate palp. X 200.

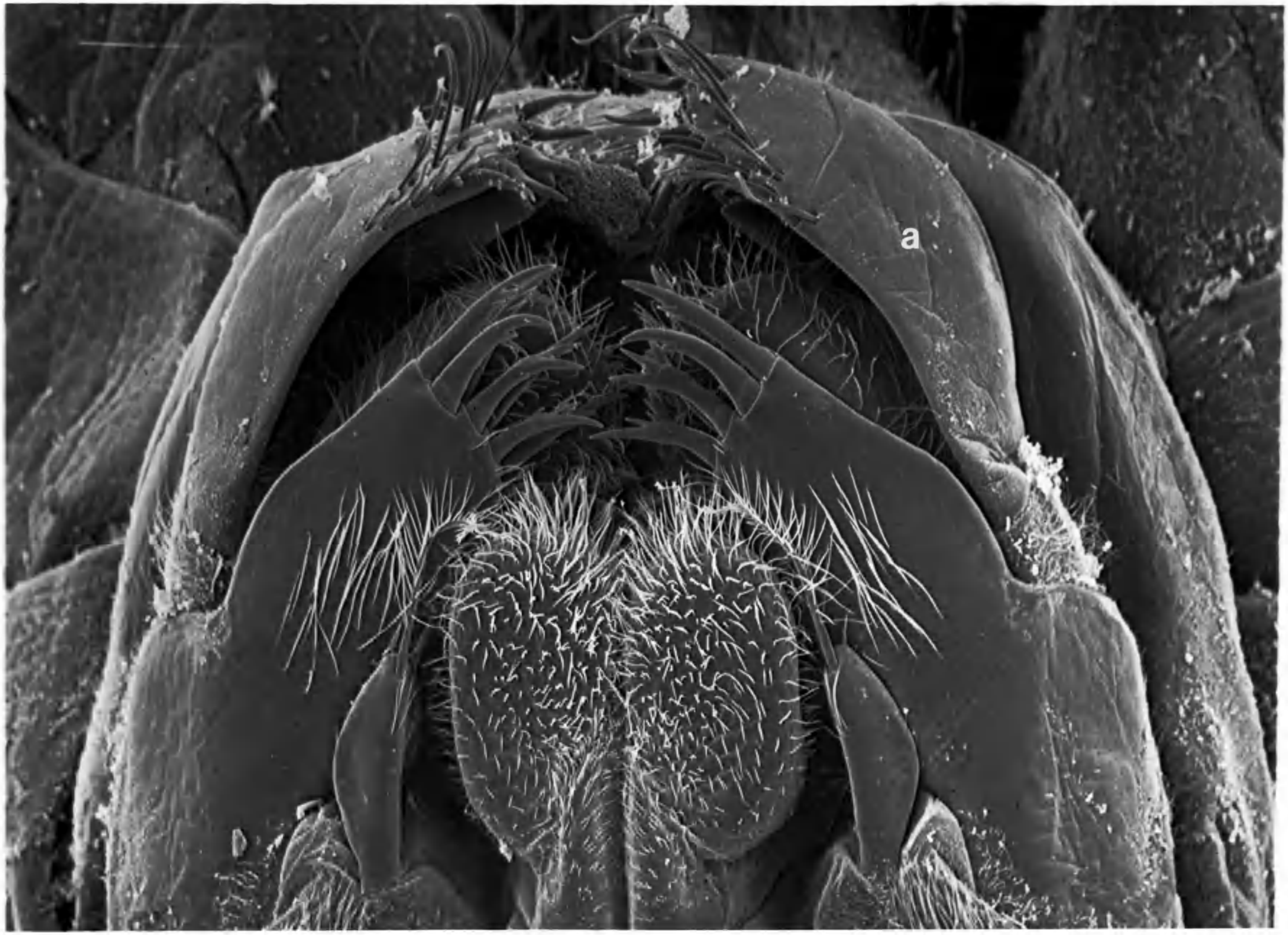

a

Figure 17. Mandible of *Unciola irrorata*. X 300.

Figure 18. Maxilliped of *Unciola inermis*. a-outer plate; b-outer plate palp. X 130.

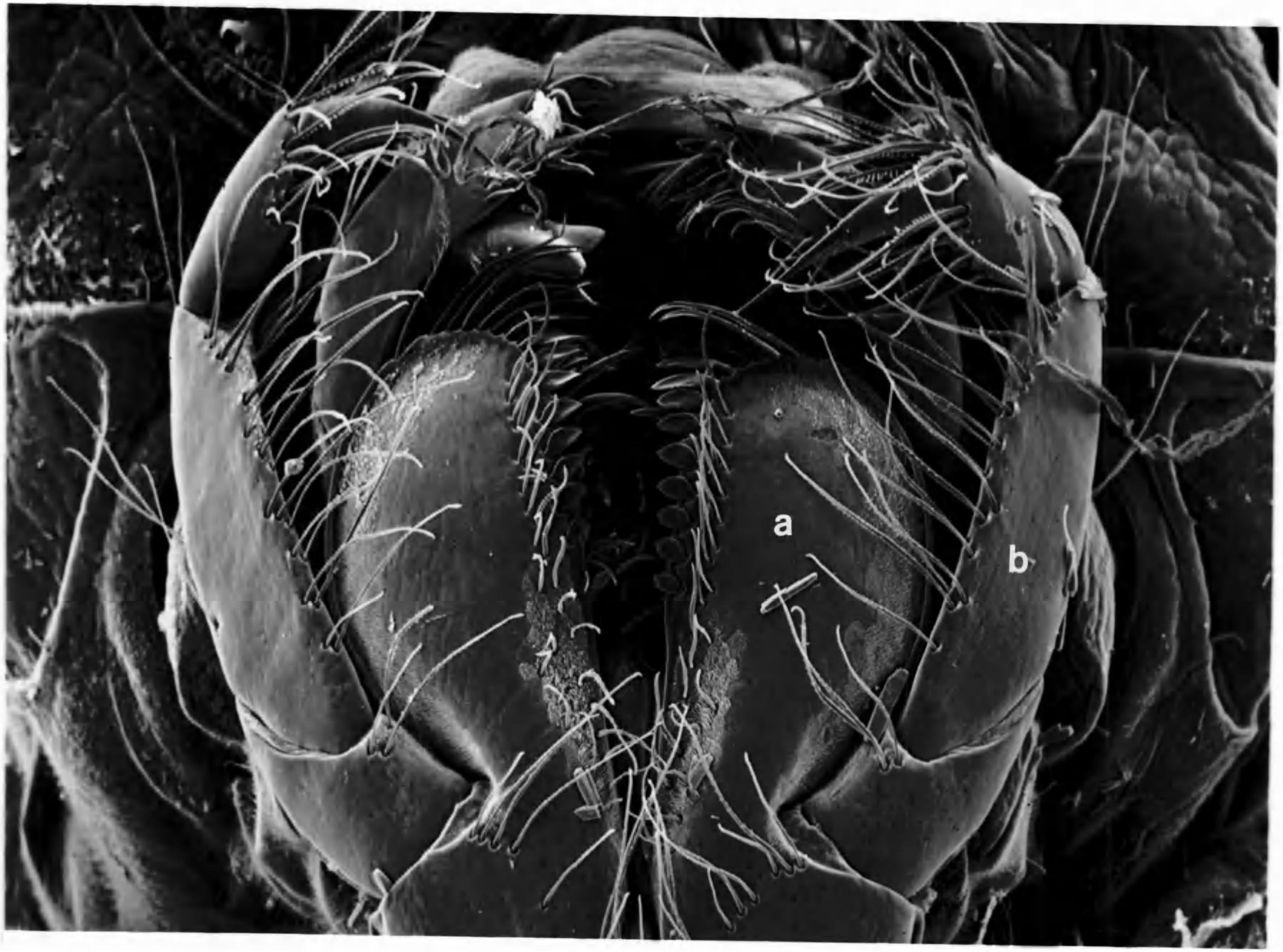

a
b

Figure 19.a. Maxilla 2 of *Unciola inermis*. X 380.

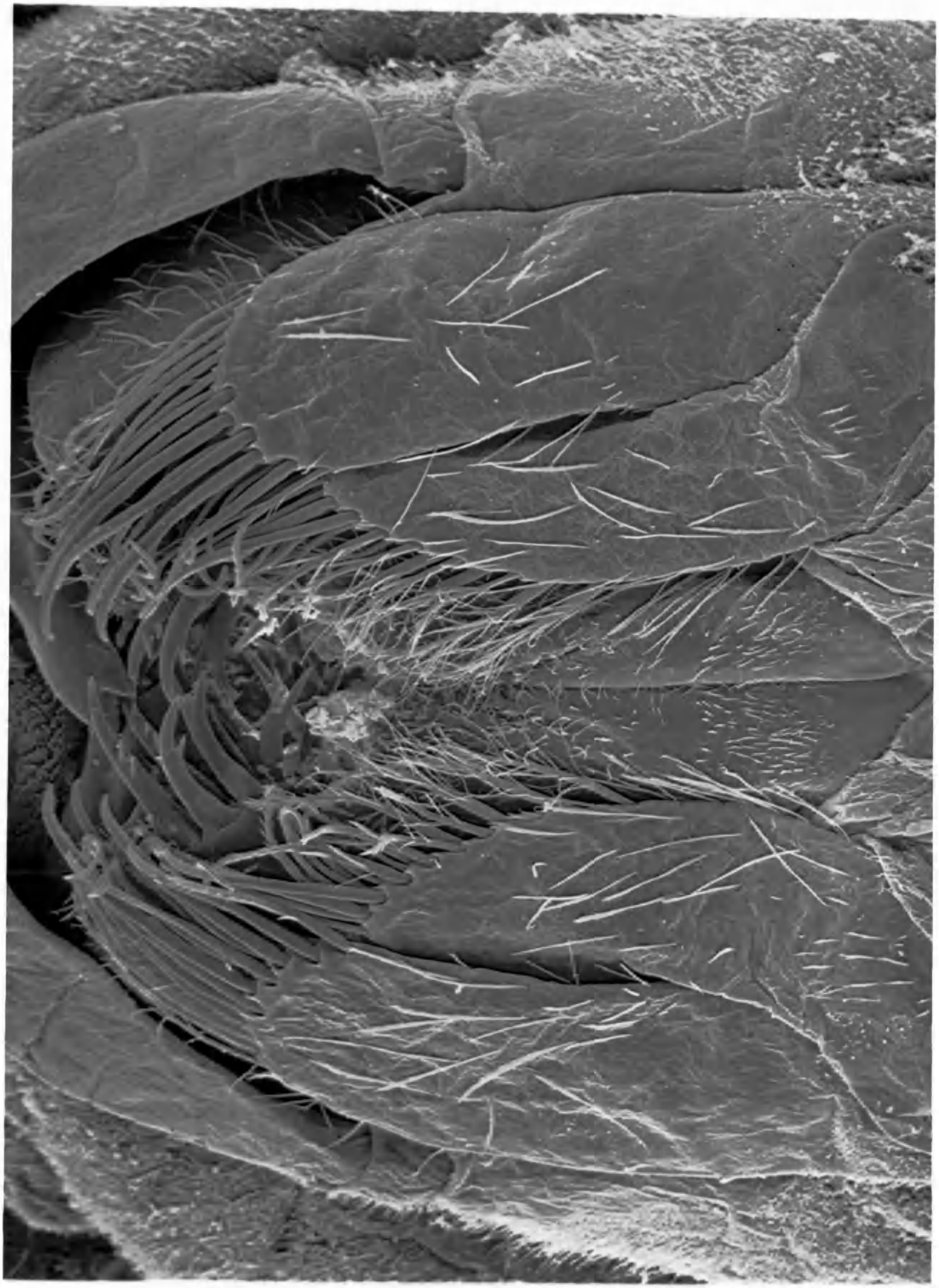


Figure 19.b. Maxilla 1 of _Unciola inermis_. a-outer plate palp. X 180.

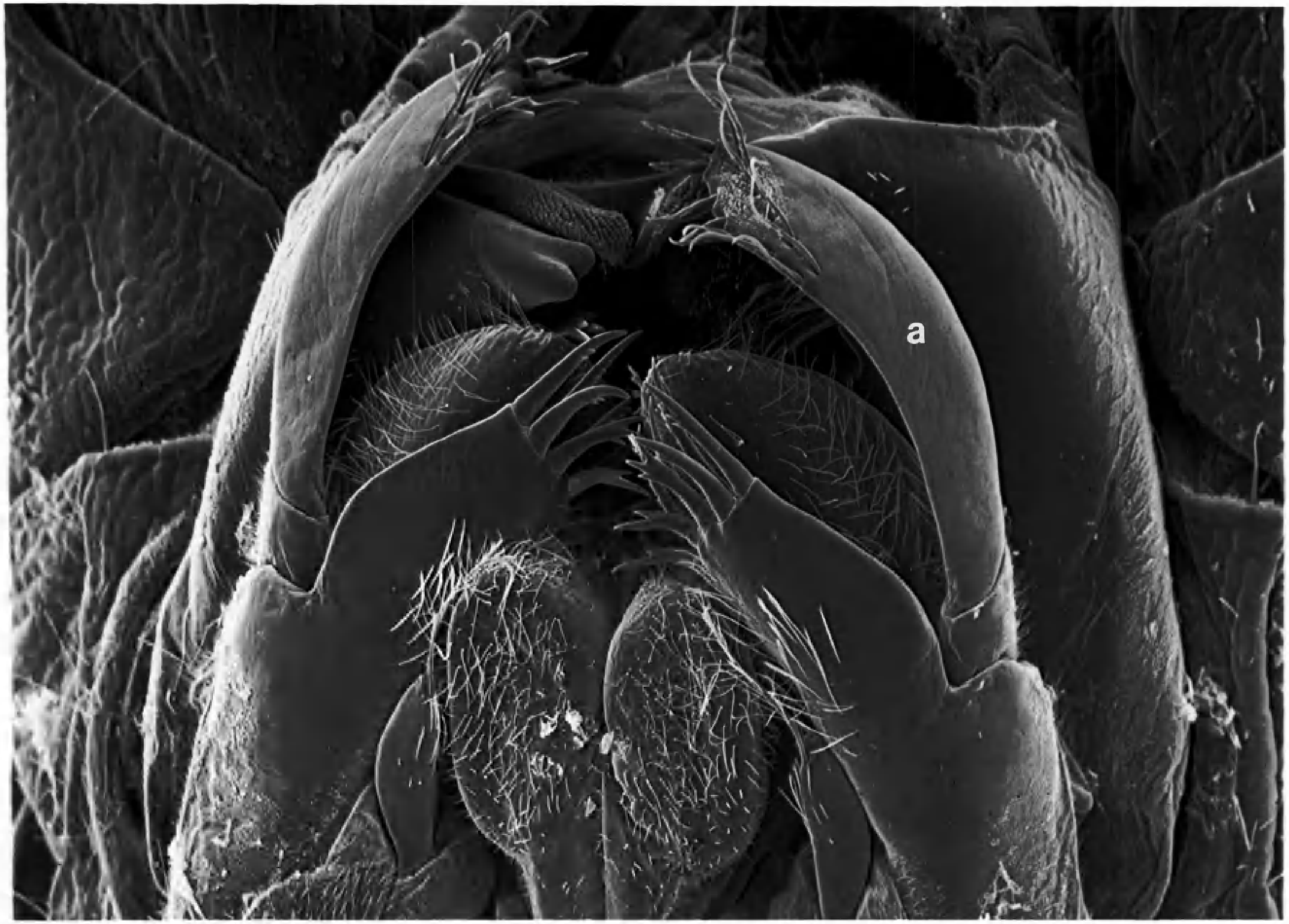

a

Figure 20. Mandible of *Unciola inermis.* X 240.

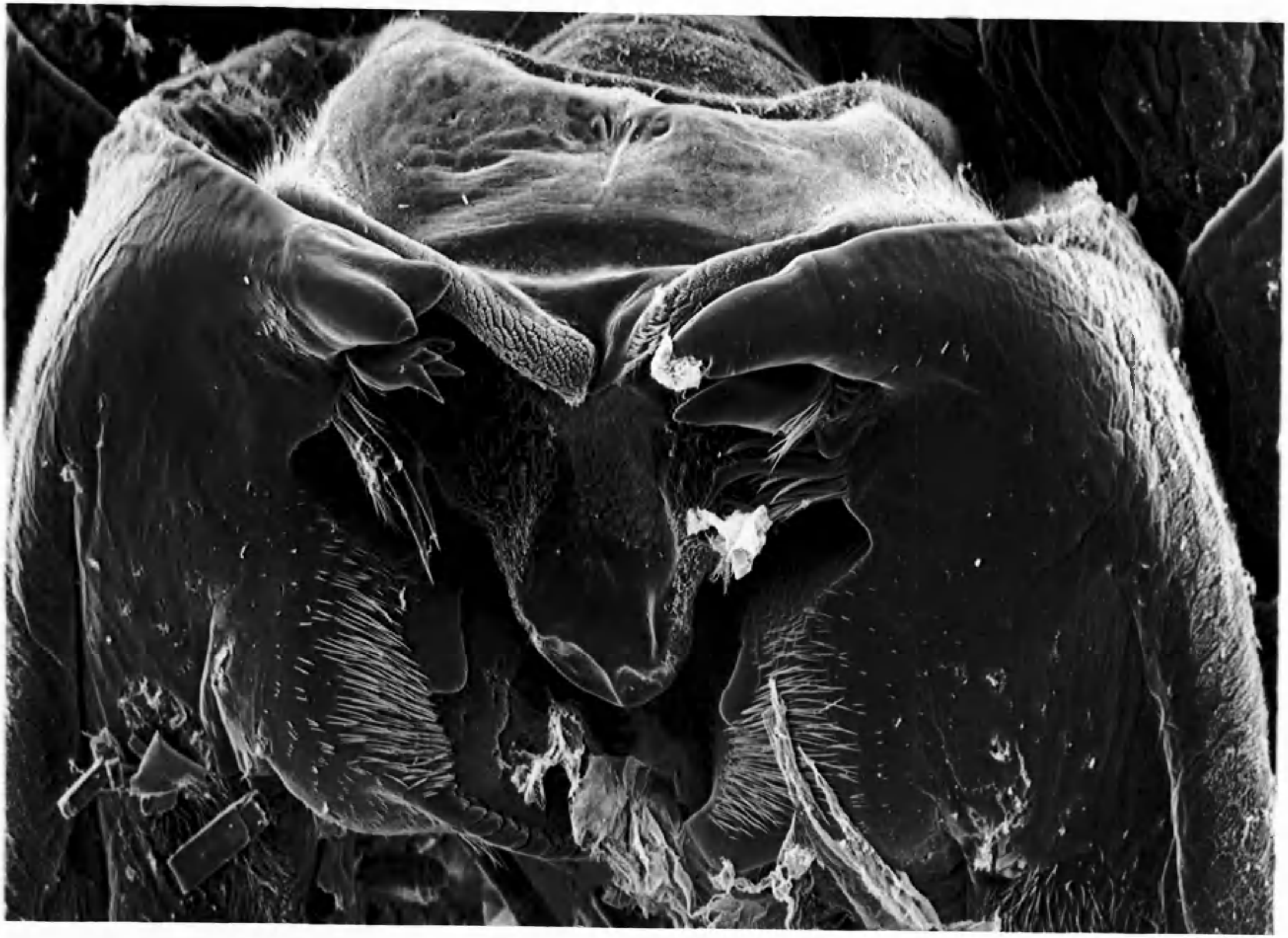


Figure 21. Maxilliped of _Erichthonius rubricornis_. a-outer plate; b-outer plate palp. X 260.

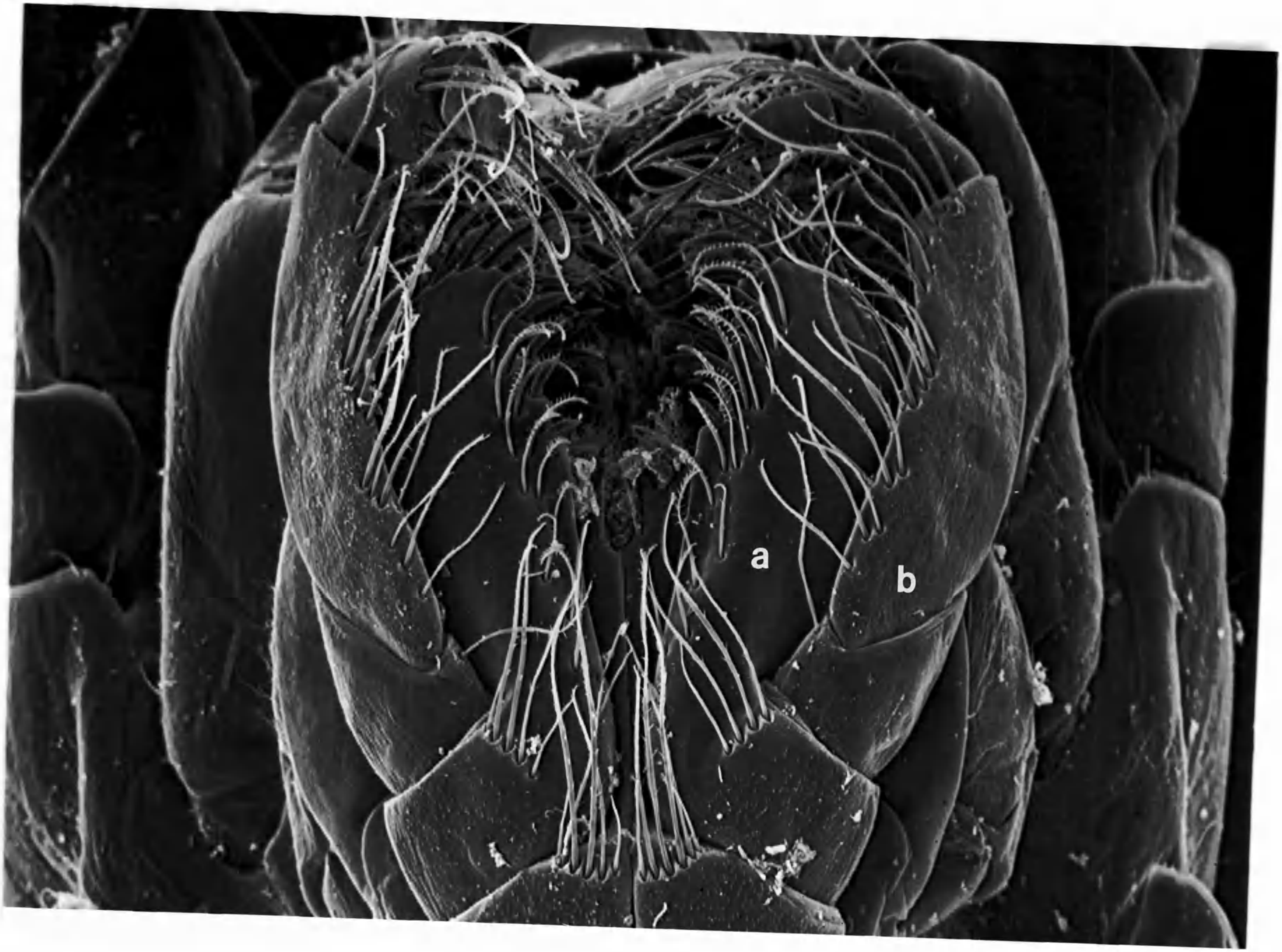

a
b

Figure 22.a. Maxilla 2 of <u>Erichthonius</u> <u>rubricornis</u>. X 330.

