

CAN PELAGIC AGGREGATIONS CAUSE BENTHIC SATIATION?
FEEDING BIOLOGY OF THE ANTARCTIC BRITTLE STAR ASTROTOMA AGASSIZII
(ECHINODERMATA: OPHIUROIDEA)

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Abstract. Information on the diet, feeding behavior, and surface morphology was obtained for Astrotoma agassizii, a large, simple-armed member of the suborder Euryalina found on the Antarctic shelf. Material was collected at South Georgia and along the Antarctic Peninsula between 1975 and 1983. Extremely long, flexible arms which can be produced into sinuous forms and tight coils, together with a combination of girdle hooklets, hooked and paddle-shaped arm spines, and long podia are employed to capture prey from the water column. Frequency-of-occurrence and points methods were used to examine the stomach contents of 115 specimens of Astrotoma agassizii, of which 78 (67.8%) contained food. Mean number of food types per feeding animal was 1.7, and mean fullness value was 1.8, on a scale of 16. The diet consisted of members of only two major taxa, Crustacea and Chaetognatha. Copepods occurred in 75.6% of brittle stars containing food and were the dominant prey group, followed by mysids (34.6%), chaetognaths (10.2%), and euphausiids (8.9%). Other prey included unidentified crustacean and organic remains, ostracodes, and amphipods. All copepods in the stomachs of Astrotoma were calanoids belonging to 12 species generally considered pelagic animals. Euchaeta antarctica and Calanoides acutus constituted about 80% of the stomach content copepods. This association of an herbivorous calanid and predatory euchaetid may result from the well-known seasonal migrations of Calanoides. Upon completing their epipelagic season, aggregations of lipid-rich, late-stage copepodids of C. acutus might be expected to attract larger pelagic predators, including the euchaetid. In shoal waters this association of downward migrating herbivores and their predators may bring these calanoids in close proximity to the substrate, thereby providing a rich, seasonally predictable food

source to the brittle stars. These interactions suggest that carbon fixed in surface waters may be transferred to the benthos within a year. In addition, frequent reports of E. antarctica to 1000 m suggest similar carbon transfer to mesopelagic depths. The extent to which this influx of epipelagic carbon affects the predatory brittle star and euchaetid and influences benthic and mesopelagic biology remains to be determined.

Introduction

Increasing uses of automatic underwater cameras, remote operating vehicles and manned submersibles, and ever deeper scuba activities are providing new opportunities for studies of the behavior of subtidal benthic invertebrates [e.g., Pawson, 1982]. Among the ecological relationships which can now be more effectively studied is the extent to which some benthic invertebrates obtain food from the water rather than through various benthic processes.

The food and feeding mechanisms of brittle stars (Echinodermata: Ophiuroidea) in particular have received recent attention (reviewed by Warner [1982]). Brittle stars exhibit diverse food capture adaptations. The structural and functional morphology of members of the suborder Euryalina is especially intriguing [Hendler and Miller, 1984]. Some genera (e.g., Asteropora, Astrochlamys) have five very long unbranched arms. Other genera show varying degrees of arm branching. In Astrocnida and Conocladus, for example, the arms are branched only a few times, while in the most complex Euryalina, the true basket stars (Gorgonocephalus and Astrophyton), the arms branch many times, resulting in a complex assemblage of "twigs." The feeding branches of these many-divided arms are raised in a fanlike posture and oriented into the current to pro-

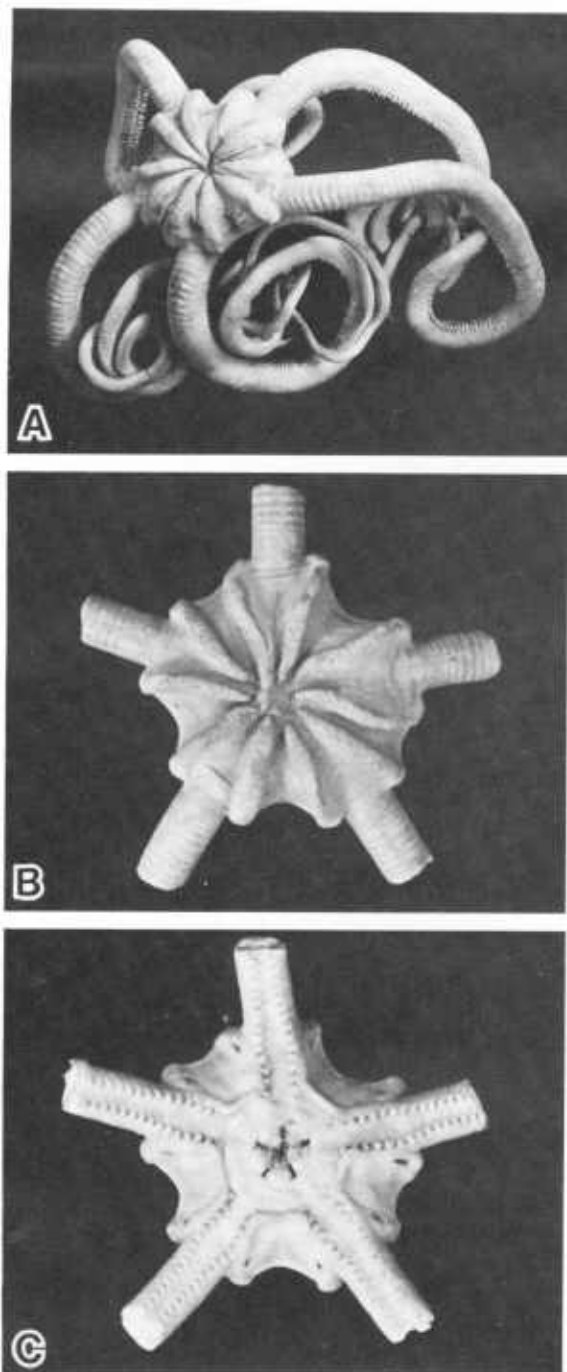


Fig. 1. *Astrotoma agassizii*; dried specimens. (A) Entire, DD = 43 mm. (B) Aboral disc surface, DD = 56 mm. (C) Oral disc surface, same specimen as that shown in Figure 1B.