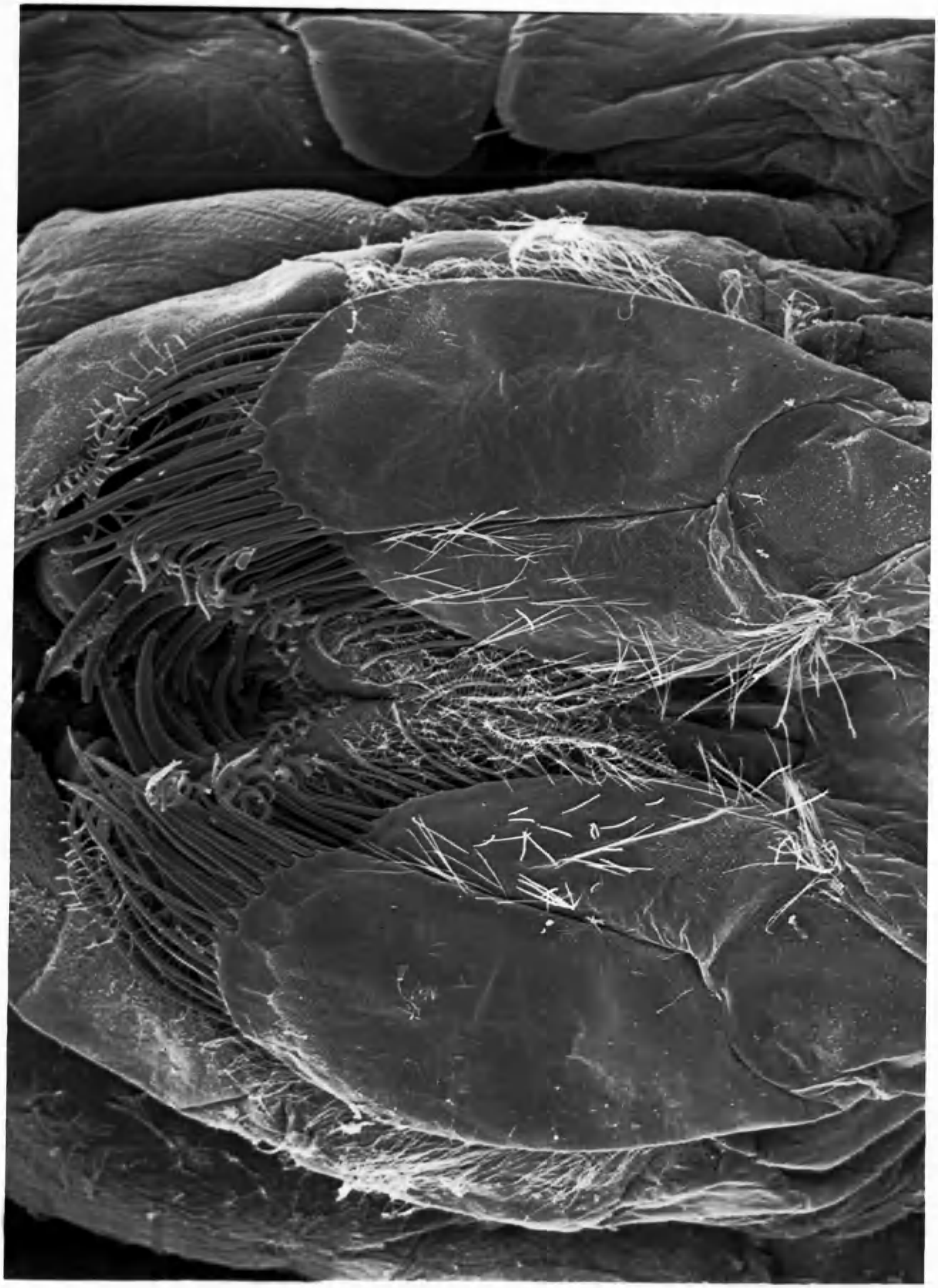


Figure 22.b. Maxilla 1 of Erichthonius rubricornis. a-outer plate palp.
X 240.

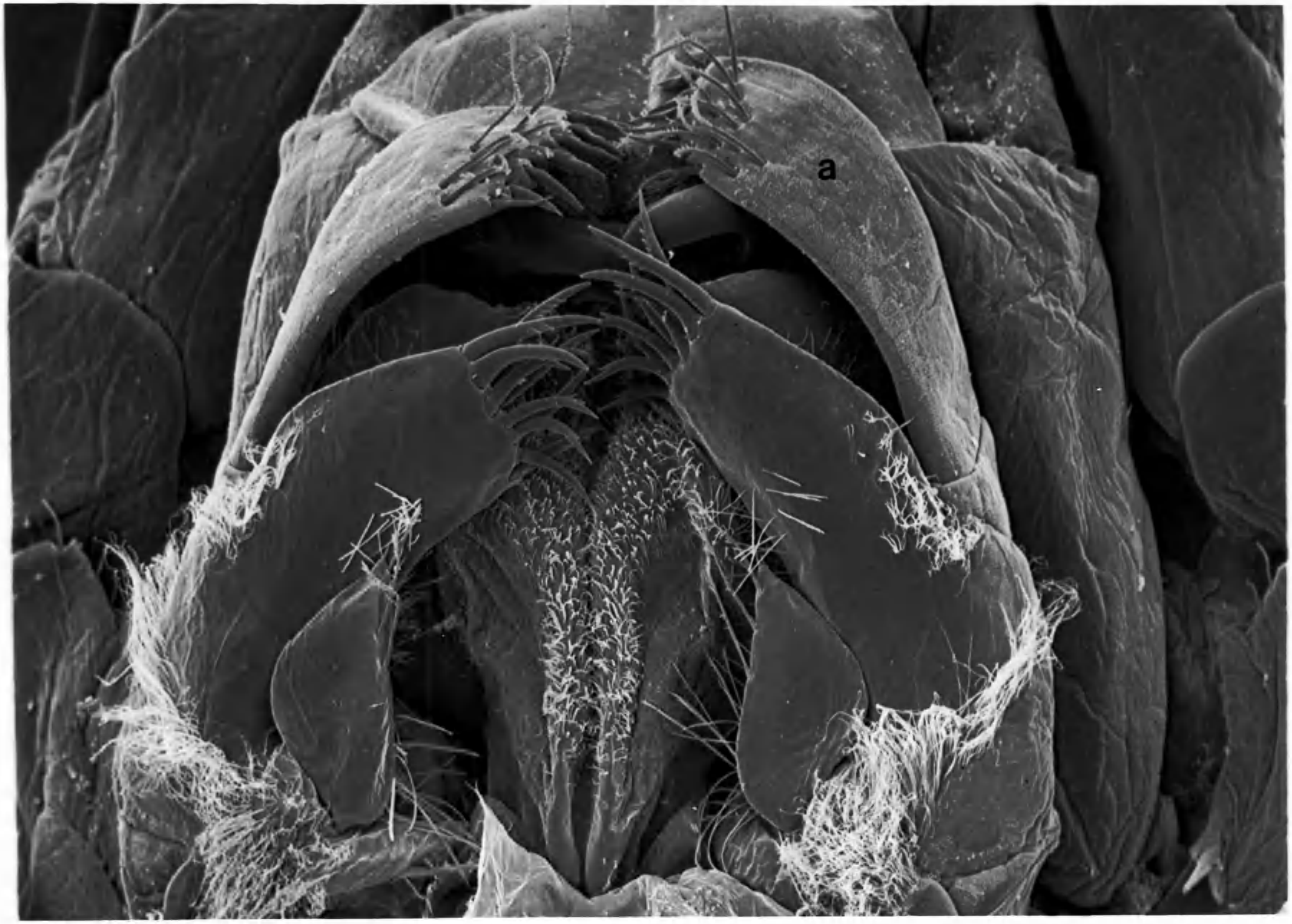

a

Figure 23. Mandible of *Erichthonius rubricornis*. X 800.

Figure 24. Maxilliped of *Ampelisca agassizi*. a-outer plate; b-outer plate palp. X 190.


a
b

Figure 25.a. Maxilla 2 of *Ampelisca agassizi*. X 270.

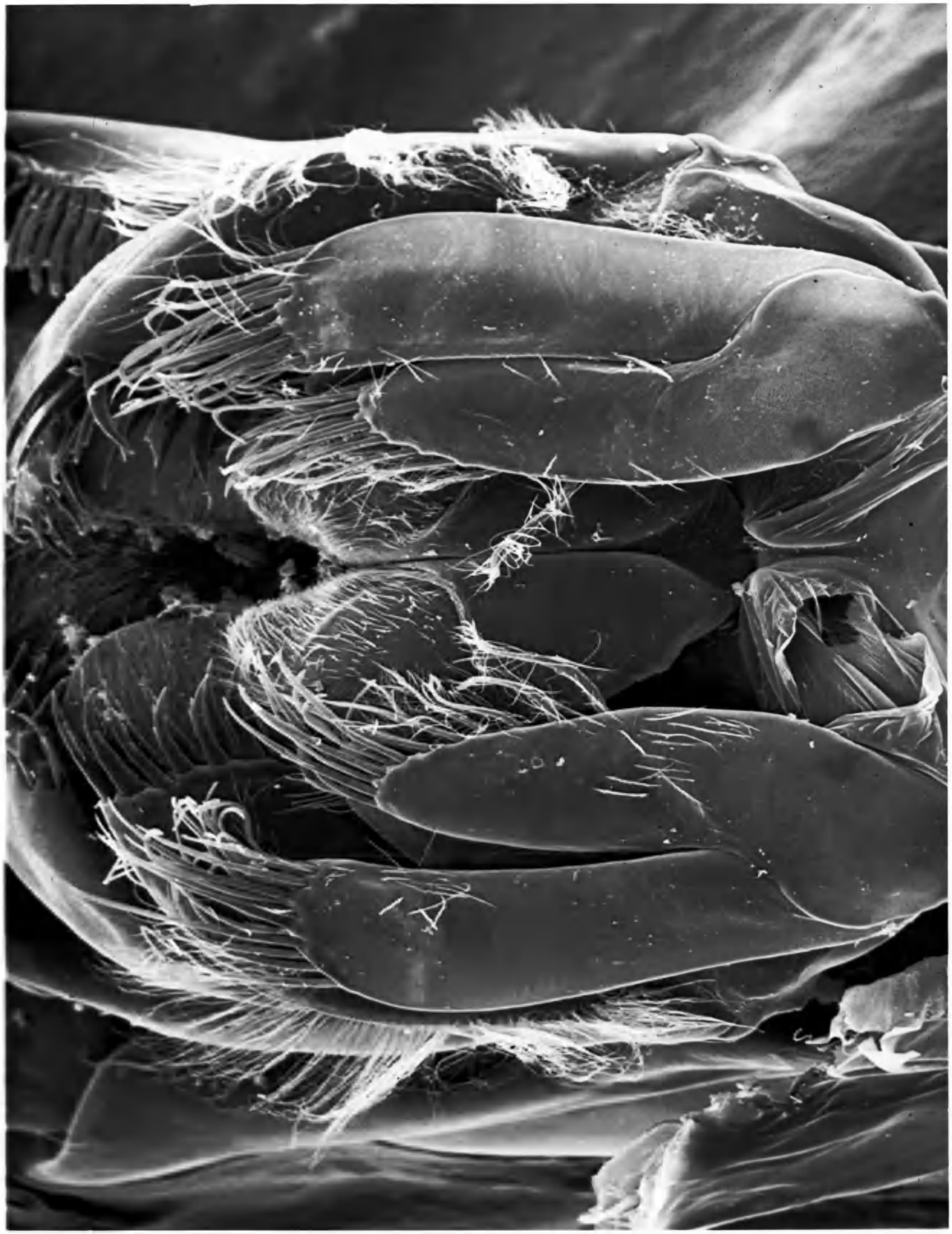


Figure 25.b. Maxilla 1 of _Ampelisca agassizi_. a-outer plate palp. X 190.

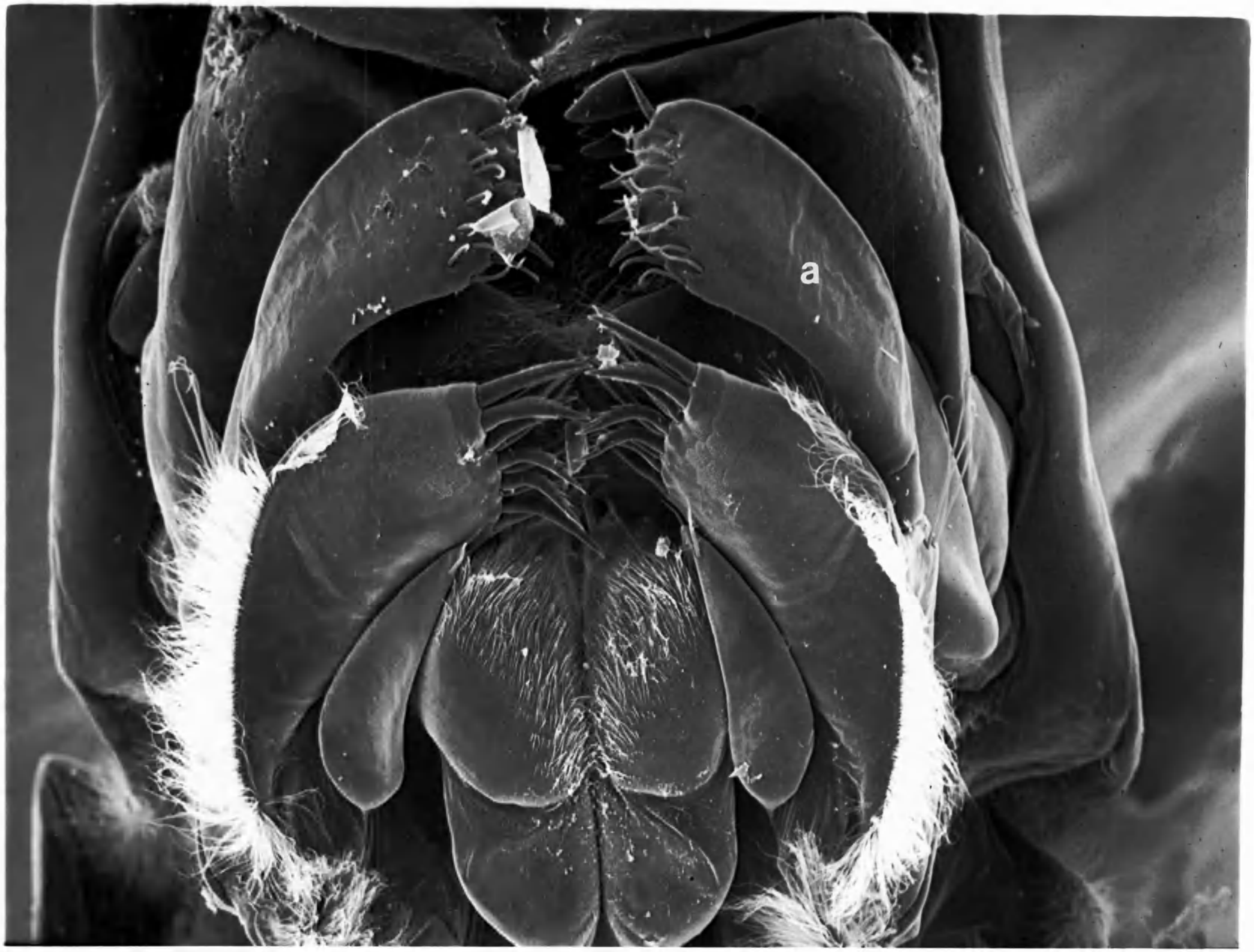

a

Figure 26. Mandible of *Ampelisca agassizi*. X 270.

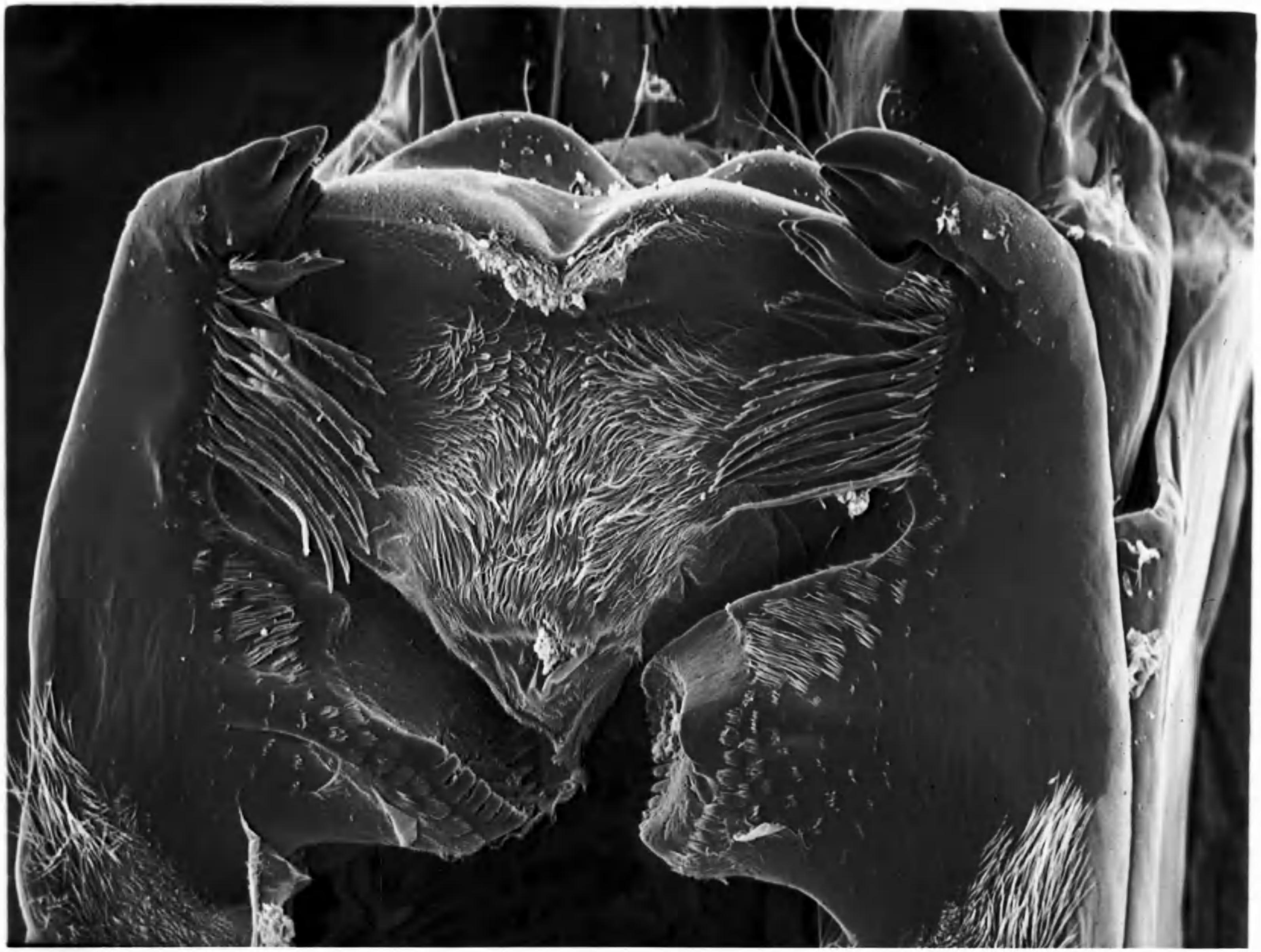


Figure 27. Maxilliped of *Ampelisca vadorum*. a-outer plate; b-outer plate palp. X 160.


b
a

Figure 28.a. Maxilla 2 of *Ampelisca vadorum*. X 320.

Figure 28.b. Maxilla 1 of *Ampelisca vadorum*. a-outer plate palp. X 180.

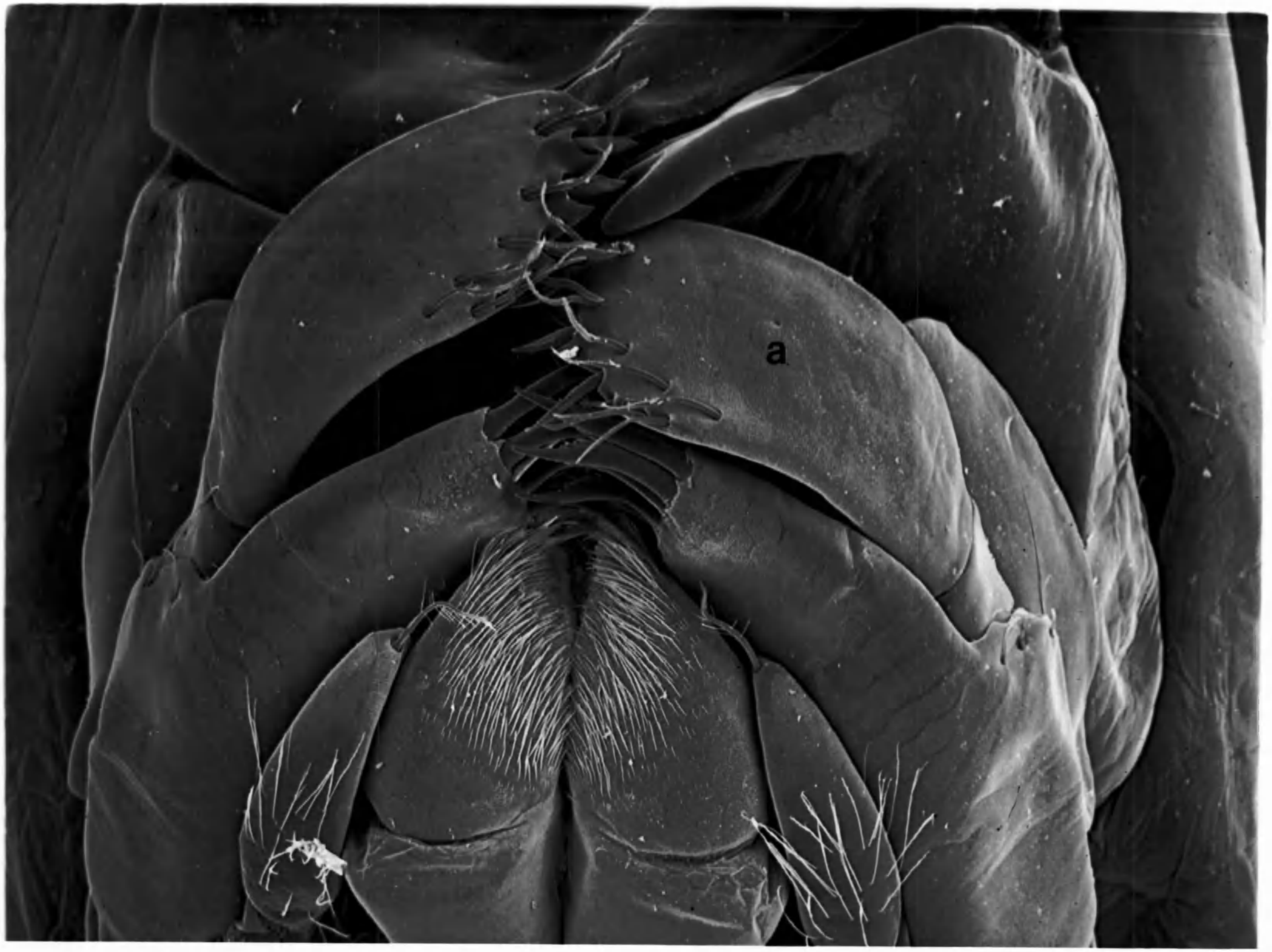

a

Figure 29. Mandible of *Ampelisca vadorum*. X 400.

Figure 30. Maxilliped of *Byblis serrata*. a-outer plate; b-outer plate palp. X 110.

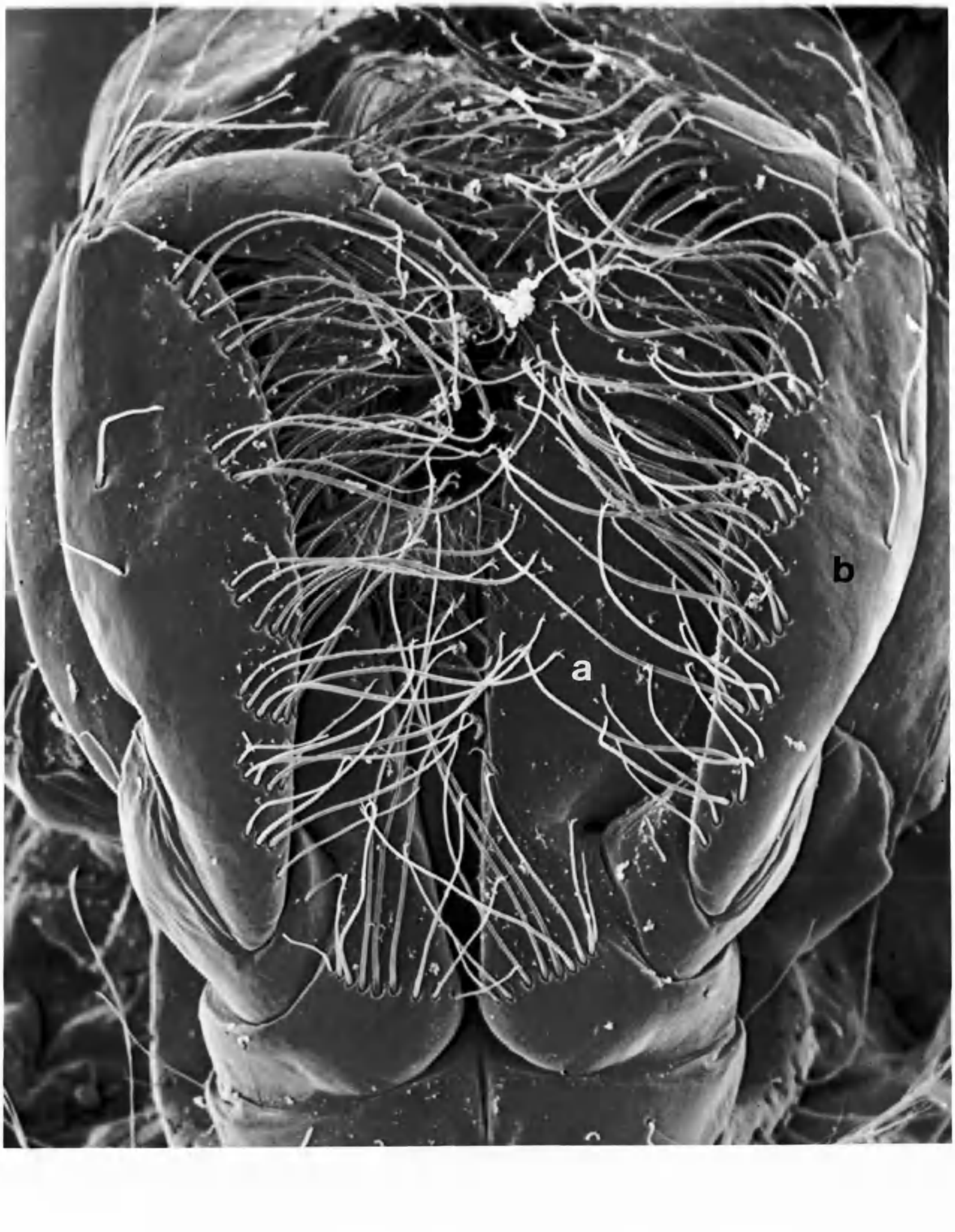

b
a

Figure 31.a. Maxilla 2 of Byblis serrata. X 210.

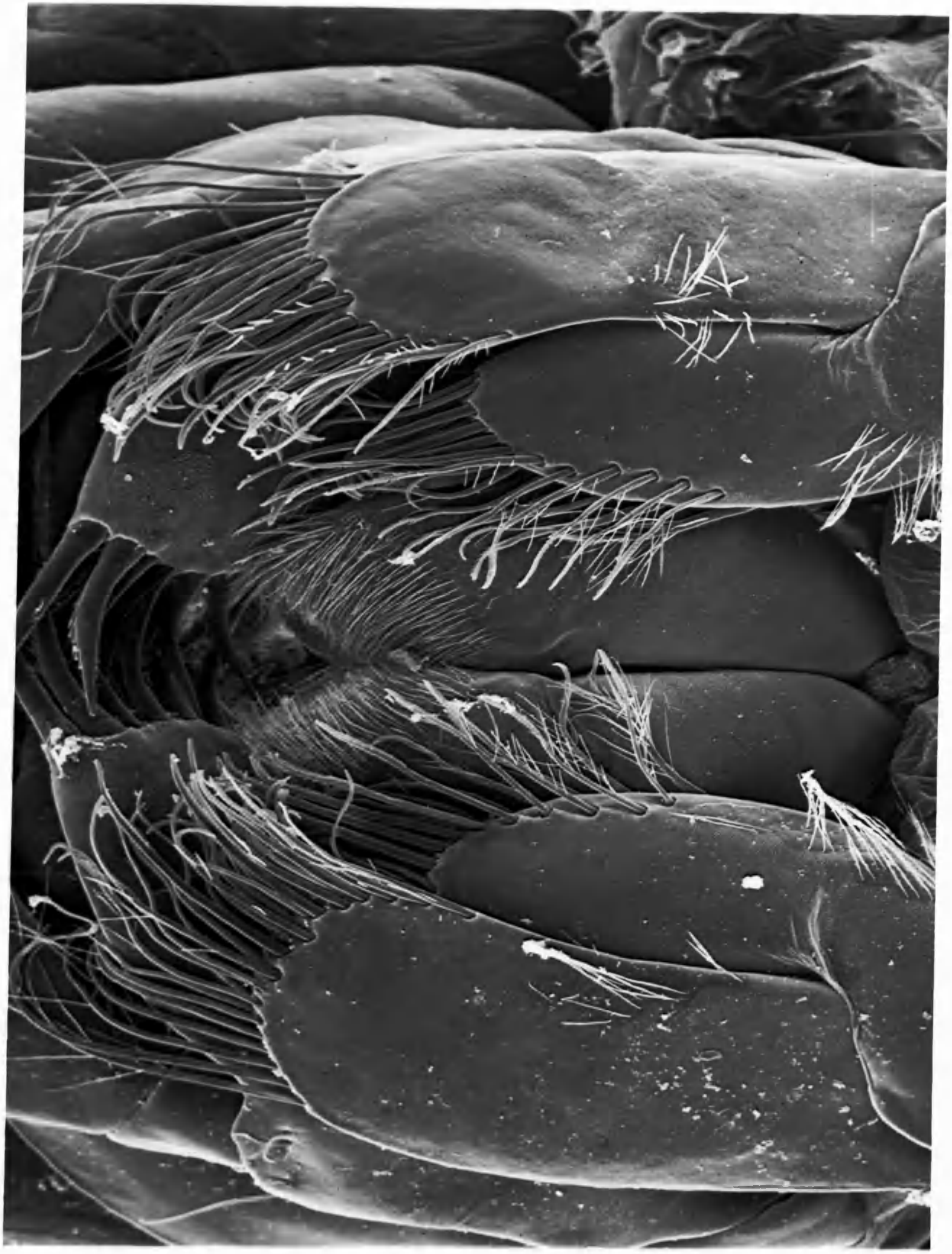


Figure 31.b. Maxilla 1 of *Byblis serrata*. a-outer plate palp. X 170.

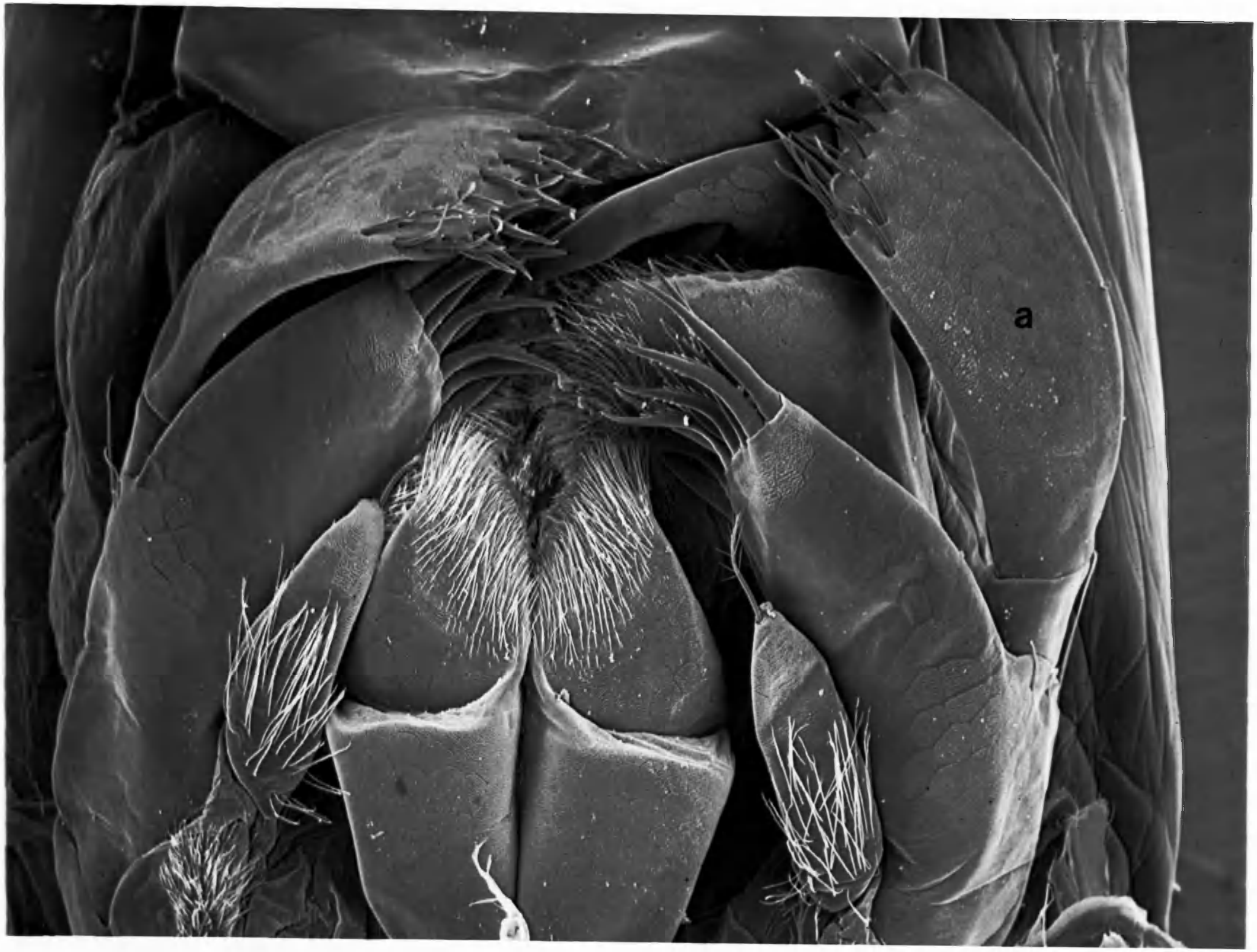

a

Figure 32. Mandible of *Byblis serrata*. X 440.

23) differs from these species by having six more slender accessory spines and a reduced molar cusp area. The right molar of *E. rubricornis* supports a small scrub-brush like appendage which projects into the cusp area.

The mandibular incisors of the ampeliscids (Figures 26, 29, 32) are similar to those of the corophiids. *B. serrata* (Figure 32) has four accessory spines while *A. vadorum* (Figure 29) has nine. In both species the molar is fairly strong and triturative. *A. agassizi* (Figure 26) has eight accessory spines. The molar, although triturative, is reduced in size relative to those of *A. vadorum* and *B. serrata*.

DISCUSSION

The Amphipoda considered in this study are conspicuous dominants in the outer shelf benthic community. They comprise six of the top ten numerically dominant species of peracaridan crustaceans in the areas of the outer shelf which we have studied extensively (Schaffner and Boesch unpublished, stations E1-4, B1-5 on Figure 1). The outer shelf represents an extensive and geologically persistent habitat and thus may be considered an important region for these species in both ecological and evolutionary terms. The results presented indicate that a complex set of physical and biological factors govern the distribution and abwndance of these species within the outer shelf zone.

Spatial patterns

Spatial patterns in abundance of the six species indicate that there was substantial habitat partitioning among the ampeliscid species. Both the grand mean data and the results of the discriminant analysis indicate little overlap between *Ampelisca agassizi* and the other ampeliscid species *Ampelisca vadorum* and *Byblis serrata*. The extremely high, persistent densities of *A. agassizi* in the deeper, finely grained sediment portions of the study area suggests that species' superior ability to utilize space in these quiescent environments. This contention is furter supported by records of *A. agassizi* at comparably high densities in similar habitats throughout the Middle Atlantic Bight (Boesch 1979a) and in shallower (35 m), but sedimentologically similar habitats in Block Island Sound off Rhode Island (S. Pratt personal communication).

The distributions of *Ampelisca vadorum* and *Byblis serrata* overlap in discriminant space suggesting less discrete habitat segregation. There was an apparent tendency for *B. serrata* to utilize the shallower, coarser grained habitats as well as intermediate habitat types. *A. vadorum* was found primarily on clean medium sands such as those found on ridge crests.

The preferences exhibited by *B. serrata* for shallow (≤ 64 m) fairly dynamic, medium sand habitats are supported by data from other areas in the Middle Atlantic Bight. Large populations of this species were found in clean, medium-fine sands at approximately 30 m depths off the south shore of Long Island near Fire Island (Boesch, et al., in press). *A. vadorum* was not found at these stations which were sampled over a five year period (1972-1977). Boesch (1979a) found *B. serrata* at three stations on the central shelf (D3, 36 m; D4, 49m; K2, 41 m) where sediments consisted of medium to medium-fine sands (median diameter ϕ = 1.5 - 2.3). Bousfield (1973) indicates that this species is common on medium to coarse sands from immediately subtidal to over 40 m. Pratt (personal communication) found this species distributed to depths of approximately 30 m in Block Island Sound. As previously noted, large populations of *A. agassizi* were found at 35 m depths in the same region.

The distribution patterns of *A. vadorum* as recorded in the literature are less well defined. In the Middle Atlantic Bight (Boesch 1979a) the species was found over a wide depth range. It was both persistent and abundant on deep, clean, medium and fine-skewed medium sand ridges and flanks (Stations E1 and E3, 64 m) near the shelf break where median sediment diameter ranged from 1.1 to 2.0 ϕ. This agrees with its distribution pattern in Area B where it was found on medium sand ridges at similar depths. *A. vadorum* was also abundant in medium-fine sands (median diameter ϕ = 2.25) at a central shelf swale (Station D4, 49 m). Although sediments in this swale contained up to 7.8% silt and clay (mean = 5.3%) *A. agassizi* was found only rarely. Biernbaum (1979) found *A. vadorum* on gravel, muddy sand and medium sand bottoms in Fisher's Island Sound (≃ 30 m) off Connecticut. Sanders (1956) and Mills (1967) found *A. vadorum* (= Species A, Sanders 1956) on gravelly sands at 10-12 m depths in Long Island Sound. These data suggest that *A. vadorum* has eurytopic sediment preferences. The absence of *A. vadorum* from the deep swales in this study may be related to the presence of the competitively superior species *A. agassizi*. This situation is paralleled in shallow water where *A. vadorum* is replaced in muddy sediments by its sibling species *A. abdita* (Mills, 1967).

As evidenced in the discriminant analysis and in grand mean abundance data populations of *A. vadorum* and *B. serrata* frequently co-occurred with all three species of corophiids. Conversely, the distribution of *A. agassizi* is overlapped widely only by the distribution of *U. irrorata*. This fact is poorly represented in the grand mean data largely as a result of the information compiled at station B5. This station is located in a dynamic transition zone between shallow swale and eroded flank habitats. The grand mean abundance data for this station is compiled from two faunally distinct habitat types (Boesch 1979a, 1979b). *U. inermis* was abundant at this station when sediments characteristic of eroded flanks were sampled (spring and summer) while *A. agassizi* was abundant when shallow swale conditions were sampled (fall and winter). The spatial overlap of *E. rubricornis* with *A. agassizi* may be greater than is evidenced in the discriminant analysis because both species exhibited high abundances at Station B5 in the winter (samples utilized in the discriminant analysis were from the fall). Nonetheless, the abundance of *E. rubricornis* was low in the deepest portions of the study area. *E. rubricornis* is an epifaunal suspension-feeding species which tends to construct small colonies of 5-10 tubes on the tubes of other species (personal observation) and probably also on shell and other hard substrates. The close spacing of ampeliscid tubes in the deep swales or lack of other suitable substrate may preclude the building of these epifaunal colonies. An alternative explanation is that the relatively quiescent environment of deep swales is not suitable for effective suspension feeding.

The distribution and abundance of *U. irrorata* seems little affected by the presence of *A. agassizi*. This species is reported in the literature as domicolous, but has lost the spinning glands present in other members of the Corophiidae (Bousfield 1973). It is known to occupy the vacated tubes of other organisms such as the polychaete *Prionospio* (Feeley and Wass 1971). The observed densities of this species in habitats supporting few tube dwellers, such as the terrace stations in Area B, suggest that the species may be a faculative tube dweller. I have observed individuals of *U. irrorata* in laboratory aquaria maintaining unlined burrows in the sediment. The organisms were also frequently observed (on the sediment surface exhibiting a high degree of mobility. The relative mobility of *U. irrorata* as well as flexible domicolous behavior presumably account for the ability of this species to coexist in deep swales with *A. agassizi*.

Spatial overlap among the corophiids is extensive. Noticeably, the particular conditions favoring dense populations of *U. inermis* are largely indistinguishable from those areas favorable for *E. rubricornis* and *U. irrorata*.

The evidence available here suggests that *U. inermis* is found primarily on poorly sorted sediments which often contain large quantities of shell hash. This is consistent with the presence of the species in the Hudson Shelf Valley (Station G3, Boesch 1979a) on shelly medium-fine sands (median diameter $\phi = 1.77$). The topography of these environments suggests that they may be hydrodynamically erosional although this is not always supported by the measured granulometric conditions. It was particularly striking to note that nearly all of the stations at which the species occurred in the study area were located in a band along the western and southern flanks of the shallow swale. Whether the species responds to increased coarse sediment components, shell hash, or some aspect of the hydrodynamic conditions is unknown. The species is poorly described and close taxonomic similarities with its congener *U. irrorata* have led to confusion in identification, particularly amongst juveniles (M. Bowen personal communication, L. Watling personal communication). Consequently there is a paucity of ecological information about the preferred habitat of *U. inermis*.

Temporal Changes in Population Abundance and Body Size

Seasonal changes in population abundances have been shown to reduce the potential for competition among species which have similar space and food requirements (Schoener 1974). Whittaker (1970) showed that partitioning of time resources to coincide with varying moisture conditions facilitates the coexistence of a wide vareity of desert plants. Broadhead and Wapshere (1966) found that seasonal changes in abundance and consequent demand for a potentially limiting food resource contributed to the ability of psocid insects to coexist on larch trees. In the benthic marine environment Croker (1967) found that some species of haustoriid amphipods with similar trophic and spatial resource requirements reached peak abundances at different times of the year.