duce an effective trap for zooplankton [Davis, 1966; Hendler, 1982]. Most reports on the behavior of Euryalina have involved these complexly branched basket stars [Davis, 1966; Fricke, 1966, 1968; Tsumamal and Marder,

1966; Patent, 1970; Macurda, 1976; Meyer and Lane, 1976; Wolfe, 1978; Hendler, 1982; LaBarbera, 1982; for general review see Warner, 1982]. These papers deal primarily with *Gorgonocephalus*, *Astrophyton*, or *Astroboa*.

The diets and feeding behavior of Euryalina with unbranched arms have received much less attention. The most informative paper to date is the account by Hendler and Miller [1984] on *Asteropora annulata* (Gorgonocephalidae). They report observations made in situ from the submersible Johnson-Sea-Link I on a population off central Florida in depths of 56-85 m. The brittle stars were found perching on clumps of *Oculina varicosa*, a scleractinian coral. The majority of individuals assumed suspension feeding postures only at night. Their diet consisted primarily of pelagic organisms, mostly copepods.

Astrotoma agassizii (Figures 1 and 2) is the largest Antarctic member of the Gorgonocephalidae with five unbranched arms. In large specimens, with a disc diameter of 50-60 mm, the arms may reach 600-700 mm in length. The arms of such an individual would typically have a basal diameter of about 12 mm and taper gradually to about 1 mm at the tip. Generally, one or two arms are used to cling to the substrate, with the remainder extended to feed (Figure 2). This species is irregular in occurrence on the Antarctic shelf, although it may be locally abundant where conditions are favorable. Information on the feeding biology of *A. agassizii* has been summarized by Dearborn [1977]. He reviewed comments by Mortensen [1936] and Fell [1961] on the planktonic nature of the food of *Astrotoma*, suggested by presence of copepods and hyperiid amphipods in stomachs, and on the basis of bottom photographs presented some new information on the extremely flexible arms and various feeding postures of this species.

We report here on the diet, feeding behavior, and morphology of 115 specimens of *A. agassizii* taken at South Georgia and along the Antarctic Peninsula between 1975 and 1983. We suggest that the dominance of pelagic calanoid copepods in stomachs of *A. agassizii* in austral autumn is correlated with seasonally episodic behavior of the prey. Further, since some prey copepods are pelagic herbivores, we infer that carbon transferred directly to the brittle star has been fixed in the water and not simply recycled by benthic copepods. Predator-prey interactions, the large body size of *Astrotoma*, and its local abundance on the Antarctic shelf make it an important macroinvertebrate for further investigation.

Materials and Methods

Sample Collection

A total of 115 specimens of *A. agassizii* were obtained by trawl from eight stations around South Georgia and along the Antarctic

Peninsula in 1975 and 1983 (Table 1). Samples were collected at five sites off South Georgia in May and June 1975 during ARA Islas Orcadas cruise 0575 [DeWitt et al., 1976]. Depths of capture ranged from 121 to 265 m. Both 1.5-m and 3-m beam trawls were used. In March and April 1983, additional specimens were taken at two sites along the Antarctic Peninsula during R/V Hero cruise 83-3 [Dearborn et al., 1984]. The southernmost location, in the Lemaire Channel between Booth Island and the Danco Coast, was sampled twice with two types of gear. Initial collections were made with a 1.5-m beam trawl. A 3-m otter trawl was used at a second station in the same general location. The otter trawl was more successful than the beam trawl in obtaining specimens of *Astrotoma agassizii*, but the extremely rough bottom of the Lemaire Channel severely damaged the net. At Hope Bay at the eastern end of the Trinity Peninsula, the second Antarctic Peninsula site, all trawling was done with a 1.5-m beam trawl. Hauls of short duration were used to minimize damage to specimens and contamination of stomach contents. The latter was unlikely, however, because *Astrotoma* has a relatively small mouth which does not gape in the same manner as it does in some noneuryalid brittle stars.

Stomach Analysis

Immediately upon capture the arms were removed from specimens of *Astrotoma agassizii* retained for stomach analyses, and the discs were fixed in 70% ethanol. Large discs were injected with ethanol to ensure proper preservation of contents. No regurgitation of stomach contents was evident upon contact with the fixative or during injection. Some live specimens were retained in circulating seawater at ambient temperature in shipboard holding tanks for behavioral observations in laboratory aquaria at Palmer station.

Prior to dissection the disc diameter (DD) and width of arm base (AB) were measured to the nearest 0.1 mm. Animals were dissected by cutting around the disc perimeter and folding back the aboral surface to expose the stomach lining. Stomach contents were examined with a Wild M5 dissecting microscope, and the types of food and relative abundance of each were recorded. Photomicrographs were taken of representative stomachs. After initial examination, all food items were removed and identified to the lowest possible taxonomic level. Copepods were identified by the second author (F.D.F.) and remaining prey by the other authors (K.C.E. and J.H.D.).