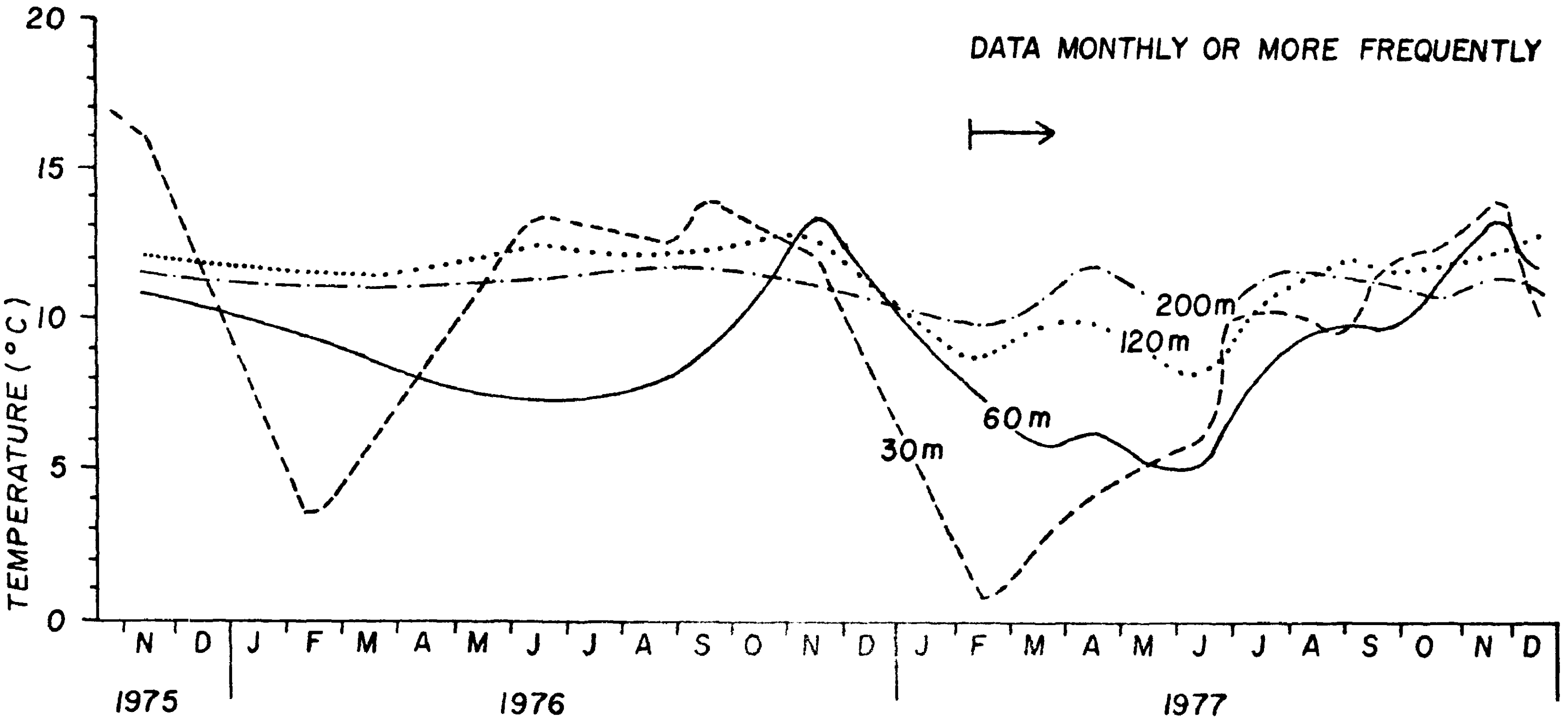
Temporal changes in abundance do not appear to play an important role in reducing potential resource competition among the species considered in this study. The spatially co-occurring populations of

A. vadorum and B. serrata responded less to temporal factors than they did to small scale spatial variability (Figures 9-13). Although the corophiids exhibited significant seasonal variations in abundance, temporal overlap remained relatively high (Figures 9-13).

The lack of strong seasonal trends in population abundances is not surprising. Boesch (1979a) noted the relative persistence of the total outer shelf community of the Middle Atlantic Bight in comparison with the strong seasonal abundance patterns exhibited by species in nearshore environments. This relative seasonal persistence may be the result of a more constant thermal regime. The net flow of water on the Middle Atlantic continental shelf is south-westward. Cold bottom water, which may originate on the Southern New England Shelf or in the Gulf of Maine (Bearsdley, Boicourt and Hansen 1976; Csanady 1976 and Bumpus 1973), flows from the northwest as a discrete "cold pool". This cold water remains on the outer shelf during the summer, maintaining strong thermal stratification, and thereby buffering the benthos from seasonal warming of surface waters. Thus, while seasonally variable bottom temperatures (3-20°C) are found on the inner shelf, bottom temperatures are relatively constant and colder (4-11°C) on the central and outer shelf (Figure 33) (Colton and Stoddard 1972, Walford and Wicklund 1968).

Size differences may facilitate the coexistence of species. Hutchinson (1959) and Schoener (1965) have indicated that closely related sympatric species often exhibit ratios of body size or size of some important feeding appendage that approximate 1.3. Recent work by

Figure 33. Variation in bottom temperatures over a two and a half year period at four depths on the continental shelf and upper slope off New Jersey (from Boesch in press)


DATA MONTHLY OR MORE FREQUENTLY
TEMPERATURE (°C)
20
15
10
5
0
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
1975
1976
1977
200m
120m
60m
30m

Fenchel (1975) and Fenchel and Kofoed (1976) has illustrated the importance of character differences and resultant changes in trophic resource use for sympatric species of hydrobiid mudsnails. Frier (1979a) has shown that two species of isopods, *Sphaeroma hookeri* and *S. rigicauda*, maintain size ratios of 1.3 to 1.7 when sympatric. These ratios fall in the range 1.0 to 1.1 for allopatric populations. The greater ratios in sympatric populations result partly from a divergence of life cycles and partly from a divergent displacement in the size of molt stages. This character displacement reportedly lessens interspecific competition for shelter space in the intertidal zone and possibly also reduces the likelihood of hybridization (Frier 1979b). Kolding and Fenchel (1979, Fenchel and Kolding 1979) have also postulated that displaced reproductive cycles which result in size differences among co-occurring *Gammarus* spp. amphipods reduce "mating competition" and may relieve spatial competition through microhabitat selection.

In this study body size ratios ranged from 1.0 to 1.5. The most closely related species which were frequently found in coexistence had the highest ratios (i.e. *A. vadorum*: *B. serrata* ratio = 1.5, *U. inermis*: *U. irrorata* ratio = 1.4). Interestingly, these differences appear to be maintained by offset modal size peaks suggesting different periods of peak reproduction (Appendix D). Data are not available for these species in allopatric habitats. Monthly sampling of both sympatric and allopatric populations, not possible in this study, would be necessary to consider this to be strong evidence of such adaptive size displacement.

Feeding Behavior and Functional Morphology

Observed differences in mouthpart morphology of the species in this study (Figures 15-32) and literature documented differences in feeding behavior for some species considered here, or closely related species suggests that differential usage of particulate detritus may occur. The feeding behavior of ampeliscids has been carefully studied by Enequist (1949) and Mills (1967). Mills identified three specific types of feeding behavior. Type 1 behavior identified a filtering mode probably not employed by any of the species considered in this study.

A. vadorum was identified as a species employing Type 2 feeding behavior. This behavior involves two modes of obtaining food particles. In the first, least important mode, sand grains are collected from the sediment surface using the second antennae. These are tossed to the midline, held in place by gnathopods while they are scraped by the mouthparts. These grains are then discarded by the gnathopods. A second, more commonly employed, feeding method involves the setting up of a feeding current by beating the pleopods and synchronously whirling the second antennae. Sand grains and detritus accumulate on the setae of pereopods 1 and 2, are scraped together by the gnathopods (where large particles are rejected) and carried towards the mouthparts. Here the long spines on the outer plate of the maxilliped are probably bent forward and used to direct particles inward where they are ground on the sclerotized molars.

Mills identified certain morphological and ecological characteristics of species exhibiting this "whirling" feeding behavior. These include subequal antennae (Antenna 1 shorter than Antenna 2) which are not especially setose, occurrence on fine to coarse sand, and in some species, such as *A. vadorum*, a well developed urosomal keel which may aid burrowing in coarse sediments.

Although the feeding behavior of *B. serrata* has not been observed the antennal morphology and sediment preferences of this species suggests that it would feed in a manner similar to *A. vadorum* (Type 2). Enequist (1949) observed the closely related species *B. gamaridi* finding that it fed in this manner.

A. agassizi conforms morphologically to the third feeding type outlined by Mills. This species has very short first antennae and extremely long second antennae. Both Mills and Enequist observed species of this type scraping fine material from the sediment surface in a circular fashion with the second antennae. The material (fine sand and detritus) was then moved to the ventral midline. Mills states that ampeliscids feeding this way are common on fine sands and mud. The reduced molar cusp area, hairlike setae on the first maxillae and long plumose setae on the maxilliped all suggest that *A. agassizi* relies on fine detrital material as a major food source. Topographic depressions on the Middle Atlantic continental shelf provide abundant fine particulate material at the sediment-water interface. The larger molar cusp and plumose setae on the maxilliped of _A. vadorum_ probably allow this species a greater flexibility in particle resource use. The habitat preferences and mouthpart morphology of _B. serrata_ suggest that this species should feed primarily on somewhat coarser detrital material. This is difficult to ascertain due to the lack of gut content analyses.

My observations of the feeding behavior of _E. rubricornis_ in laboratory aquaria indicate that its behavior is very similar to that described by Enequist (1949) for _E. rubricornis_ (= _E. hunteri_) and _E. brasiliensis_ by Zavattari (1920). These animals remain in the upper opening of the tube with the antennae, head, and first few thoracic appendages exposed. The antennae are held vertically outstretched in the water column. In the presence of suspended particulates the antennae and any adhering detritus are independently bent towards and combed by the gnathopods. From the gnathopods the detrital material is transferred to the mouthparts. Enequist indicates that pleopodal currents are probably not important in detritus capture or transfer. _Erichthonius_ spp. will leave its tube to collect sediment particles and detritus when water conditions are stagnant, but this is probably not an important feeding mechanism. The small molar and fine hairlike setae on the first maxillae of this species suggests that its primary food source is fine, detrital material which is easily suspended. The lack of long or plumose setae on the palp of the maxilleped probably reflects the decreased importance of this appendage in the actual collection of detrital material as might be expected in the ampeliscids. The long spines along the inner margin of the maxilliped outer plate are similar to those observed in <u>Ampelisca</u> spp. suggesting similar function.

No observations of <u>Unciola</u> spp. feeding behavior are recorded in the literature. The lack of long or plumose setae on the maxilliped the robust incisors and large, strong mandibular molars all suggest that these species feed on larger food particles. The teeth-like spines on the maxilleped differ in shape from those in the ampeliscids and <u>Erichthonius</u>. The stoutness of these spines suggests their possible use as scraping spines for removing encrusted material from sand grains.

Although some overlap certainly exists with respect to the choice of food particle size by each species some general trends, which relate well to observed habitat requirements, are apparent. Those species commonly found on fine substrates or in areas where there is a sizeable fine component in the substrate (<u>A</u>. <u>agassizi</u> and <u>E</u>. <u>rubricornis</u>) employ feeding methods and exhibit mouthpart morphology which more effectively utilize this type of resource. Species found most commonly in a wide range of habitat types or where sediments contain significant coarse components (<u>Unciola</u> spp.) have robust mandibles and little setation. It is interesting to note that the only quarterly sampled station which consistently supported abundant populations of all six species was B5 where sediments were characteristically mixed thus, potentially supplying the necessary trophic resources for each species.

The Relative Importance of Resource Axes

As was previously stated in this discussion habitat partitioning is of major importance within the ampeliscid family. Evidence from stations on the central shelf sampled by Boesch (1979a) suggests that this partitioning is the result of the superior ability of *A. agassizi* to monopolize fine sediments on the outer shelf rather than the inability of *A. vadorum* and *B. serrata* to utilize fine sediments. Populations of both *A. vadorum* and *B. serrata* equal to or greater than those maintained within the study area, were found at central shelf swales (D4-Fall 1975 to Spring 1976 and D1-Winter 1976). The granulometric conditions in these swales were similar to or in some cases finer than those in outer shelf swales, yet *A. agassizi* was not present.

Except where dense populations of amphipod are found in topographic depressions the populations of amphipods in the study area do not appear to be limited by spatial resources. Average total densities for these six species in the ridge, flank, and terrace habitats ranged from 20 to 134 individuals/m^2 (Figure 4). These densities yield average potentially exploitable surface areas ranging between 75 and 500 cm^2/individual.

Both *A. vadorum* and *B. serrata* occasionally exhibit greatly increased populations densities on the shelf which cannot be explained by changes in sedimentary conditions. These increased densities have generally occurred in central shelf regions (Boesch 1979a). Boesch et al. (in press) documented a series of population increases and decreases for *B. serrata* and other benthic species off southern Long Island. These temporal variations were apparently related to episodic enrichment of the overlying water column as a result of heavy phytoplankton blooms chiefly composed of the dinoflagellate *Ceratium tripos*. If populations of *A. vadorum* and *B. serrata* are food limited body size differences may allow them to differentially utilize this resource and thereby facilitate coexistence.

The relatively even distributions of *U. irrorata* throughout the study area, and over much of the outer shelf, suggest that this species is a generalist not limited by spatial or trophic resources. The distribution and abundance patterns of *E. rubricornis* suggest that it is excluded from habitats that are either too dynamic (the terrace) or too quiescent and lacking in suitable substrate (deep swales). As was previously suggested competition for space with *A. agassizi* may also exclude *E. rubricornis* from deep swales. The rather specialized spatial requirements of *U. inermis* suggest that this species may utilize a particular microhabitat or feed in a manner which subtly differs from its congener. The close similarity in functional morphology of the *Unciola* spp. suggests that the microhabitat distribution of *U. inermis* is the more important factor facilitating coexistence between these species.

The Role of Predation

Predation by demersal fishes and epibenthic invertebrate predators has been increasingly recognized as an important structuring mechanism in benthic communities, particularly in shallow subtidal areas (Connell 1975, Virnstein 1977, Petersen 1979). Epibenthic predators play an important role in limiting the abundances of some of the species considered in this study. On the outer shelf the pericaridans, particularly *U. irrorata* and *E. rubricornis*, were of major importance in the diets of bottom feeding fishes (Table 6) (Sedberry 1979, Boesch 1979a). The ampeliscids *A. vadorum* and *B. serrata* were generally of secondary importance to most fishes. *A. agassizi* was of importance in the diet of only one fish species, the scup (*Stenotomus chrysops*) while the corophiid *U. inermis* was not reported as a food item in the diet of any of the fishes examined.

Although evidence exists which indicates that partitioning of both spatial and trophic resources is occurring among these species the potential role of predation in facilitating coexistence seems high. Resource partitioning may be important to these species on a time scale which differs from the one examined here. Zimmerman et al. (1979) noted that an amphipod guild within a seagrass bed of the Indian River, Florida appeared to be partitioning trophic resources although their abundances were known to be strongly limited by predation. He postulated that this partitioning may have been a relic of competitive interactions in ancient or fluctuating environments

Table 6. Importance of species of peracaridan crustaceans as prey for bottom feeding fishes on the outer continental shelf as indicated by their index of relative importance (from Boesch 1979a, Sedberry and Musick 1979).

	Predator Species									
Prey Species	*Raja erinacea*	*Urophycis chuss*		*Urophycis regius*	*Merluccius bilinearis*	*Macrozoarces americanus*	*Stenotomus chrysops*	*Citharichtys arctifrons*	*Hippoglossina oblonga*	
		JUV.	ADULT		JUV.				JUV.	ADULT
AMPHIPODA										
Ampeliscidae										
Byblis serrata	xxx	x	x	x	xx		x	xx	xx	x
Ampelisca agassizi							xx			
Ampelisca vadorum	xx		x		x	x	x	xx		
Corophiidae										
Erichthonius rubricornis	xxx	xx	xxx	x		xxx	xxx	xxx	xx	
Unciola irrorata	xxx	xxx	xxx	xx		xxx	xx	xxx	xxx	x
Leptocheirus pinguis	x									
Phoxocephalidae										
Trichophoxus epistomus	x		x	x						
Phoxocephalus holbolli							x			
Lysianassidae										
Hippomedon serratus				x						
Hyperiidae										
Parathemisto gaudichaudi		xxx		xx	xxx		xx	x		
CUMACEA										
Diastylis bispinosa	xx	x			x			x		
Diastylis sculpta	xx					x		x		
ISOPODA										
Cirolana polita			x	x						

x - minor importance
xx - secondary importance
xxx - major importance

where competition may be intense for short time periods but occurring with enough regularity to maintain the selective advantage.

Most of the important fish predators feeding on the amphipods in this study are present on the shelf year-round (Foell and Musick 1979). Additionally, the lack of strong seasonal trends in population abundance for each amphipod species suggests that the selective advantage of maintaining resource partitioning mechanisms is not facilitated on an annual basis. Longer terms changes in amphipod abundance on the shelf have been noted. Boesch (1979a) found some species principally *Unciola* spp., *A. vadorum* and *B. serrata* were more abundant during 1975-1977 than they were during 1974 when Radosh et al. (1978) sampled macrobenthos in the same area examined for this study. One might hypothesize that resource partitioning mechanisms, such as those observed in this suite of species, would be of adaptive significance in facilitating coexistence and maintenance of community structure when intrinsic or extrinsic factors permitted concordant rises in population abundances.

Evolutionary and Ecological Trends in Ampeliscoidea and Corophioidea

Accommodation to competitive interactions may be expressed in an evolutionary rather than ecological time frame. This factor must be considered when examining suites of species that may have coexisted in communities though long periods of geological time.

The early evolutionary history of the Amphipoda is poorly understood primarily because no fossil record exists prior to the

Eocene (Bousfield 1978). A relatively recent evolution from within the peracaridan stock may be inferred from numerous characteristics of the order outlined by Bousfield. These include: a) advanced morphology of mouthparts, thoracic and abdominal appendages; b) numerical dominance in coastal marine and freshwater environments; c) relatively low subordinal diversity (four vs. ten suborders in Isopoda) including none that are parasitic; and d) decreased diversity and abundance in the deep sea and on land as compared with the older order Isopoda.

Bousfield places the probable origin of the Amphipoda in the late Paleozoic from a caridoid- or mysid-like ancestor in response to the increasing availability of primary plant food resources. The more advanced (apomorphic) amphipod superfamilies (including the Ampeliscoidea and Corophioidea) may have radiated during the Cretaceous in response to the evolution and development of coastal salt marshes, seagrasses, and mangrove swamps. This contention corresponds well with inferences on possible evolutionary trends in the Ampeliscidae drawn from zoogeographic considerations by Mills (1965). He noted the likelihood that A. agassizi (= A. compressa) moved from an eastern Pacific flock of ampeliscids to the western Atlantic Basin during the Miocene or early Pliocene. The high phenotypic stability of this species, as evidenced by our inability to distinguish between Atlantic and Pacific populations, suggests that the species was widely distributed and abundant in the Atlantic prior to the complete formation of the central American land bridge in the

Pliocene. Mayr (1977) has noted that when large, stable gene pools are isolated speciation is often slow or nonexistent. *A. vadorum* may have arisen from members of a West African stock of ampeliscids during the late Mesozoic or early Cenozoic when cooling trends isolated populations on North American coasts from the stock species in temperate waters on the eastern side of the Atlantic (Mills 1965). Unfortunately, similar biogeographic and evolutionary assessments for the Corophiidae and *B. serrata* do not exist. It is interesting to note that, with the exception of *A. agassizi*, all of the species considered in this study are endemic to the North Atlantic Basin (Bowen et al. 1979, Watling 1979). This suggests that co-evolution may have played an important role in shaping community structure as it is observed in its present ecological sense.

Both superfamilies, and therefore the families considered in this study, exhibit specific morphological and behavorial features which have presumably led to their success in soft-bottom benthic marine habitats. The major advancement to arise independently in each superfamily was the evolution of tube-spinning glands and domiculous behavior (Barnard 1969, Bousfield 1978), thus facilitating the exploitation of environments otherwise offering little protection from predators. Associated with this change in living position were other functional and behavioral adaptations which further strengthened the advantages of a domiciliary life style. These changes as well as their adaptive significance are outlined in Table 7. Both superfamilies maintained the basic gammaridean mouthpart morphology

Table 7. Morphological and behavioral adaptations exhibited by Ampeliscoidea and Corophiodea.

FUNCTIONAL OR BEHAVIORAL CHANGE	ADAPTIVE SIGNIFICANCE	NOTES
A. elongation and increased setation of antennae	increased ability to gather food without leaving the protection of the tube	characteristic of both superfamilies
B. deposit or trypton feeding	enables organisms to utilize environments where primary plant materials are not major food source	same as above
C. fusion or rigidization of urosome	increased leverage within the tube structure	same as above
D. reduction and modification of the third uropods	increased leverage within the tube structure and increased ability to rapidly withdraw from tube opening	Corophioidea only
E. reduction of coxae	facilitates cylindricization of body and tubes	same as above
F. increased cephalization and elongated occular lobes	allows animal to utilize anterior portion of body in collecting food material	same as above
G. loss of pelagic male stage	decreased risk of loss of males to planktonic predators	same as above

Compiled from Barnard 1969 and Bousfield 1973 suggesting that this plan was particularly well suited for deposit feeding behavior. The larger number of functional and behavioral changes exhibited by the Corophoidea seemed to have allowed this superfamily to radiate into a greater spectrum of habitats and feeding positions (i.e. the epifaunal realm utilized by *Erichthonius* and occupation of the tubes of other organisms or perhaps burrows coupled with a loss of tube-spinning glands by *Unciola irrorata*) which may facilitate their coexistence with both competitors and predators.

Appendix A. Instructions for preparation of mounting medium.

MOUNTING MEDIUM FOR SEM SPECIMENS

To: 4 ml 100% ethanol

Add: 10 drops silver paint (such as #1481 (Ernest F. Fullam, Inc.)

Shake well. Allow to settle undisturbed for approximately 15 minutes. Carefully decant off the top 3 ml of suspended metal and ethanol. The object is to leave the coarse particles behind.

To: 3 ml suspended metal-ethanol mixture

Add: 2.5 ml "Diaphane" mounting medium (Will Scientific, Inc.)

5 ml 100% ethanol

Shake well. For convenient use store the mixture in a small bottle with a dropper top.

To use:

Place one drop on a stub. Mixture should spread out to coat surface of stub, although it will be somewhat thicker at the edges. In a few minutes the mixture will begin to turn milky and will then begin to clear. As it clears the surface will become tacky. This is the point at which the specimens should be mounted. After mounting place specimens in a dessicator and allow medium to set for at least four hours before coating.

Appendix B. Measured environmental parameters for quarterly sampled and stratified random stations. See end of appendix for note concerning Cruise Number.

Station/ Cruise		med dia (φ)	mean dia (φ)	sort	skew	gravel %	co sand %	med sand %	fine sand %	silt+clay %	org C (mg/g)
B1	01	1.54	1.59	0.40	0.60	0.9	3.6	79.9	13.1	2.5	0.58
	02	1.56	1.61	0.40	1.19	0.7	5.7	79.5	12.8	1.3	0.54
	03	1.56	1.60	0.48	0.18	0.5	10.1	69.9	17.6	1.7	1.72
	04	1.63	1.66	0.52	0.10	0.8	8.2	68.4	20.7	1.3	0.86
	05	1.78	1.76	0.45	-0.07	0.5	4.8	62.7	28.4	3.5	0.97
	06	1.79	1.80	0.42	0.04	0.7	2.8	68.9	23.0	4.4	1.19
	07	1.90	1.92	0.35	0.09	0.5	0.7	60.8	36.3	1.4	1.02
	08	1.79	1.77	0.46	-0.06	0.9	5.1	62.8	27.5	3.4	1.22
B2	01	1.07	1.04	0.74	-0.65	8.6	30.4	53.2	4.5	0.3	0.37
	02	1.29	1.28	0.61	0.41	2.6	24.5	62.6	8.6	1.4	0.66
	03	1.13	0.94	0.96	-0.15	8.3	29.2	54.1	7.5	0.6	0.41
	04	1.11	0.99	0.83	-0.32	8.9	32.3	52.1	5.9	0.2	0.34
	05	1.47	1.37	0.66	-0.21	2.6	19.7	62.0	15.1	0.4	0.40
	06	1.33	1.12	0.83	-0.33	7.5	23.0	59.1	9.4	0.7	0.67

Station/ Cruise		med dia (ø)	mean dia (ø)	sort	skew	gravel %	co sand %	med sand %	fine sand %	silt+clay %	org C (mg/g)
	07	1.47	1.47	0.53	0.02	7.6	9.2	66.3	16.4	0.3	0.31
	08	1.31	1.18	0.78	-0.21	5.0	24.1	58.7	11.7	0.3	0.77
B3	01	1.95	2.04	0.56	-0.07	5.5	1.9	45.8	41.1	5.1	1.98
	02	2.05	.10	0.63	0.50	2.8	3.1	39.9	47.7	6.4	2.50
	03	2.13	2.09	0.68	-0.04	5.1	2.7	28.5	58.1	5.3	2.53
	04	2.13	2.15	0.66	-0.05	13.3	2.2	25.6	52.4	6.3	2.46
	05	2.36	2.31	0.58	1.04	5.3	2.6	18.5	66.1	7.2	1.95
	06	2.32	2.32	0.57	-0.13	5.8	2.1	19.1	64.6	8.2	3.02
	07	2.36	2.30	0.52	-0.14	2.7	1.1	20.7	69.2	6.2	1.94
	08	2.35	2.10	0.97	-0.35	12.6	3.8	13.9	62.1	7.4	2.35
B4	01	0.88	0.70	0.79	-0.36	10.3	49.2	39.2	1.1	0.1	0.49
	02	0.90	0.71	0.82	-0.04	9.0	49.1	39.7	1.8	0.2	0.05
	03	0.87	0.80	1.14	-0.35	18.1	38.7	39.3	2.4	0.1	0.34

Station/	Cruise	med dia (ø)	mean dia (ø)	sort	skew	gravel %	co sand %	med sand %	fine sand %	silt+clay %	org C (mg/g)
	04	1.07	1.02	0.73	-0.16	14.9	28.6	52.0	4.3	0.1	0.29
	05	1.09	0.96	0.70	-0.26	7.9	31.9	56.1	3.8	0.0	0.26
	06	1.16	0.95	0.81	-0.41	10.4	28.5	56.0	4.9	0.0	0.44
	07	1.29	1.32	0.48	-0.07	11.0	15.3	65.9	7.1	0.0	0.76
	08	1.10	1.10	0.79	-0.31	15.8	23.6	53.5	6.8	0.1	0.60
B5	05	1.63	1.54	0.59	-0.23	4.2	15.6	57.9	19.2	3.1	-
	06	1.92	1.79	0.74	-0.26	10.6	7.8	37.0	38.7	5.9	1.90
	07	1.71	1.65	0.69	-0.07	8.3	12.5	39.4	36.1	3.7	1.11
	08	1.41	1.78	0.61	0.06	10.9	15.6	50.3	19.8	3.4	1.20
P0	05	1.12		0.64		3.1	36.6	54.9	4.8	0.6	0.25
P1	05	1.05		0.93		11.7	34.4	49.4	4.4	0.1	0.49
P2	05	0.98		0.66		1.2	39.5	54.3	4.9	0.0	0.26
P3	05	1.20		0.79		10.0	28.8	56.7	4.5	0.0	0.24

Station/	Cruise	med dia (ϕ)	mean dia (ϕ)	sort	skew	gravel %	co sand %	med sand %	fine sand %	silt+clay %	org C (mg/g)
P4	05	1.18		0.83		7.8	26.7	63.5	1.8	0.2	0.77
P5	05	1.26		0.58		4.7	25.7	65. 7	3.8	0.1	0.33
P6	05	1.19		0.40		0.9	30.7	65.4	3.0	0.1	0.36
P7	05	1.24		0.68		3.5	30.9	60.8	4.8	0.1	0.30
P8	05	1.37		0.43		1.0	17.8	75.2	5.9	0.1	0.29
P9	05	1.34		0.54		2.2	23.	63.1	10.7	0.7	0.25
R1	05	2.04		0.30		0.6	1.9	41.9	51.4	4.3	1.60
R2	05	1.38		0.52		4.1	21.9	64.8	8.6	0.6	1.22
R3	05	1.95		0.58		2.5	2.6	43.2	43.2	1.5	0.47
R4	05	1.07		1.15		14.6	30.7	52.0	2.6	0.2	0.68
R5	05	1.25		0.60		0.5	33.8	58.7	7.0	0.1	0.64
R6	05	1,47		0.52		1.8	17.6	68.5	11.7	0.4	1.75
R7	05	1.29		1.02		11.0	24.9	49.8	11.2	3.1	0.40
R8	05	1.85		0.57		3.3	8.3	50.6	33.1	4.7	0.29

Station/ Cruise		med dia (ø)	mean dia (ø)	sort	skew	gravel %	co sand %	med sand %	fine sand %	silt+clay %	org C (mg/g)
R9	05	1.57		1.10		11.3	14.5	53.1	12.9	8.2	0.46
F1	05	0.72		0.89		6.1	52.6	37.6	3.8	0.0	0.29
F2	05	1.16		0.91		2.6	38.9	52.6	5.8	0.0	0.31
F3	05	1.33		0.74		1.6	31.4	59.9	6.9	0.3	0.59
F4	05	2.00		0.48		2.4	2.9	45.2	48.1	1.4	1.67
F5	05	1.92		0.31		1.1	1.0	60.0	35.8	0.4	0.95
F6	05	1.76		0.34		1.2	3.9	73.4	19.6	2.0	1.12
M1	05	2.39		0.37		0.9	0.9	15.0	77.8	5.4	2.15
M2	05	0.38		-		36.1	32.8	20.8	9.5	0.9	1.12
M3	05	1.61		0.45		3.1	6.7	71.3	17.1	1.8	0.55
M4	05	1.98		0.27		0.7	2.0	51.4	45.4	0.5	0.81
M5	05	1.35		0.57		0.7	25.2	61.9	9.7	2.6	0.54
M6	05	1.87		0.36		0.6	1.0	67.0	27.7	3.4	1.16
D1	05	1.51		0.38		0.4	7.0	82.6	10.0	0.1	1.16

Station/	Cruise	med dia (φ)	mean dia (φ)	sort	skew	gravel %	co sand %	med sand %	fine sand %	silt+clay %	org C (mg/g)
D2	05	1.48		0.52		0.2	17.9	68.6	12.9	0.4	1.48
D3	05	1.63		0.49		2.7	7.6	68.4	19.0	2.3	0.96
D4	05	1.58		0.49		5.3	10.4	72.6	11.3	0.4	0.84
D5	05	1.61		0.41		2.9	9.7	77.6	9.7	0.1	0.44
D6	05	2.07		0.54		3.0	5.7	36.8	51.9	2.7	2.14
D7	05	1.39		0.52		1.3	23.6	64.9	9.8	0.3	0.47
S1	05	2.00		0.43		2.1	3.7	45.2	43.4	1.8	0.81
S2	05	1.39		1.09		7.7	26.4	42.2	19.3	4.4	1.05
S3	05	2.02		0.44		2.9	3.7	41.4	46.9	5.2	1.08
S4	05	1.79		0.91		8.1	11.8	43.0	29.5	7.5	1.11
S5	05	1.67		0.53		4.1	10.8	64.7	14.4	6.0	1.48
S6	05	2.08		0.74		5.3	9.7	29.9	48.4	6.8	1.77
S7	05	1.13		1.29		12.9	31.8	43.0	9.9	4.4	1.85
S8	05	2.25		0.52		0.5	2.8	27.6	61.6	7.5	1.85

Station/	Cruise	med dia (ϕ)	mean dia (ϕ)	sort	skew	gravel %	co sand %	med sand %	fine sand %	silt+clay %	org C (mg/g)
S9	05	2.26		0.52		1.9	3.7	23.0	65.4	6.1	1.72

Cruise Number:	Sampling Date:
01	November 1975
02	February 1976
03	June 1976
04	August 1976
05	November 1976
06	February 1977
07	June 1977
08	August 1977

Appendix C. Actual numbers of individuals collected at each station. Quarterly station samples represent 0.6m^2 areas while stratified random samples represent o.1m^2 sample size.

STATION/	CRUISE	*A. agassizi*	*A. vadorum*	*B. serrata*	*U. irrorata*	*U. inermis*	*E. rubricornis*
B1	01	33	11	61	40	-	58
	02	39	19	175	74	-	52
	03	62	51	321	294	-	306
	04	14	40	225	134	-	109
	05	78	70	163	128	9	104
	06	92	420	413	466	-	526
	07	59	243	397	375	40	431
	08	48	180	294	252	-	613
B2	01	2	28	39	42	-	19
	02	-	656	520	300	-	15
	03	1	206	189	544	-	83
	04	1	91	96	400	-	100
	05	-	225	176	137	2	32
	06	1	212	183	173	2	66
	07	31	71	69	155	8	63
	08	-	134	121	130	9	210

STATION/	CRUISE	*A. agassizi*	*A. vadorum*	*B. serrata*	*U. irrorata*	*U. inermis*	*E. rubricornis*
B3	01	5569	8	3	229	-	64
	02	5909	10	12	314	-	85
	03	7012	7	0	442	-	137
	04	5018	2	5	488	-	154
	05	4097	10	1	124	1	11
	06	3332	8	12	85	-	65
	07	9022	71	28	536	-	407
	08	4457	12	2	357	5	323
B4	01	-	-	-	16	-	-
	02	-	-	-	4	-	-
	03	-	-	5	66	-	14
	04	-	1	2	128	-	6
	05	-	2	3	52	42	2
	06	5	2	6	127	3	3
	07	3	-	-	126	44	5
	08	-	3	-	340	89	52

STATION/	CRUISE	*A. agassizi*	*A. vadorum*	*B. serrata*	*U. irrorata*	*U. inermis*	*E. rubricornis*
B5	05	1032	81	118	132	91	590
	06	3116	69	121	897	25	1315
	07	1560	50	90	643	722	1557
	08	309	82	242	354	633	2520
P0	05	-	-	-	10	3	-
P1	05	-	-	-	16	-	-
P2	05	1	-	-	6	1	-
P3	05	-	-	-	5	-	-
P4	05	-	-	-	16	-	1
P5	05	-	-	4	10	-	-
P6	05	-	-	-	9	1	2
P7	05	1	-	1	15	-	7
P8	05	1	-	1	34	-	13
P9	05	1	-	-	11	-	-
R1	05	14	4	30	59	-	42
R2	05	-	50	22	16	1	19

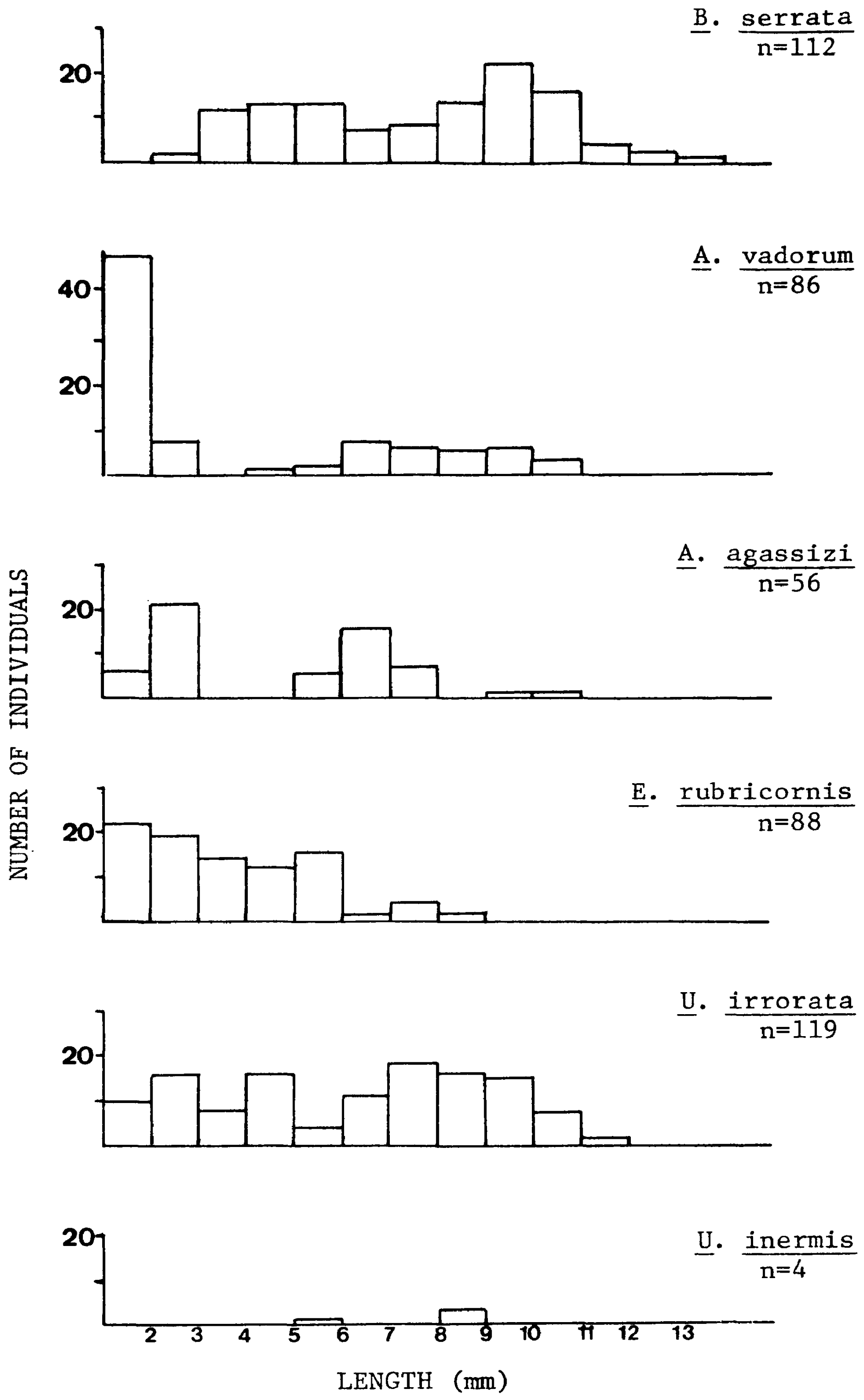
STATION/	CRUISE	*A. agassizi*	*A. vadorum*	*B. serrata*	*U. irrorata*	*U. inermis*	*E. rubricornis*
R3	05	52	2	9	10	-	1
R4	05	-	18	1	4	-	4
R5	05	-	16	55	31	-	11
R6	05	-	5	9	22	61	21
R7	05	-	3	57	36	2	145
R8	05	51	7	64	48	3	27
R9	05	-	5	11	33	24	6
F1	05	-	-	25	19	2	2
F2	05	1	-	18	12	2	-
F3	05	-	3	62	27	1	15
F4	05	7	-	2	9	-	28
F5	05	5	-	73	129	1	7
F6	05	55	-	11	69	-	51
M1	05	79	-	1	15	7	1
M2	05	1	-	-	78	106	-
M3	05	-	1	18	108	72	6

STATION/	CRUISE	*A.agassizi*	*A. vadorum*	*B. serrata*	*U. irrorata*	*U. inermis*	*E. rubricornis*
M4	05	2	-	35	66	1	11
M5	05	1	-	39	4	4	8
M6	05	34	6	15	20	-	20
D1	05	-	31	10	7	-	4
D2	05	-	37	53	5	1	2
D3	05	1	36	30	10	8	19
D4	05	1	7	8	16	3	2
D5	05	-	7	5	-	-	-
D6	05	701	15	2	49	2	2
D7	05	-	36	21	12	-	30
S1	05	185	1	2	24	2	106
S2	05	-	-	25	9	77	4
S3	05	411	1	9	32	3	32
S4	05	2	-	2	-	5	1
S5	05	54	13	9	14	15	46
S6	05	319	4	5	17	3	6

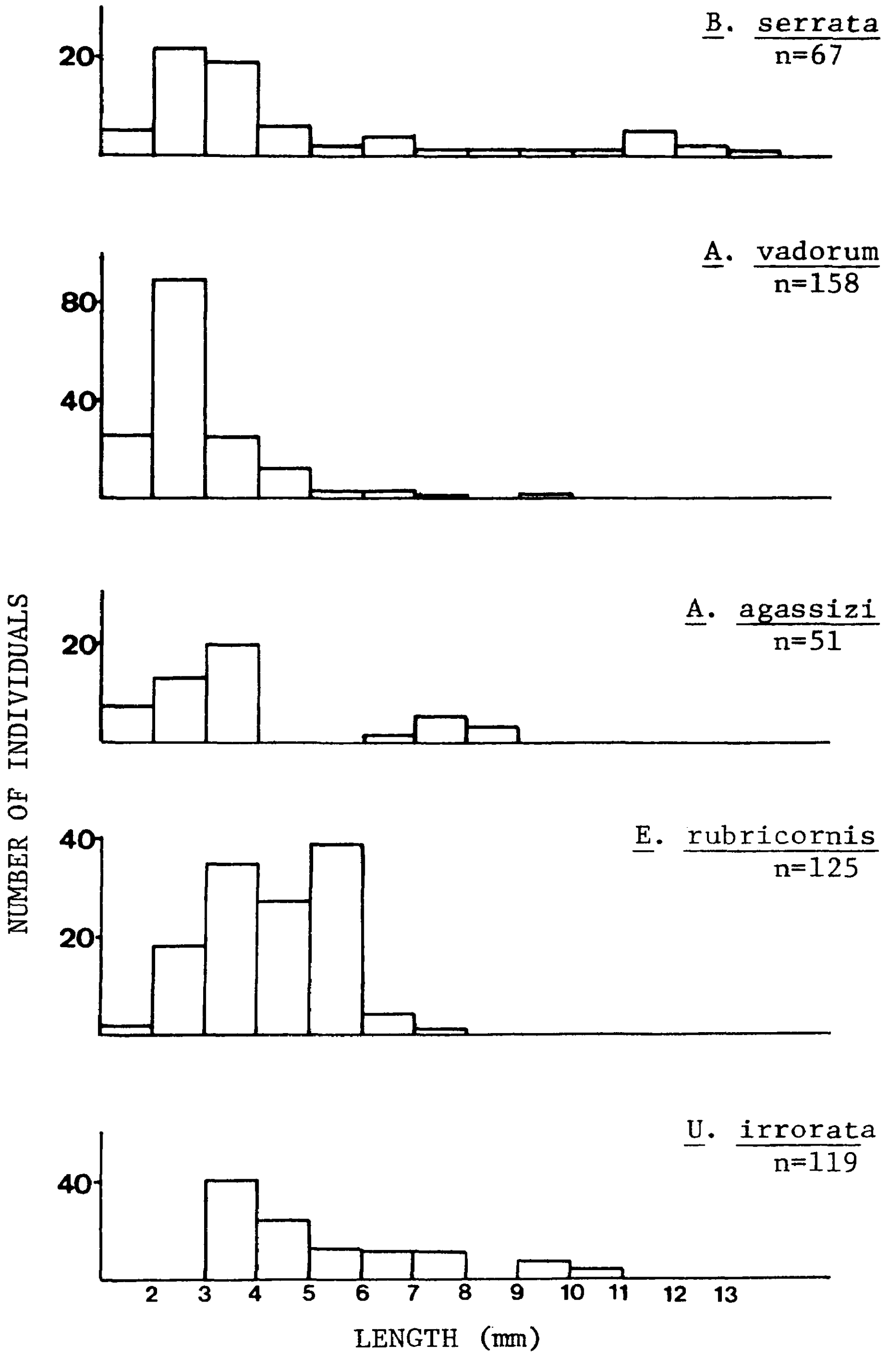
STATION/	CRUISE	*A. agassizi*	*A. vadorum*	*B. serrata*	*U. irrorata*	*U. inermis*	*E. rubricornis*
S7	05	10	13	3	31	71	5
S8	05	379	2	-	22	-	2
S9	05	652	1	-	11	-	7
S0	05	28	-	39	17	4	26

Appendix D. Length-frequency histograms for each species at each of the quarterly sampled stations (November 1976 - August 1977 only).