Diets of *A. agassizii* were described by three methods, one giving the frequency of occurrence of food items and the other two, both points methods, giving different volumetric contributions of food items. All animals were analyzed by the first procedure. Presence or absence of food was noted to determine

the number of specimens feeding. Frequency of occurrence of individual food items was then expressed as a percentage of feeding animals. The first points method of analysis followed the general methods of Brun [1972] and Fratt and Dearborn [1984]. In this method, upon initial dissection, the stomach was assigned an estimated overall fullness value of 0 (empty), 1 (trace), 2, 4, 8 (one-half full), 12, or 16 (maximum fullness). Food items, if any, in the gut were then catalogued and assigned a point value from the same scale according to their estimated volume contribution to the food bolus (see Fratt and Dearborn [1984] for details). Results were expressed as the proportion of total points awarded to a particular food item compared to the total points assigned to all food items.

The third method of analysis was a modification of the first points method by which we attempted to mitigate the inflationary effect of stomachs containing only a trace of a single food item on the totals for that food item. Under Brun's [1972] and Fratt and Dearborn's [1984] unmodified points methods a gut with a trace of a single item and a gut filled with the same item would both have contributed 16 points to the total for that prey species because these earlier methods did not include the overall fullness index in calculating the point totals for each food item and thus did not take into account the absolute amount of each item present. Our modification involved multiplying the point value assigned to each food item by the fullness index. For example, if ophiuroid A had a nearly empty gut, with only a trace of sediment present, it would have been assigned a fullness index of 1 and 16 points for sediment (having been the only item present). In the final summation, earlier methods would have assigned this animal 16 points for sediment, as would our new modification. If, on the other hand, ophiuroid B had a gut that was packed absolutely full of copepods (fullness index of 16 and a point value for copepods of 16 because copepods were the only food item present), the two methods would have given very different results. Upon summing, earlier methods would have assigned a total of 16 points to copepods, whereas our modification assigned 256 (16 x 16) points to copepods. The earlier methods would have set equal values for sediment and copepods in the above examples. By comparison, our modified points method considered both the total volume of the food bolus and the relative volume of the particular prey items. This provided a more realistic evaluation of the relative importance of the individual food items in the diet of the sample population.

A portion of the specimens from station 90 were inadvertently processed by the percent frequency-of-occurrence analysis only. We later designated material from that location as coming from station 90 (all three diet analyses completed) or station 90a (analysis

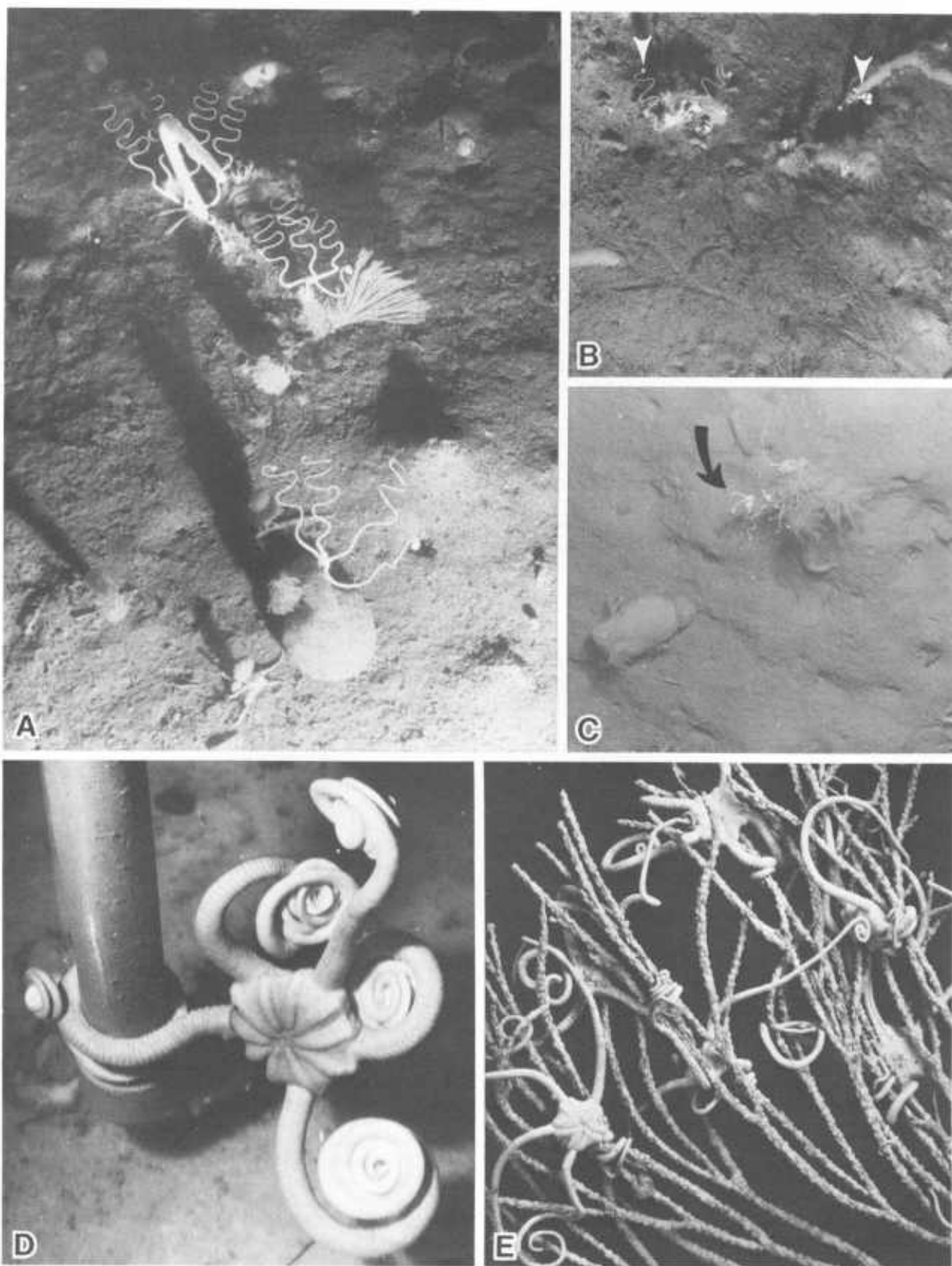


TABLE 1. Summary of Sampling Stations at Which *Astrotoma agassizii* Were Obtained

Station	Date	Latitude, S	Longitude, W	General Locality	Depth, m	Number of Specimens Taken
<u>Cruise IS0575</u>						
11	May 12, 1975	53°38.0'	38°01.8'	South Georgia	132-143	12
12	May 12, 1975	53°38.2'	37°54.7'	South Georgia	130-137	28
83	June 6, 1975	55°08.8'	35°45.4'	South Georgia	121-139	2
89	June 7, 1975	54°44.2'	37°11.2'	South Georgia	225-265	4
90*	June 7, 1975	54°50.6'	37°23.8'	South Georgia	223-227	13
90a*	June 7, 1975	54°50.6'	37°23.8'	South Georgia	223-227	15
<u>Cruise HE83-3</u>						
8-2	March 10, 1983	65°03.7'	63°57.0'	Antarctic Peninsula (Lemaire Channel)	360-375	7
15-2	March 21, 1983	65°03.7'	63°57.0'	Antarctic Peninsula (Lemaire Channel)	320-400	32
20-4	April 2, 1983	63°23.2'	57°01.1'	Antarctic Peninsula (Hope Bay)	164-190	2

*Same station, but different treatment of specimens (see text).

of percent frequency of occurrence only) in Tables 1-3 and elsewhere in the text.

Identification of Copepods

Preservation status of copepods varied. A number were in good condition--the exoskeleton was complete and unbroken, and the musculature and internal organs appeared whole. Most specimens showed degrees of degradation of internal tissue, with the exoskeleton intact or sometimes broken. Breakages generally involved partial detachment of the ventral sclerites and head appendages or of the head and swimming appendages. Occasionally, ventral sclerites plus appendages were separated. Usually, a complete urosome was attached to a complete prosome or to detached, ventral, prosome sclerites. Rarely, one or both caudal rami were lost.

The ontogeny of free-swimming copepods generally includes five postnaupliar copepodid stages (CI-CV) prior to the terminal adult

molt. Stage VI copepodid (CVI) specimens (adults) were identified if the swimming legs and urosome were intact. Assignment of earlier copepodids, except those of *Calanoides acutus* [see Andrews, 1966], to a species was based on smaller body size (e.g. see Farran, [1929], for *Calanus propinquus*) and reduced number of body segments or appendage elements. Most immature copepodids were identified with species whose adults were found among the stomach contents. In rare instances (e.g., *Euchirella rostrata*), if distinctive enough, they were assigned a specific name on the basis of the reported presence of the species in the area. This method, while conservative and thereby underestimating species diversity, seems a reasonable solution to lack of ontogenetic data for most of these calanoids.

All euchaetids are referred to the genus *Euchaeta*, as proposed by Vervoort [1957] and Park [1978]. Species of *Gaidius* are referred to *Gaetanus* following Park [1975].

Fig. 2. *Astrotoma agassizii*. (A) Three large specimens in feeding posture with arms held in sinuous positions and with some tight terminal coiling. Enlargement of portion of frame 8, camera sta. 23, *Eltanin* cruise 32; 76°26'S, 170°20'W; ~ 550 m; January 29, 1968. Courtesy Smithsonian Oceanographic Sorting Center (SOSC). (B) Two specimens (white arrows), in feeding postures, clinging to small sponges. Arms of individual on right in very tight coils. Portion of frame 5, camera sta. 14, *Eltanin* cruise 32; 77°03'S, 178°08'W; ~ 585 m; January 21, 1968. Courtesy SOSC. (C) Individuals, in feeding postures, associated with sponges and several specimens of comatulid crinoids. Portion of frame 5, camera sta. 9, *Eltanin* cruise 27; 75°25.4'S, 168°52'E; 342 m; January 17, 1967. Courtesy SOSC. (D) Adult specimen clinging by one arm to the inlet pipe in a seawater tank at Palmer station; remaining arms in tight coils. (E) Juveniles clinging to a gorgonian; preserved material from sta. 90, South Georgia (see Table 1). Note the tendency even among juveniles to climb to the highest available level.

TABLE 2. Summary Statistics From Stomach Analyses of 115 *Astrotoma agassizii*

Variable	ARA Islas Orcadas (South Georgia) Stations, 1975										RV Hero (Antarctic Peninsula) Stations, 1983			
	Total	11	12	83	89	90	90a	8-2	15-2	20-4				
Number examined	115	12	28	2	4	13	15	7	32	2				
Size range (disc diameter), mm	6.9-62.4	18.8-48.8	6.9-38.9	26.2-43.0	49.3-55.9	9.2-56.0	47.0-61.9	25.0-62.4	11.7-61.1	28.8-47.3				
Mean size, mm	34.9	39.5	14.0	34.6	52.9	29.9	55.1	51.3	37.9	38.1				
Percentage of feeding animals	67.8	66.7	46.4	50.0	100	38.5	93.3	85.7	81.3	50.0				
Percentage of feeding animals containing more than one food	55.5	25.0	8.0	0.0	100	0.0	57.1	66.7	76.9	100				
Mean number of foods per feeding animal	1.7	1.3	1.2	1.0	2.5	1.0	1.6	2.0	2.0	2.0				
Mean fullness (points method only)	1.8	1.7	1.5	0.5	8.0	0.9	F0	1.6	2.0	1.0				

F0, analyzed for frequency of occurrence only.