STATION B1 NOVEMBER 1976

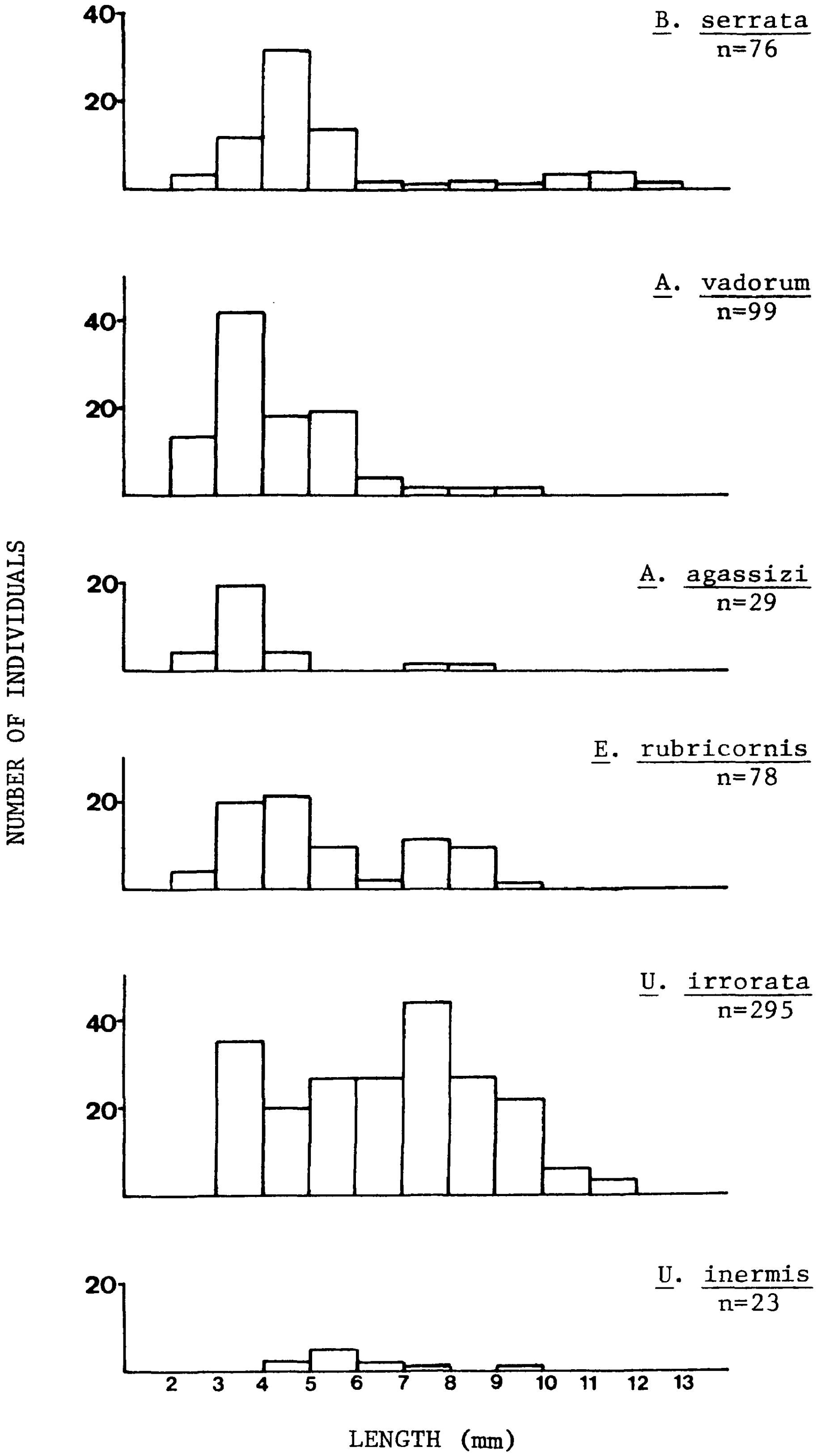


STATION B1 FEBRUARY 1977

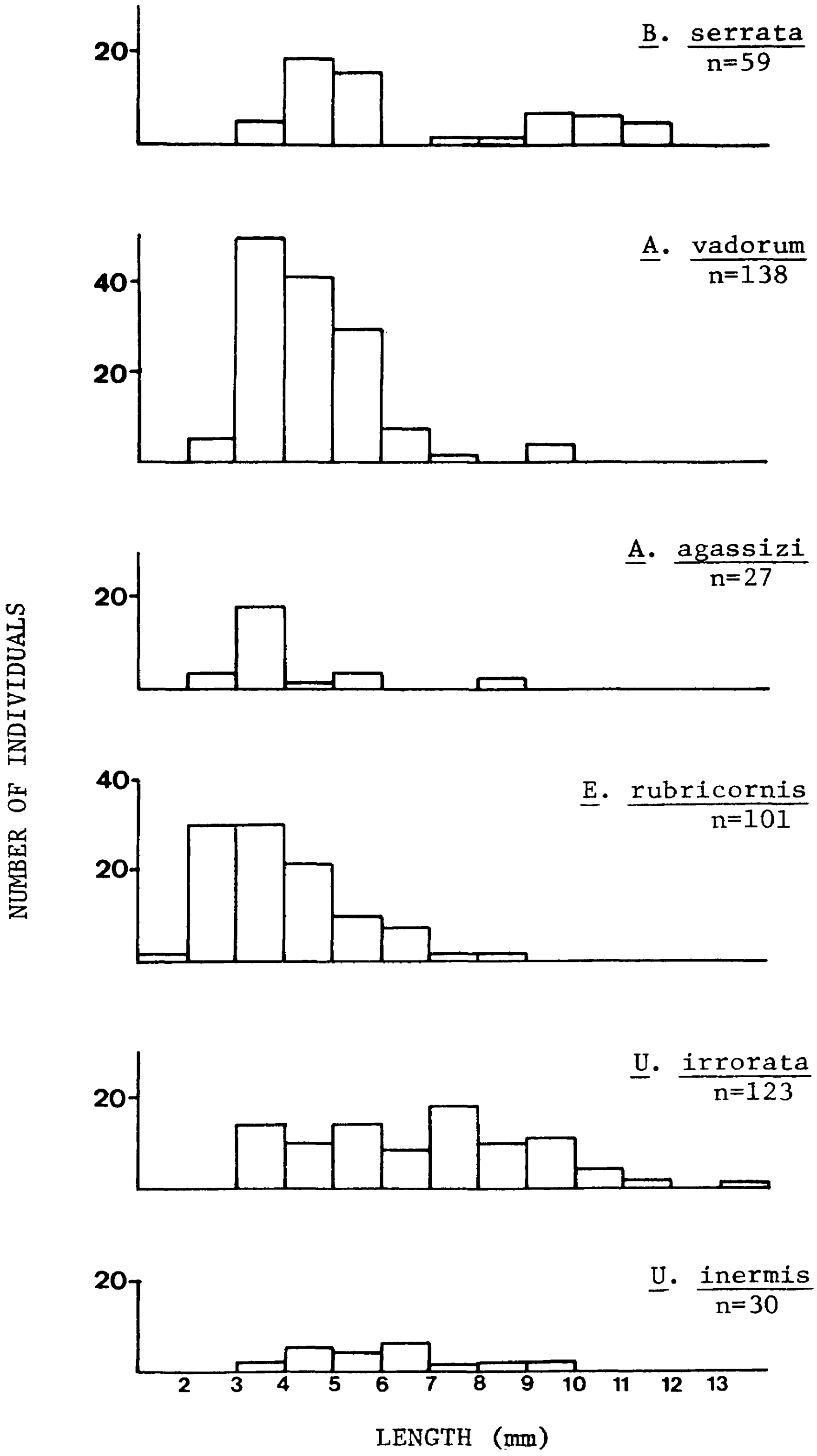


U. inermis absent

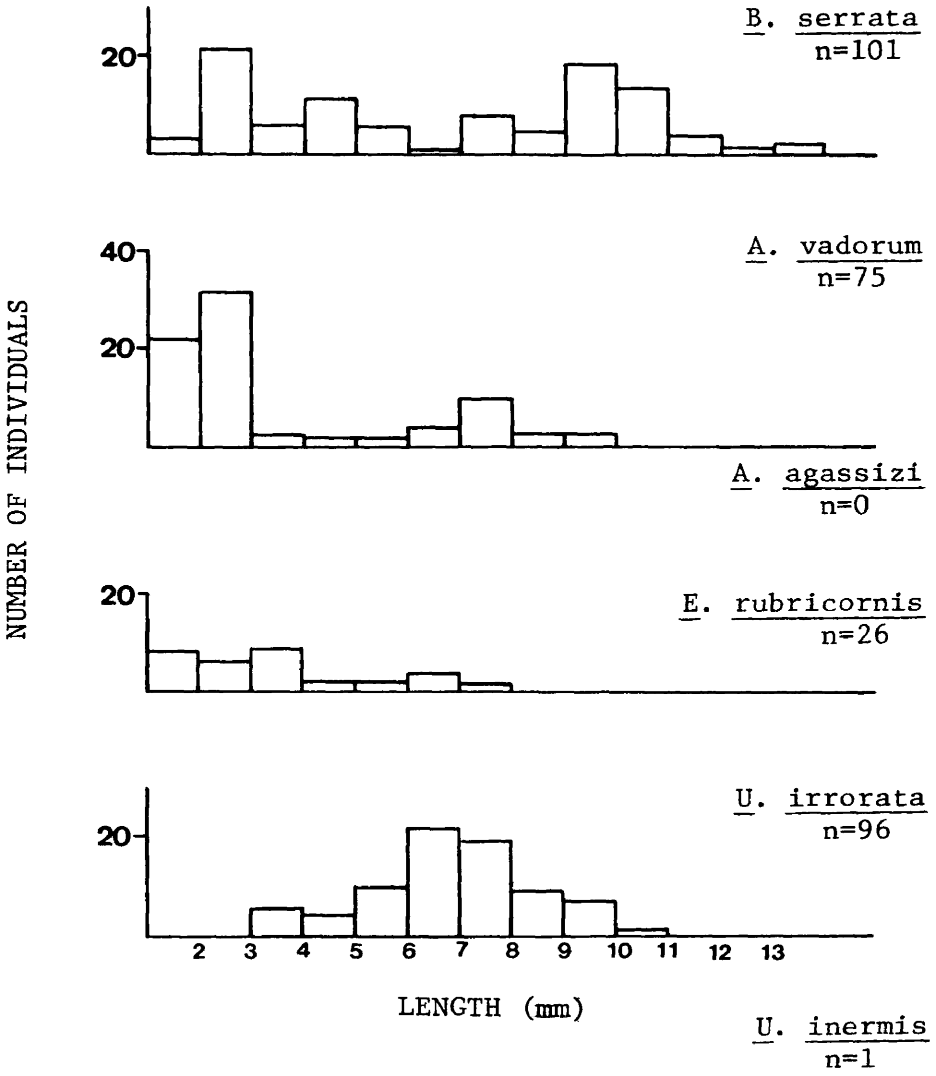
STATION B1 JUNE 1977



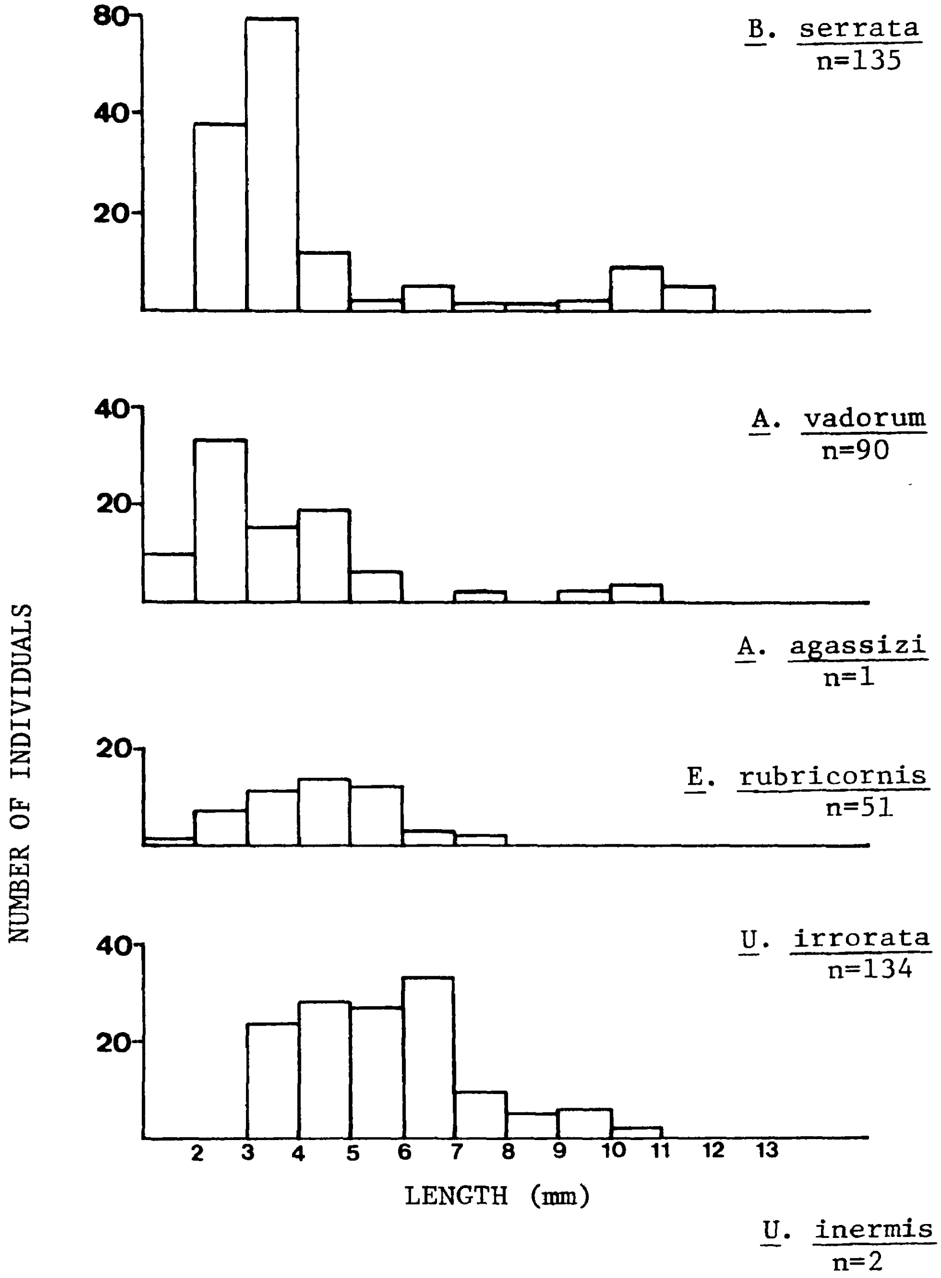
STATION B1 AUGUST 1977



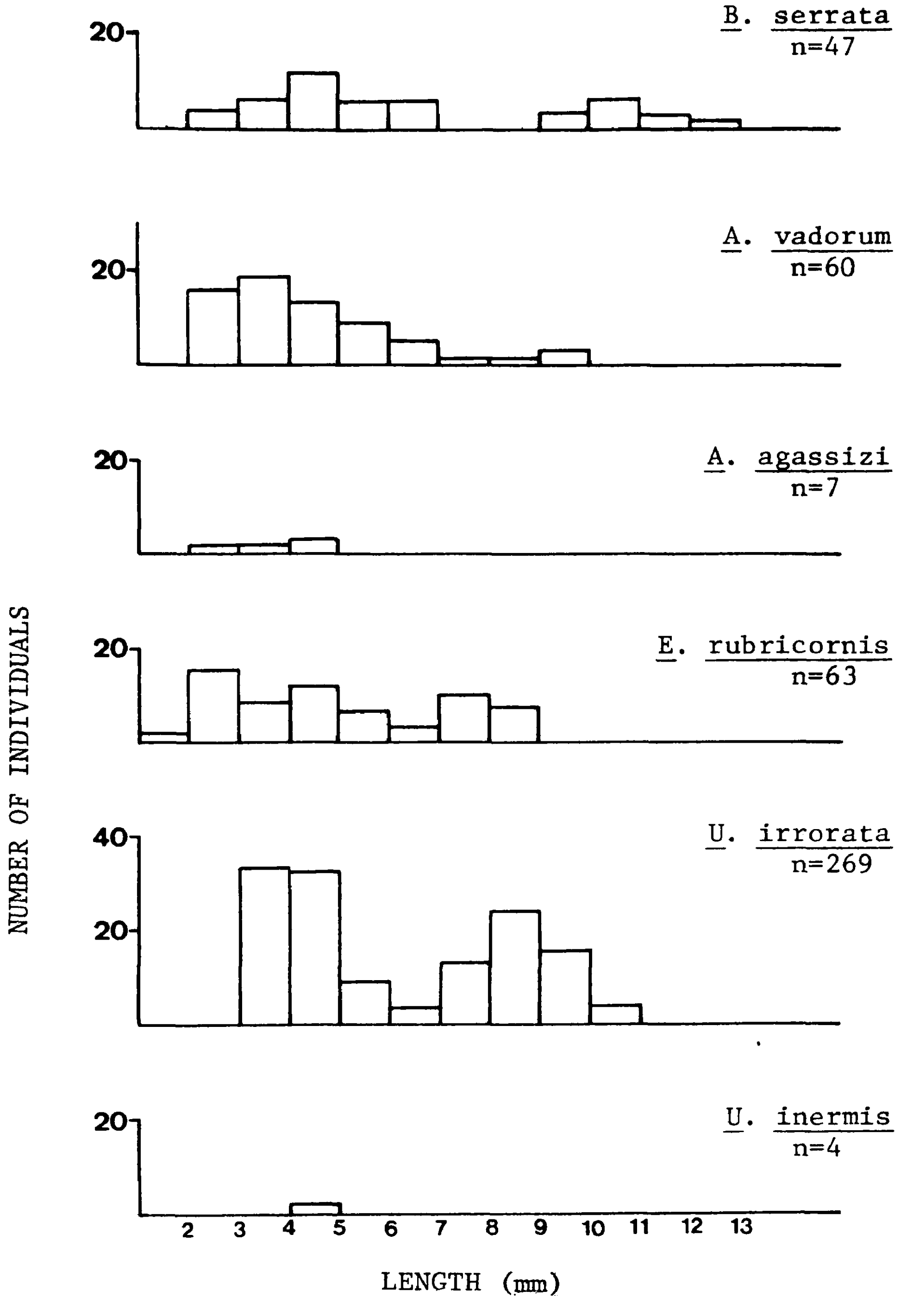
STATION B2 NOVEMBER 1976



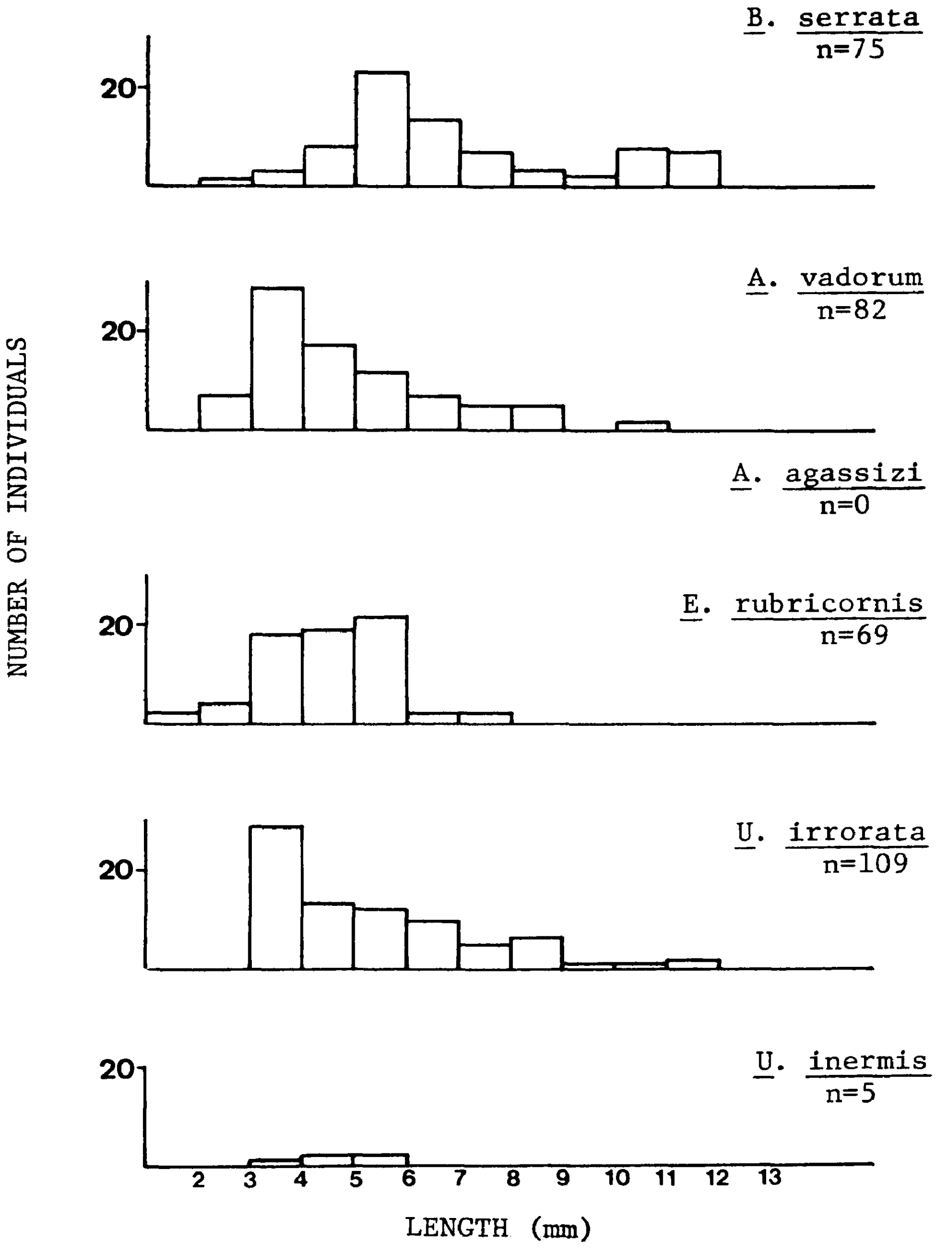
STATION B2 FEBRUARY 1977



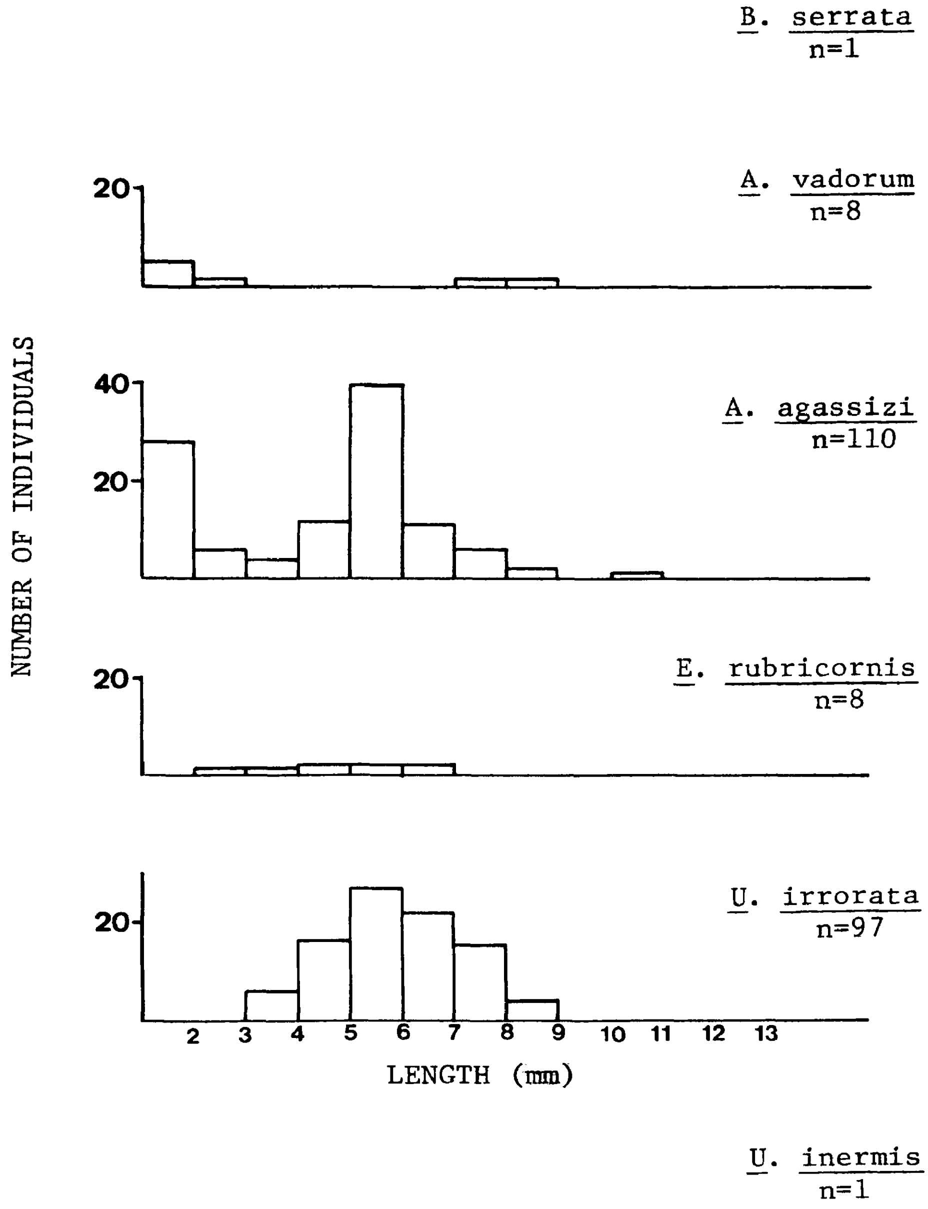