Scanning Electron Microscopy

Specimens of *A. agassizii* destined for scanning electron microscopy (SEM) were dissected immediately after capture, and duplicate samples were placed in two fixative solutions. The first consisted of a 4% formalin, 1% glutaraldehyde mixture in 0.1 M phosphate buffer [McDowell, 1978], chosen for its suitability for long-term storage of specimens. Because of occasional precipitation problems with the phosphate buffer a seawater-based fixative [Holland and Jespersen, 1973] was used, in which 4% formalin and 1% glutaraldehyde were mixed in 77% seawater. To date, the seawater fixative has proven as suitable for long-term storage as the phosphate-buffered formulation. Fixed specimens were refrigerated until preparation for examination at the University of Maine.

Because of the delicate nature of most echinoderms and the tendency of the epidermis to crack and tear with the occurrence of any shrinkage during tissue processing, the method of Wollweber et al. [1981] was utilized. This technique hardens tissues against shrinkage by post fixing in 1% osmium tetroxide, followed by incubations in 1% tannic acid and 0.5% uranyl acetate, with thorough washings between each step.

After hardening, samples were dehydrated in an ethanol series in which dilutions of 80%, 85%, and 90% were substituted for the more usual 95% step. Boyde et al. [1977] found that the greatest shrinkage rate during ethanol dehydration occurred between the 80% and 90% dilutions and that little shrinkage occurred between the 90% dilution and 100%. After dehydration, specimens were critical point dried from CO₂ and mounted on specimen stubs by using double-sided tape or silver paste. Obvious specimen damage due to shrinkage seemed to be nearly eliminated by this procedure.

Examples of bare ossicles were prepared by digesting away the tissue of dried specimens with liquid household bleach (sodium hypochlorite). Ossicles were then washed thoroughly with distilled water and mounted on specimen stubs by using double-sided tape. All specimens were sputter coated with 400 Å of gold and examined with an AMR 1000A scanning electron microscope.

Results and Discussion

Food Habits and Feeding Behavior

A total of 115 specimens of *Astrotoma agassizii* were examined for stomach contents, and 78 (67.8%) of these contained food (Table 2). The mean DD of all specimens was 34.9 mm (Table 2). The mean number of food types per feeding animal was 1.7, and the mean fullness value was 1.8, for the 100 individuals analyzed by the points methods.

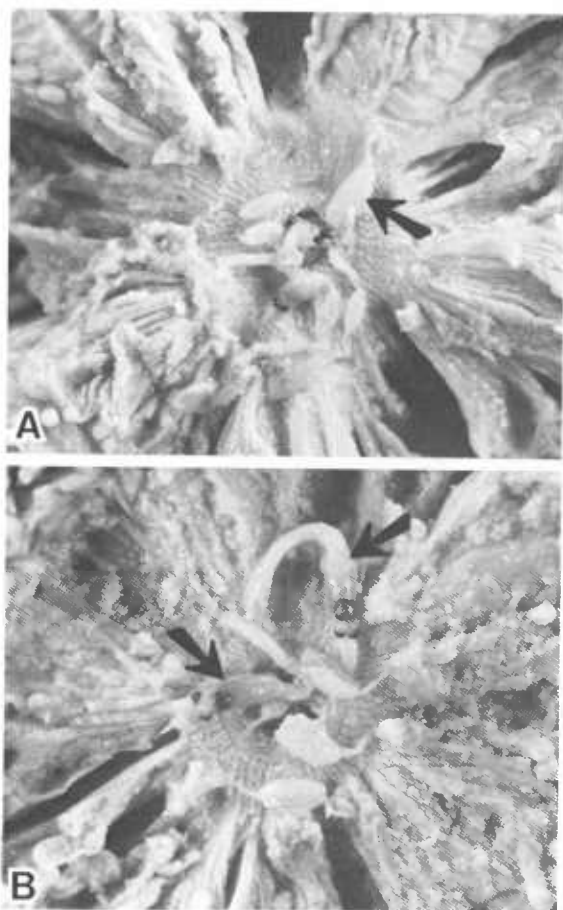


Fig. 3. Dissected specimens, oral view of stomach, aboral surface of disc removed. (A) Several copepods (arrow) in gut; note excellent condition of prey. (B) Juvenile *Euphausia superba* (arrows) and copepods in gut. Condition of prey suggests recent ingestion.

The diet of *A. agassizii* included members of only two major taxa, Crustacea and Chaetognatha (Table 3). Food items were separated into eight categories for further analysis. Occurrences and frequency and volume percentage results for these categories are listed in Table 3. Copepods dominated the diet of *A. agassizii* at both the South Georgia and the Antarctic Peninsula locations (Table 3).

Copepods as prey. With one exception each, no benthic amphipods and no benthic ostracodes were found in stomachs of *A. agassizii*. Demersal mysids were the only substrate-oriented crustaceans collected (we assume that juvenile euphausiids are primarily pelagic animals). Among copepods we found no harpacticoid or calanoid with known substrate affinities, either living in or on substrates or directly above them; no free-swimming cyclopoids or poecilostomatoids, particularly the smaller but abundant *Oithona* or *Oncaea*; no small

free-swimming calanoids, e.g., *Ctenocalanus*, *Clausocalanus*, *Stephos*, or *Microcalanus*; with one exception, no early (and small) developmental stages (CI-CIII) of the larger pelagic calanoids captured.

Copepod specimens were recovered from stomachs of 59 individual *A. agassizii*, which represented 51.3% of all *A. agassizii* captured and 75.6% of brittle stars containing food (Table 3, Figure 3). Previously, Mortensen [1936] reported unidentified copepods from specimens of *A. agassizii* taken by the *Discovery* expedition. We found 448 copepods in the brittle star stomachs; 442 were identified to species, stage, and often sex (Table 4). All specimens are calanoids usually considered inhabitants of pelagic waters. Two *Drepanopus*, two calanids, and a *Rhincalanus*, all missing urosomes, plus a small CIII *Euchaeta*, were not considered in further analyses.

We considered copepods and brittle stars synoptically collected from contiguous areas and sampling times as listed in Tables 6-9 and 11-13. However, we discuss copepod prey in the context of two general areas: South Georgia in May-June 1975 (Table 5, being a summary of Tables 6-9) and the Antarctic Peninsula in March-April 1983 (Table 10, being a summary of Tables 11-13).

Euchaeta antarctica was the most abundant copepod taken by *Astrotoma*, (Table 4); it is a large, predatory copepod (CVI females reported to 10.00 mm), generally considered an inhabitant of oceanic intermediate waters south of the Antarctic Convergence [Farran, 1929; Verwoort, 1965; Yamanaka, 1976]. Hopkins [1985] noted that *E. antarctica*, collected from Croker Passage in the Antarctic Peninsula in March and April 1983, has a broad vertical distribution (0-1000 m); he suggests that this calanoid may undergo diel vertical migration toward the surface at night. Early and recent observations indicate that *E. antarctica* may be collected in shallow waters, under ice [Farran, 1929; Bradford, 1981], or in fjords around South Georgia (P. Ward, personal communication, 1985); little is known of its life history.

A total of 238 specimens of *Euchaeta antarctica* were found in stomachs of 39 *A. agassizii*. More adults were taken around South Georgia in May-June 1975 (adult/immature ratio is $113/85 = 1.33$) than along the Antarctic Peninsula in March-April 1983 ($1/39 = 0.03$) (Tables 5 and 10). The percentage of males for both CVI and CV also varied (around South Georgia, CVI ratio is $33/113 = 29\%$, and CV ratio is $30/82 = 37\%$; along the Antarctic Peninsula, CVI ratio is $0/1 = 0\%$, and CV ratio is $24/36 = 67\%$).

These ratios can be compared to net-collected *E. antarctica* from various seasons. Zvereva [1972] reported adult females and males in August and September at Molodezhnaya, but only CV males during October and November. In the Mirnyy area, immature

TABLE 4. Number of Individuals in Various Life History Stages From a Total of 442 Copepods Taken From Stomachs of 52 *Astrotoma agassizii*, All Locations

Species	Developmental Stage								Totals
	VI		V		IV		V	IV	
	F	M	F	M	F	M	Unsexed	Unsexed	
<i>Euchaeta antarctica</i>	81	33	64	54	3	3	238
<i>Calanoides acutus</i>	17	5	99	1	122
<i>Drepanopus forcipatus</i>	7	5	13	9	1	35
<i>Calanus propinquus</i>	1	2	11	1	15
<i>Calanus simillimus</i>	3	0	10	0	13
<i>Pleuromamma robusta</i>	4	3	0	0	0	0	7
<i>Metridia gerlachei</i>	3	0	0	0	0	0	3
<i>Euchaeta biloba</i>	1	0	0	0	0	0	1
<i>Euchirella rostromagna</i>	0	0	0	1	0	0	1
<i>Gaetanus tenuispinis</i>	1	0	1	0	0	0	2
<i>Gaetanus intermedius</i>	0	1	0	1	0	0	2
<i>Rhincalanus gigas</i>	1	0	0	1	0	1	3

Three dots indicate not applicable.

females and males were found in January and February, CV males in July, and CVI females and males in September. Collections for these animals were made in less than 100 m. Bradford [1981] reported on sample sizes of *E. antarctica* similar to ours collected with plankton nets under ice of the Ross Sea in 1977. On June 27, CVI males comprised 18/49 = 37% of adult animals, while on August 10 the value decreased slightly to 22/69 = 32%.

The only seasonal study of similar ratios for a euchaetid was compiled by Hopkins [1982] for *E. norvegica* in Loch Etive, Scotland. We

have inferred the reproductive condition of *E. antarctica* by comparison to those ratios. From samples of at least 500 individuals, Hopkins found that the percentage of CVI males increased from September 1971 toward a major peak in March 1972 (31.38% in northern spring), then decreased, and then redeveloped a minor peak in early July (15.10% in northern summer). The percentage of CV males showed a reverse trend, comprising almost all CV specimens in September 1971, with a precipitous drop beginning January 1972. The nadir was reached in March (about 25% from his Figure

TABLE 5. Number of Individuals in Various Life History Stages From a Total of 355 Copepods Taken From Stomachs of 32 *Astrotoma agassizii* Collected Off South Georgia, May-June 1975

Species	Developmental Stage								Totals
	VI		V		IV		V	IV	
	F	M	F	M	F	M	Unsexed	Unsexed	
<i>Euchaeta antarctica</i>	80	33	52	30	1	2	198
<i>Calanoides acutus</i>	1	5	74	1	81
<i>Drepanopus forcipatus</i>	7	5	13	9	1	35
<i>Calanus propinquus</i>	1	2	10	1	14
<i>Calanus simillimus</i>	3	0	10	0	13
<i>Pleuromamma robusta</i>	4	3	0	0	0	0	7
<i>Euchaeta biloba</i>	1	0	0	0	0	0	1
<i>Euchirella rostromagna</i>	0	0	0	1	0	0	1
<i>Gaetanus tenuispinis</i>	1	0	1	0	0	0	2
<i>Rhincalanus gigas</i>	1	0	0	1	0	1	3

Three dots indicate not applicable.