STATION B2 JUNE 1977



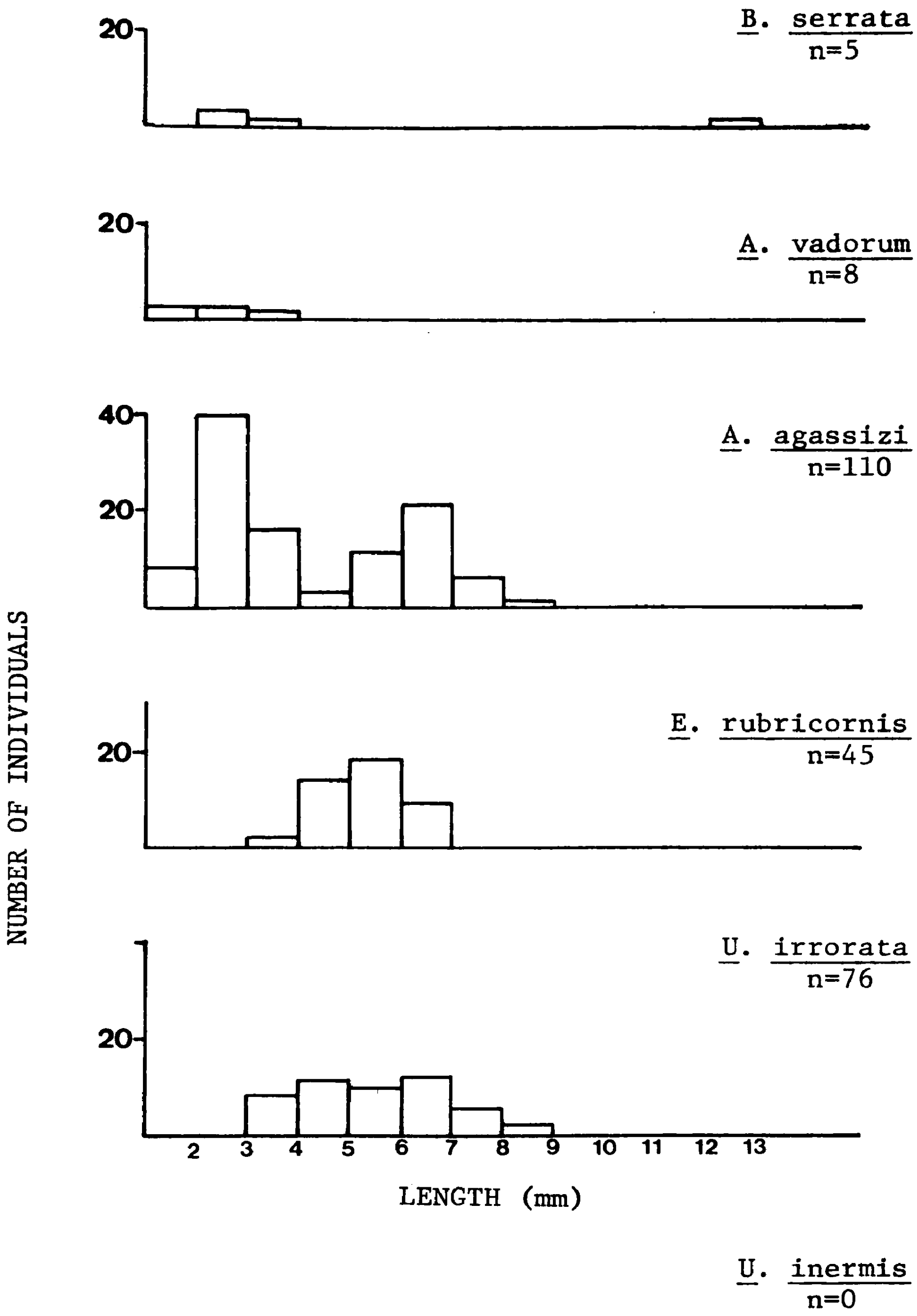
STATION B2 AUGUST 1977



STATION B3 NOVEMBER 1976



STATION B3 FEBRUARY 1977



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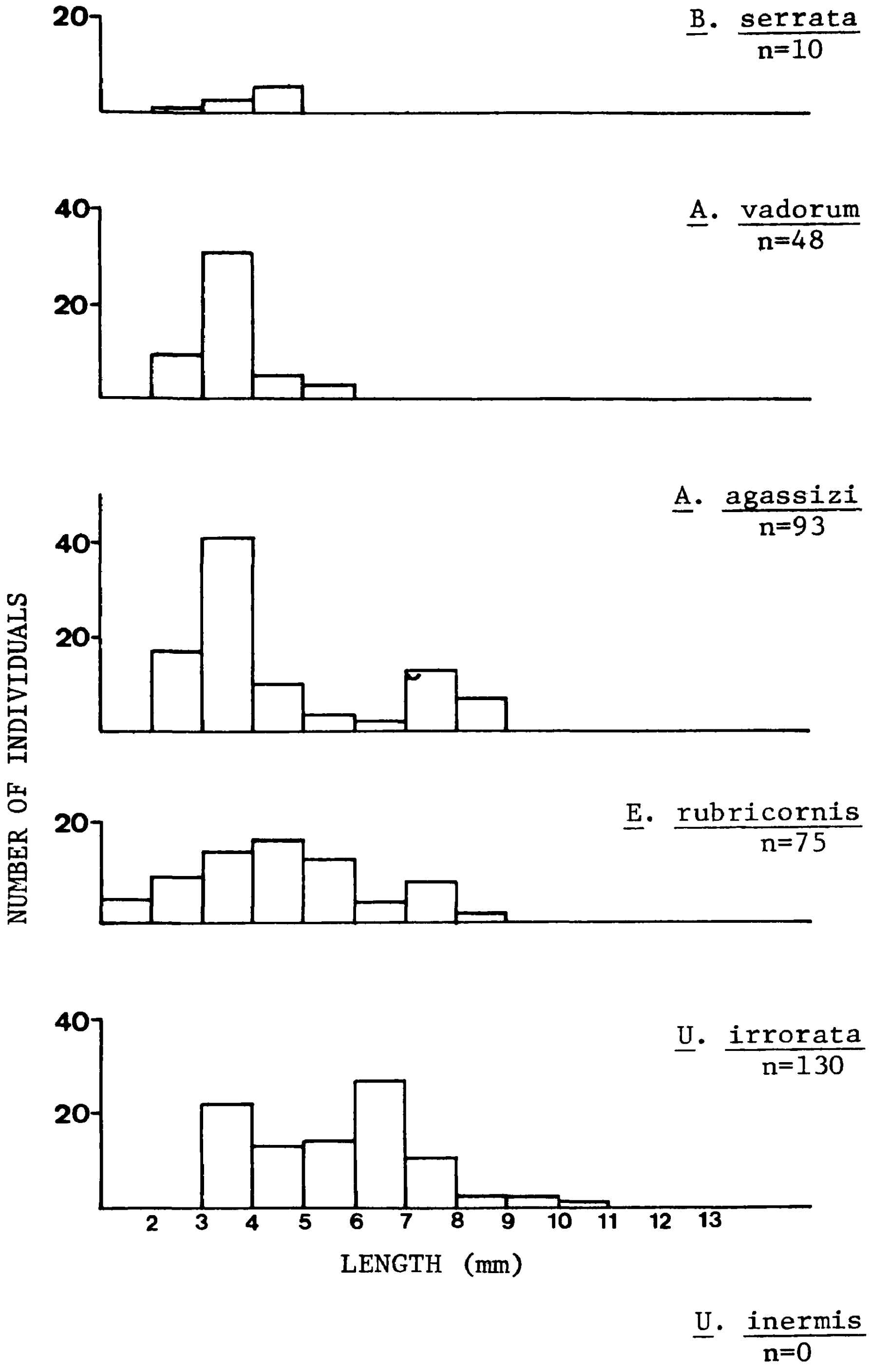
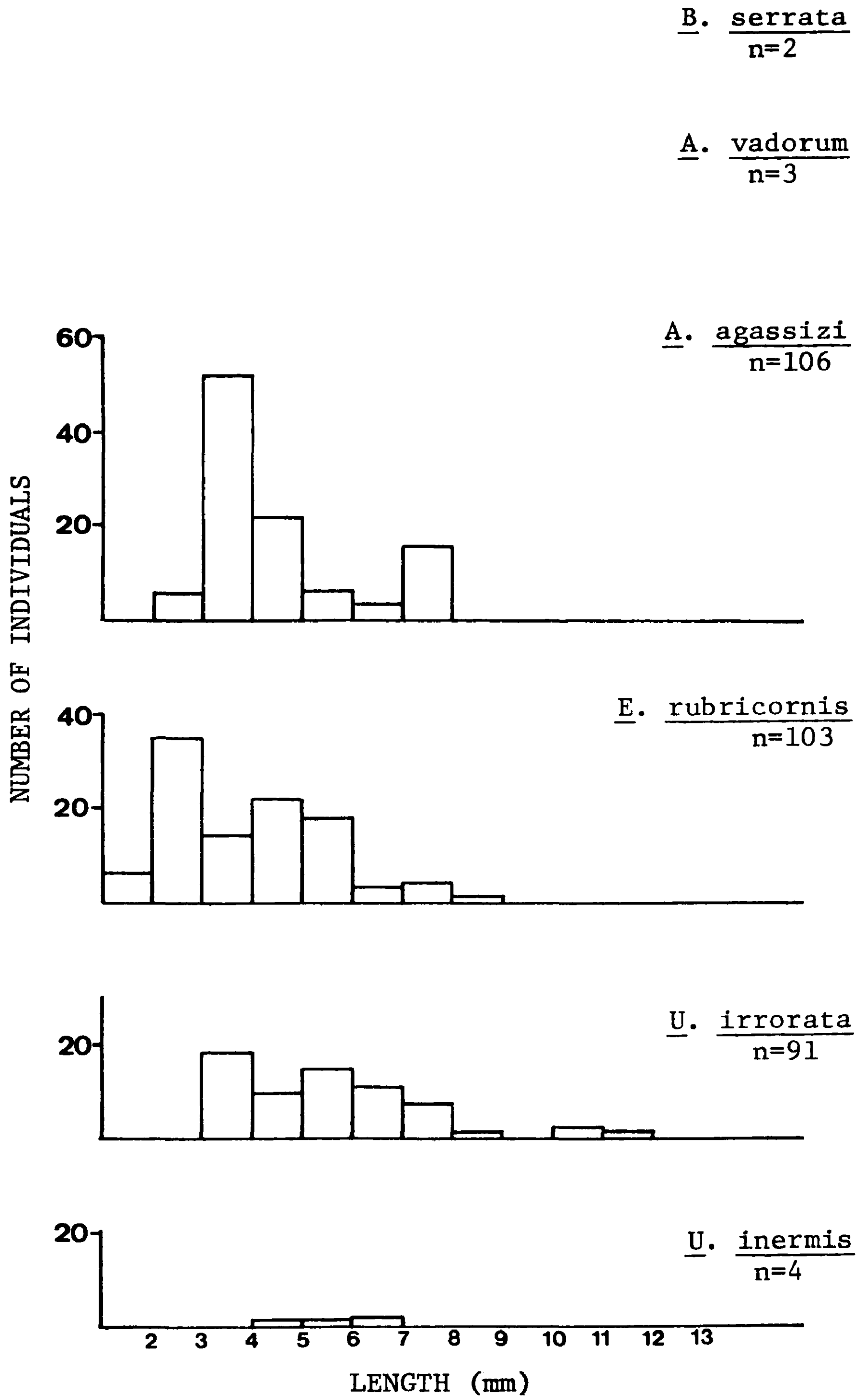
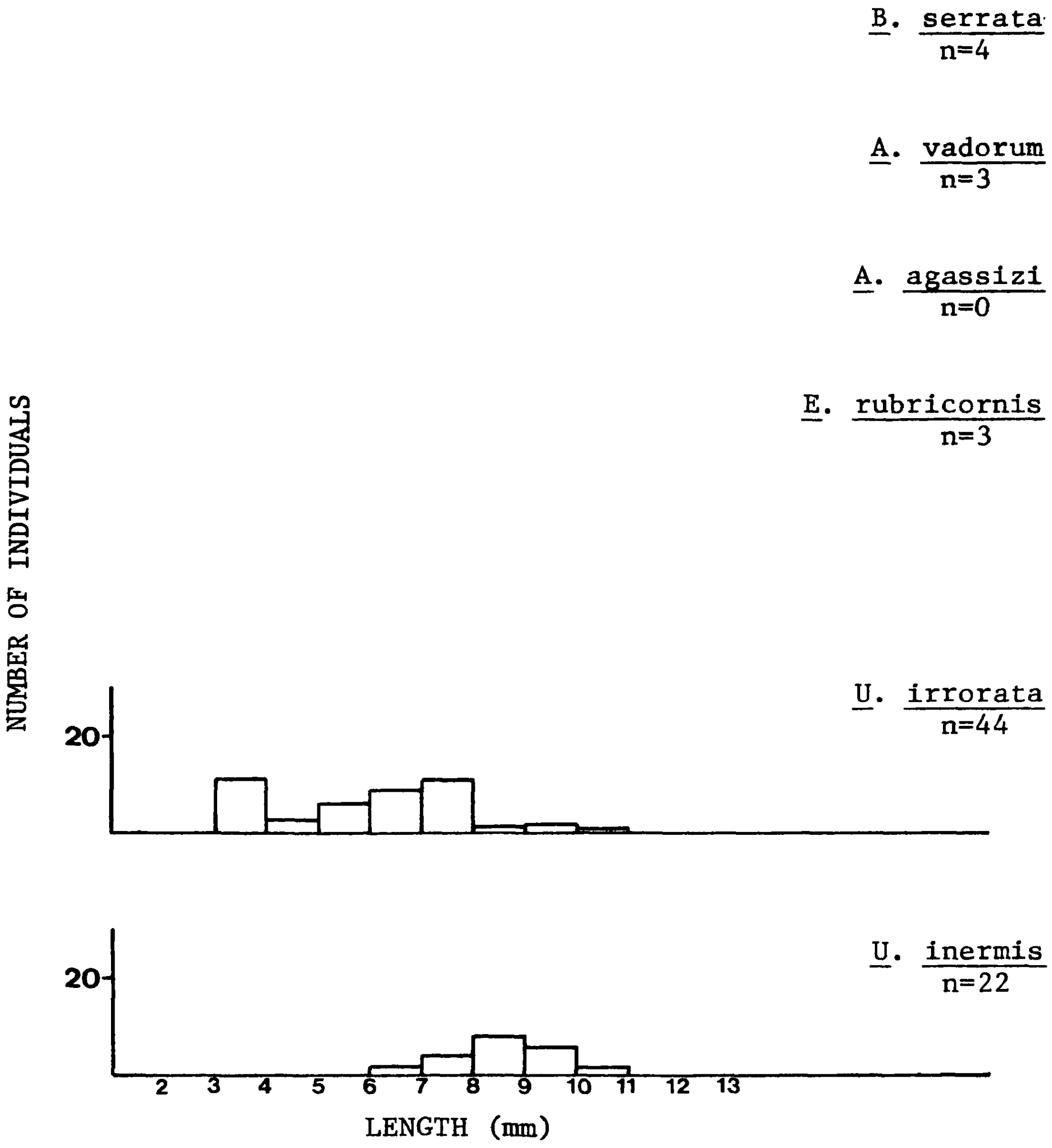


STATION B3 AUGUST 1977



STATION B4 NOVEMBER 1976



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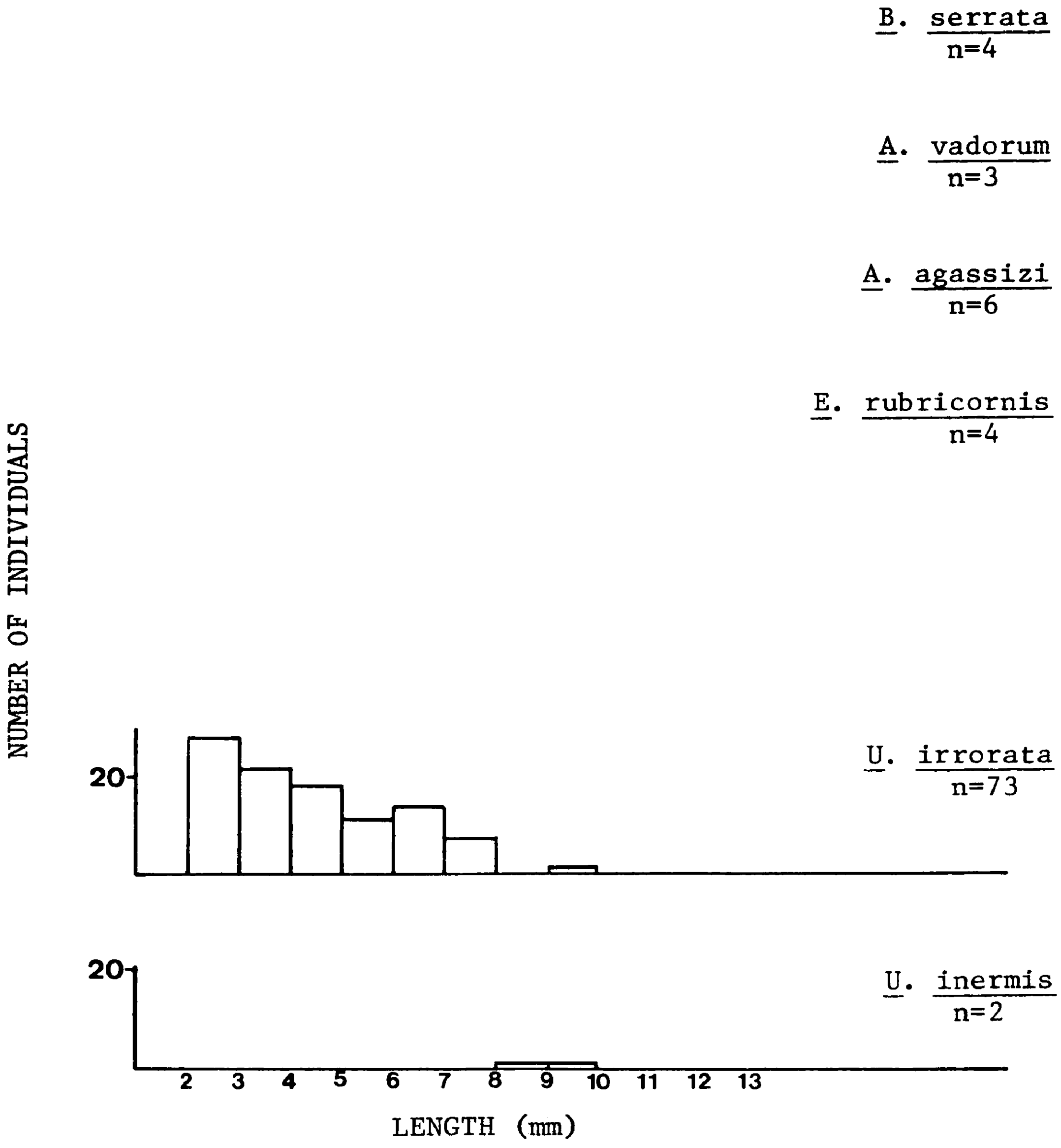