TABLE 6. Number of Individuals in Various Life History Stages From a Total of 13 Copepods Taken From Stomachs of 9 Astrotoma agassizii From Stations 11 and 12, South Georgia, May 1975

Species	Developmental Stage								
	VI		V		IV		V	IV	Totals
	F	M	F	M	F	M	Unsexed	Unsexed	
<u>Euchaeta antarctica</u>	0	0	0	0	0	1	1
<u>Calanoides acutus</u>	0	0	6	0	6
<u>Drepanopus forcipatus</u>	0	0	2	1	0	3
<u>Calanus propinquus</u>	0	0	0	1	1
<u>Calanus simillimus</u>	1	0	0	0	1
<u>Rhincalanus gigas</u>	0	0	0	0	0	1	1

Three dots indicate not applicable.

1), followed by a slower, uneven rise ending in August. Hopkins noted a close correlation between the percentage of CVI males and the proportion of CVI females with spermatophores; he chose the latter as a measure of mating intensity.

The percentage of males (29%) for CVI E. antarctica taken by A. agassizii collected in June (onset of southern winter) approaches the peak value for E. norvegica in March (31.38%). The corresponding value for CV (37%) is comparable to E. norvegica (about 25%) at the CVI male peak. The percentage of CV males of 67% along the Antarctic Peninsula in March/April (early southern fall) may correspond to values for E. norvegica either in late northern winter or in early northern summer. On the basis of Hopkins' [1982] correlation between the percentage of CVI males and the proportion of CVI females with spermatophores, our data suggest that significant mating activity by E. antarctica may have occurred prior to capture by the brittle stars.

Despite the possibility of mechanical dist-

urbance during capture and ingestion, nine CVI females from the South Georgia area had one spermatophore attached to the genital segment. In seven cases the single spermatophore was placed on or near one of two symmetrically situated small ridges anterior to the genital prominence; two of these females were the only ones found with egg sacs. An asymmetrical ridge is found on females of E. norvegica and marks a similar alternate site for 60% of all attached spermatophores [Ferrari, 1978]. The percentage of females with spermatophores (11%) collected by Astrotoma is lower than the value reported by Bradford [1981] (26%) on June 27 but similar to her value of 13% on August 10, 1977. All values for Euchaeta antarctica are much lower than the lowest one for E. norvegica [Hopkins, 1982] recorded during May (about 33% from his Figure 2A).

Calanoides acutus is another oceanic copepod usually found south of the Antarctic Convergence. This crested calanid was the second most abundant copepod, taken by 27 brittle stars. A total of 122 specimens were identified (Table 4), with 81% CV; one CIV was

TABLE 7. Number of Individuals in Various Life History Stages From a Total of 4 Copepods Taken From the Stomach of Specimens of Astrotoma agassizii From Station 83, South Georgia, June 6, 1975

Species	Developmental Stage								Totals
	VI		V		IV		V	IV	
	F	M	F	M	F	M	Unsexed	Unsexed	
<u>Euchaeta antarctica</u>	0	0	0	0	0	1	1
<u>Drepanopus forcipatus</u>	1	1	0	1	0	3

Three dots indicate not applicable.

TABLE 8. Number of Individuals in Various Life History Stages From a Total of 91 Copepods Taken From Stomachs of 4 Astrotoma agassizii From Station 89, South Georgia, June 7, 1975

Species	Developmental Stage								Totals
	VI		V		IV		V	IV	
	F	M	F	M	F	M	Unsexed	Unsexed	
<u>Euchaeta antarctica</u>	48	9	17	10	0	0	84
<u>Calanoides acutus</u>	1	0	5	0	6
<u>Calanus similimus</u>	0	0	1	0	1

Three dots indicate not applicable.

found. Andrews [1966] reported extensively on the biology of C. acutus. During the two periods that brittle stars collected this calanid, late March to early April and May to early June, Andrews found C. acutus undergoing a seasonal migration from oceanic surface waters (0-250 m) to below 500 m; this migration is complete by July. In addition, ontogenetic development was proceeding from CIII to CIV and CV during the migration. Calanoides acutus spends the southern winter months of July, August, and September primarily as CIV and CV below 500 m.

Andrews found that CIII through CVI comprised 18%, 34%, 40%, and 5% of the population in March to early April. During the same months in 1983, Hopkins [1985] describes the

capture of only late stages throughout the upper 1000 m in Croker Passage. Samples taken by the brittle stars during the same period along the Antarctic Peninsula (Tables 10-12) include only CV and CVI, the latter being 16/41 = 39% of the population. In May and June, Andrews found mostly CIV and CV, comprising 33-45% and 62-54%, respectively, with CVI less than 2%. In the same months off South Georgia (Tables 5-6, 8-9) the brittle stars again found only CV and CVI, the latter being 6/74 = 8%. Most noteworthy, five of six adults were males.

There are very few reports of C. acutus males. Although Andrews noted the presence of CVI males, he did not mention how many were collected or when. Ottestad [1932] examined

TABLE 9. Number of Individuals in Various Life History Stages From a Total of 247 Copepods Taken From Stomachs of 18 Astrotoma agassizii From Stations 90-90a, South Georgia, June 7, 1975

Species	Developmental Stage								Totals
	VI		V		IV		V	IV	
	F	M	F	M	F	M	Unsexed	Unsexed	
<u>Euchaeta antarctica</u>	32	24	35	20	1	0	112
<u>Calanoides acutus</u>	0	5	63	1	69
<u>Drepanopus forcipatus</u>	6	4	11	7	1	29
<u>Calanus propinquus</u>	1	2	10	0	13
<u>Calanus similimus</u>	2	0	9	0	11
<u>Pleuromamma robusta</u>	4	3	0	0	0	0	7
<u>Euchaeta biloba</u>	1	0	0	0	0	0	1
<u>Euchirella rostromagna</u>	0	0	0	1	0	0	1
<u>Gaetanus tenuispinis</u>	1	0	1	0	0	0	2
<u>Rhincalanus gigas</u>	1	0	0	1	0	0	2

Three dots indicate not applicable.