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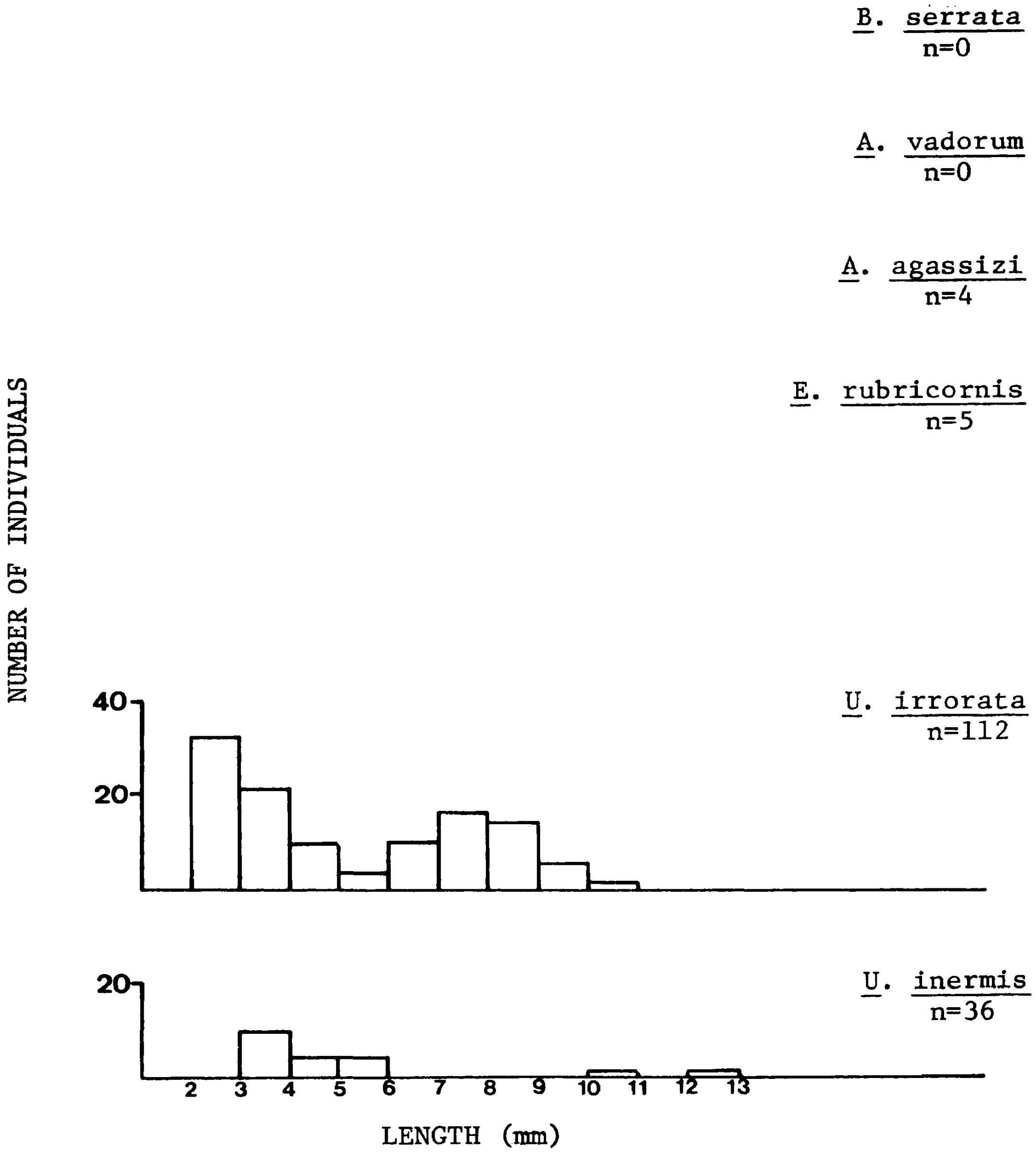

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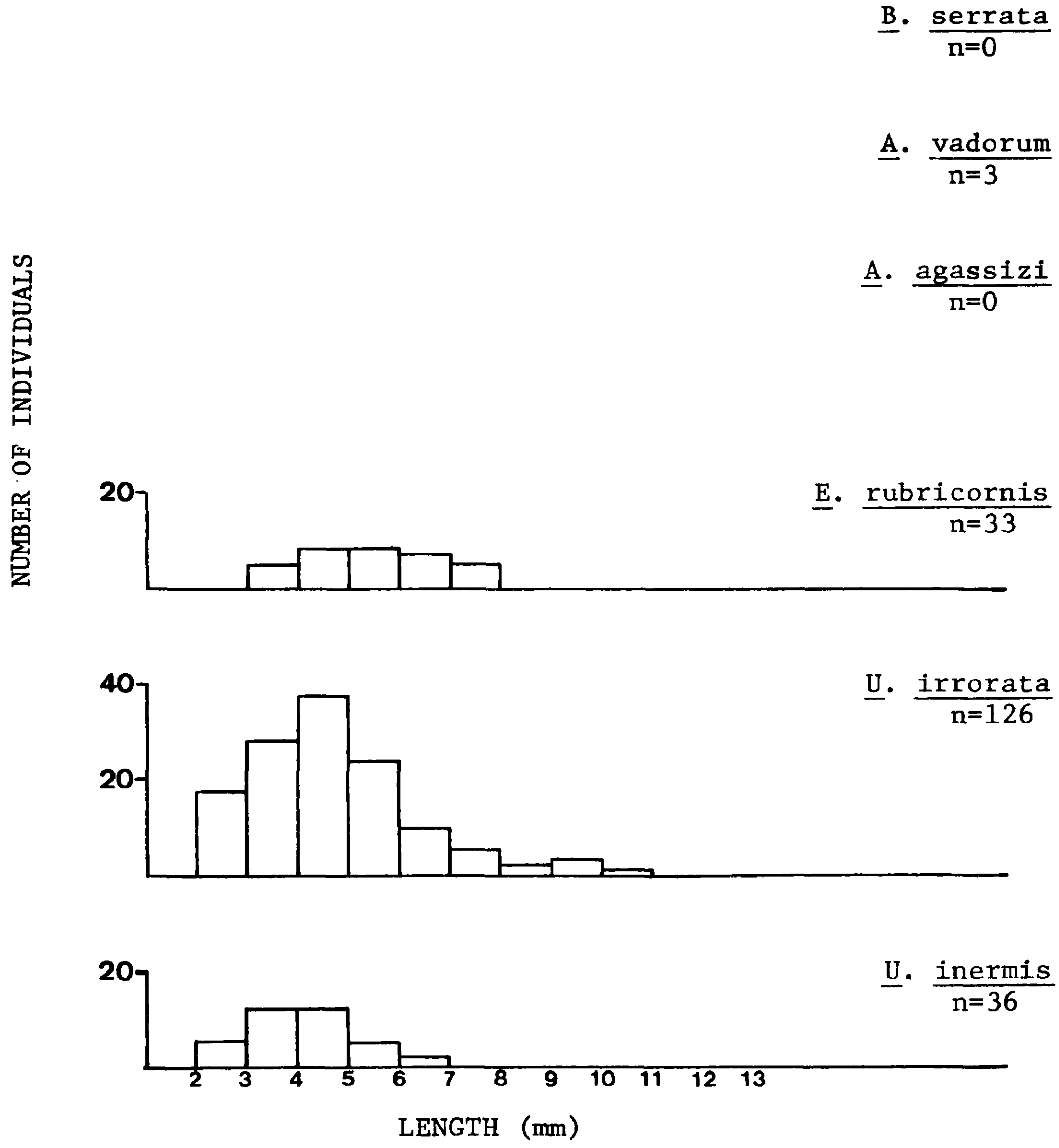

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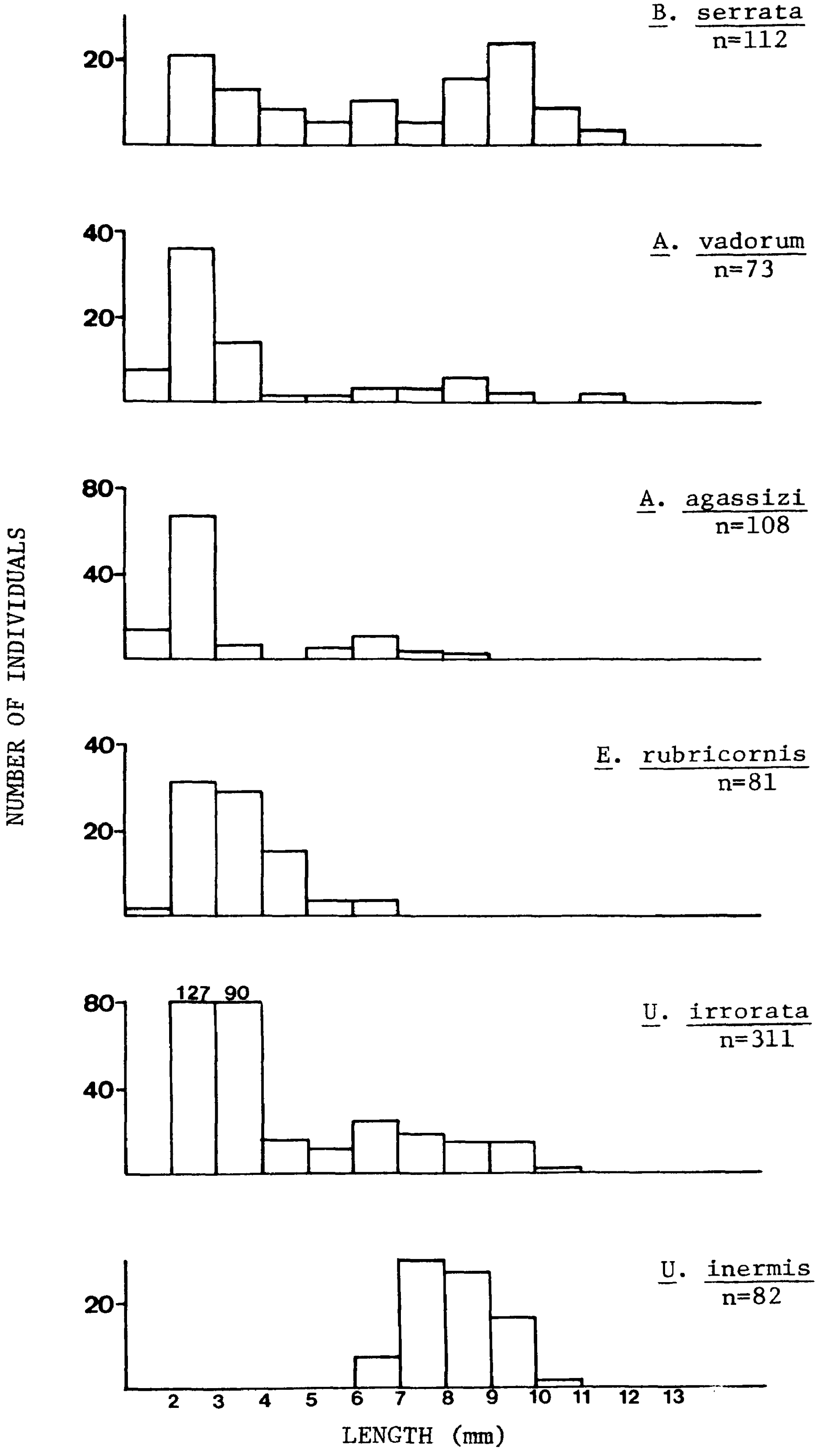
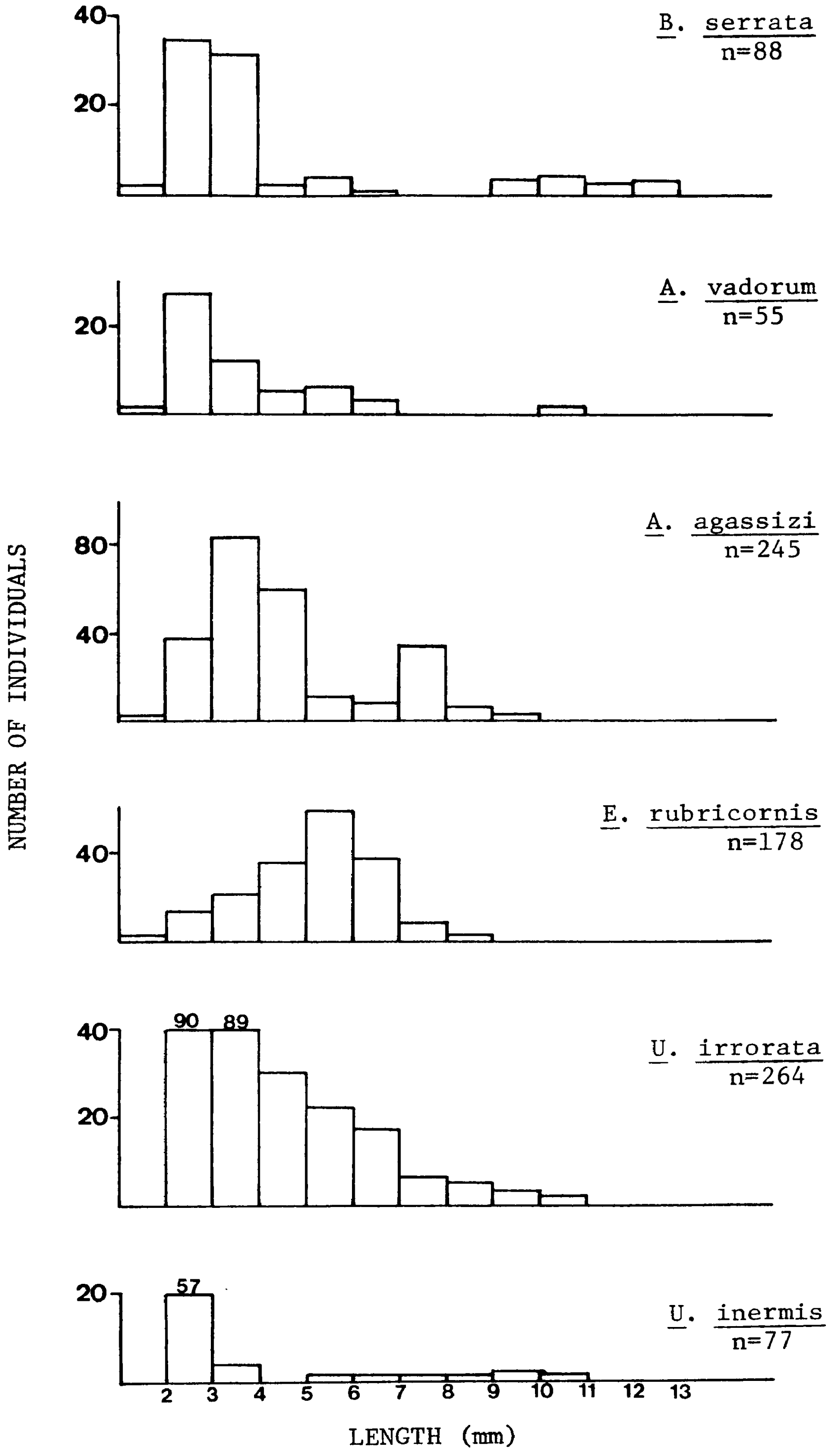


STATION B5 FEBRUARY 1977



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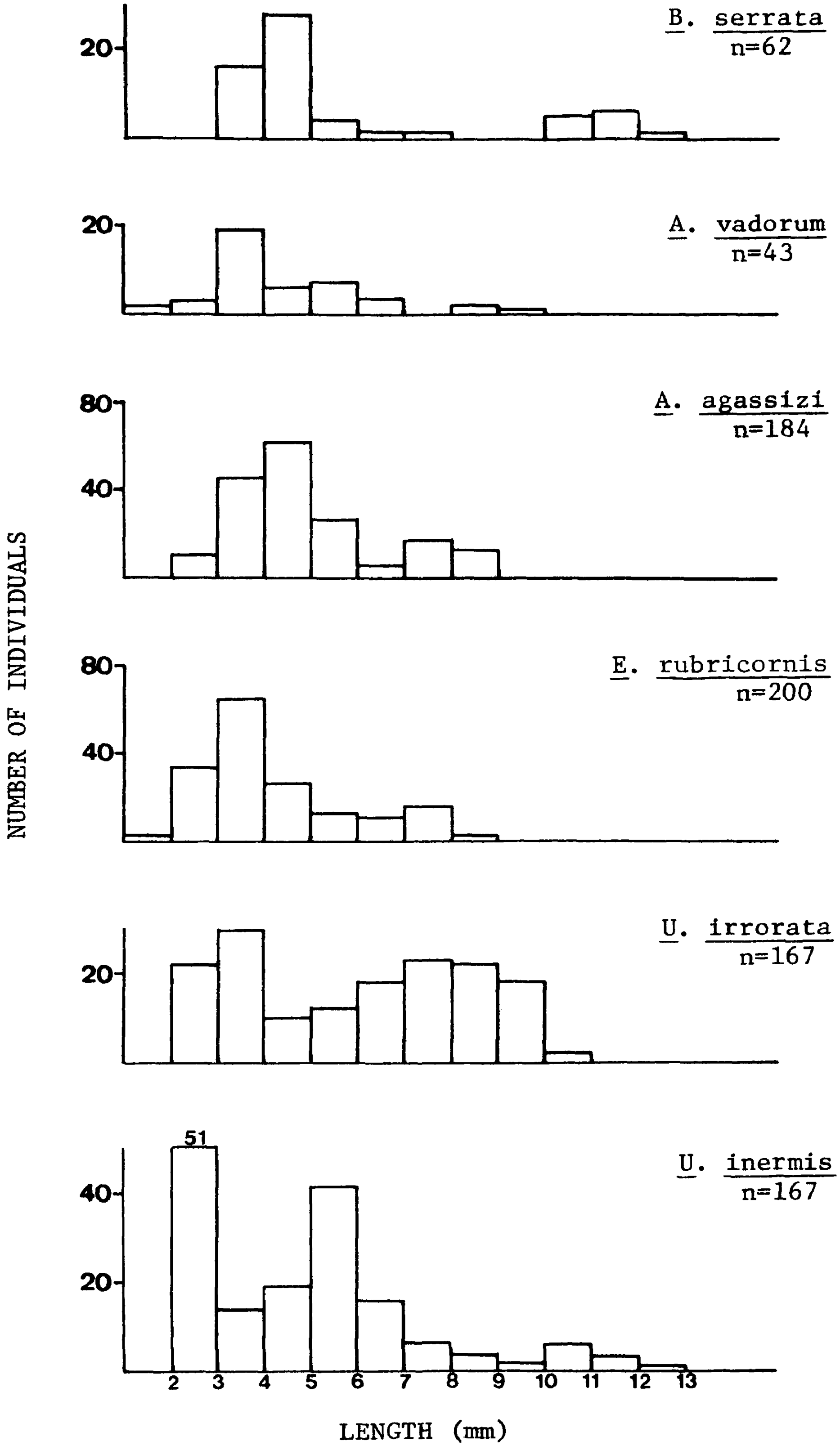

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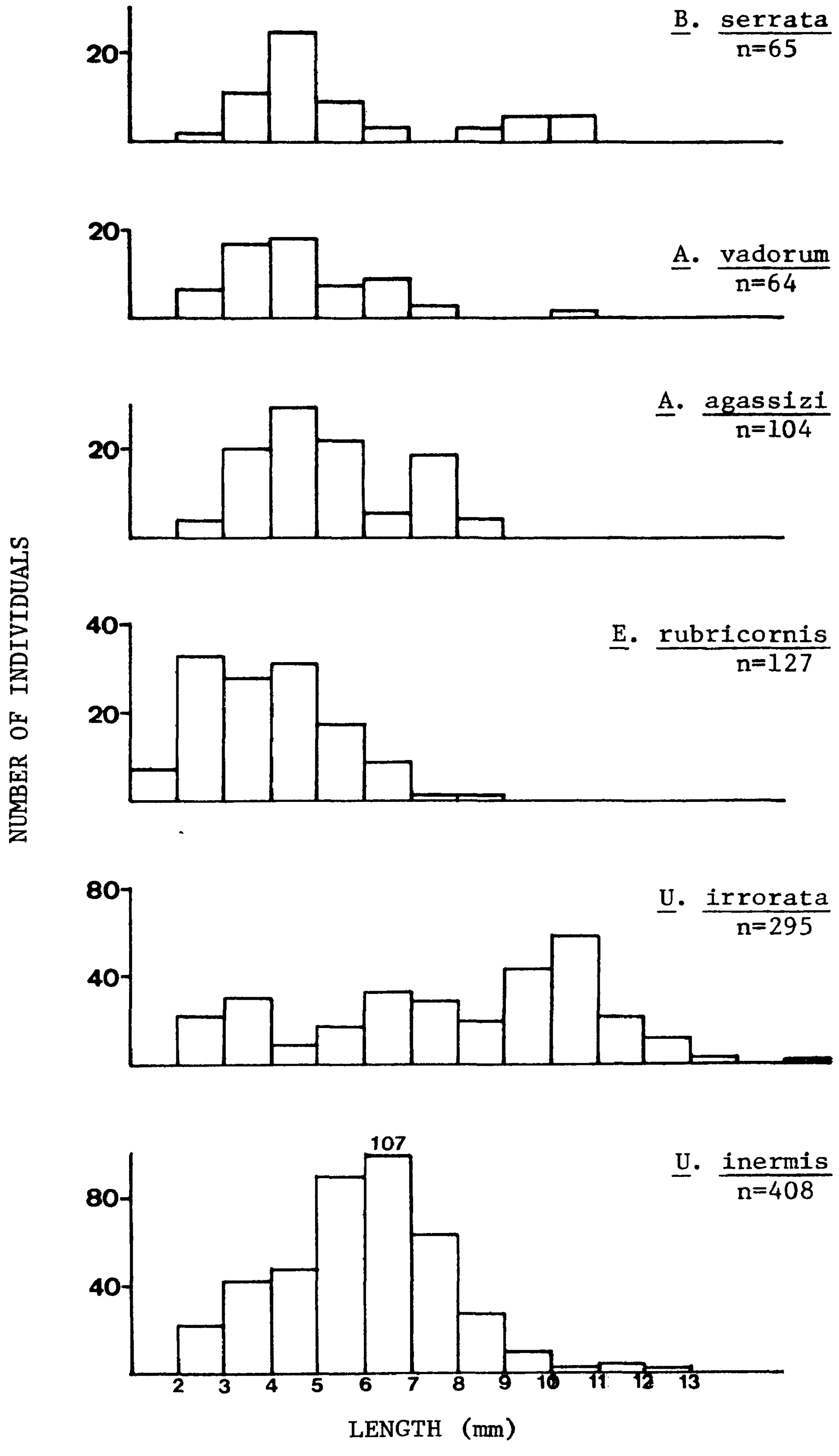

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