TABLE 10. Number of Individuals in Various Life History Stages From a Total of 87 Copepods Taken From Stomachs of 20 Astrotoma agassizii From Three Stations Along the Antarctic Peninsula, March-April 1983

Species	Developmental Stage								
	VI		V		IV		V	IV	Totals
	F	M	F	M	F	M	Unsexed	Unsexed	
<u>Euchaeta antarctica</u>	1	0	12	24	2	1	40
<u>Calanoides acutus</u>	16	0	25	0	41
<u>Calanus propinquus</u>	0	0	1	0	1
<u>Metridia gerlachei</u>	3	0	0	0	0	0	3
<u>Gaetanus intermedius</u>	0	1	0	1	0	0	2

Three dots indicate not applicable.

samples from 0 to 450 m in the Weddell Sea taken between October 27, 1929, and February 17, 1930. Large numbers of C. acutus (reported as Calanus acutus) were collected in November and December; almost 50% were CVI, none of which were males. Vervoort [1951] initially described detailed male morphology from a single specimen. Zvereva [1972, Table 3] reported males in September at Molodezhnaya and in February and September at Mirnyy; no numbers were presented. Kaczmaruk [1983] examined samples collected from the upper 50 m along the ice edge of the Weddell Sea during January and February 1980; most C. acutus were CIV and CV; no CVI males were found.

Drepanopus comprises four boreal/polar species of clausocalanids inhabiting coastal or nearshore waters [Bayly, 1982]. The distribution of D. forcipatus is restricted to southern South America from 45°S [Lee, 1966] and Atlantic sector islands. Previous reports from South Georgia include Cumberland West Bay [Pesta, 1930] and numerous points around the

island [Hardy and Gunther, 1935]. Thirty-five specimens were taken by brittle stars collected only around South Georgia (Tables 5-7, 9). Thirty-four percent were CVI (5/12 = 42% males) and 65% were CV (9/22 = 41% males); one CIV was identified, but its sex could not be determined. A single CVI female carried a spermatophore placed directly over the genital opening.

Two round-headed calanids of the genus Calanus were taken by Astrotoma. Calanus propinquus and C. similis differ in size and general distribution [Farran, 1929; Ottestad, 1932; Vervoort, 1951, 1965; Tanaka, 1964; Bradford, 1971]. Calanus propinquus (with CVI females to 5.5 mm) is generally restricted to waters south of the Antarctic Convergence, while C. similis (CVI females to 3.5 mm) has a Subantarctic distribution. Occasionally, both have been reported from the same plankton samples. Brittle stars took 15 specimens of the larger species and 13 of the smaller, the latter only from South Georgia (Tables 5-6, 8-9); most were CV. The percent-

TABLE 11. Number of Individuals in Various Life History Stages From a Total of 11 Copepods Taken From Stomachs of 5 Astrotoma agassizii From Station 8-2, Lemaire Channel, March 10, 1983

Species	Developmental Stage								
	VI		V		IV		V	IV	Totals
	F	M	F	M	F	M	Unsexed	Unsexed	
<u>Euchaeta antarctica</u>	0	0	3	4	1	0	8
<u>Calanoides acutus</u>	1	0	0	0	1
<u>Metridia gerlachei</u>	2	0	0	0	0	0	2

Three dots indicate not applicable.

TABLE 12. Number of Individuals in Various Life History Stages From a Total of 72 Copepods Taken From Stomachs of 14 Astrotoma agassizii From Station 15-2, Lemaire Channel, March 21, 1983

Species	Developmental Stage								Totals
	VI		V		IV		V	IV	
	F	M	F	M	F	M	Unsexed	Unsexed	
<u>Euchaeta antarctica</u>	1	0	8	18	1	1	29
<u>Calanoides acutus</u>	15	0	25	0	40
<u>Calanus propinquus</u>	0	0	1	0	1
<u>Gaetanus intermedius</u>	0	1	0	1	0	0	2

Three dots indicate not applicable.

age of CV/CVI for C. propinquus ($3/11 = 27\%$) is much lower than the value reported by Ottestad [1932] for his latest summer station (14) on February 17 ($51/57 = 90\%$). The presence of C. propinquus CVI males has been reported by Zvereva [1972] during the same months farther south at Mirnyy. Brittle stars found two while collecting only three adults.

The following notes are from various authors [Farran, 1929; Ommanney, 1936; Vervoort, 1951, 1957, 1965; Tanaka, 1964; Bradford, 1971; Park, 1978; Hopkins, 1985] and pertain to the remaining copepods captured by Astrotoma. Euchaeta biloba was initially described by Farran (as Paraeuchaeta biloba) from around Auckland and Campbell islands; Park found it extensively in Antarctic and Subantarctic waters. Gaetanus intermedius, G. tenuispinis, Pleuromamma robusta, and Rhincalanus gigas are found in both Subantarctic and Antarctic waters. The first three are seldom collected in the upper 50 m during the day. The latter three were taken only by Astrotoma at South Georgia (Tables 5-6, 9). Euchirella

rostromagna and Metridia gerlachei also are found away from the upper 50 m and usually collected south of the Antarctic Convergence. Metridia gerlachei can be very abundant in samples from Antarctic intermediate waters [Pinero de Verdinelli, 1981]. Among copepods of the family Metridiidae in brittle star stomachs, only CVI animals were taken. Metridia gerlachei was captured by Astrotoma from both the Lemaire Channel and Hope Bay (Tables 11 and 13), and Pleuromamma robusta by the South Georgia brittle stars (Tables 5 and 9). Only one brittle star had more than one metridiid (two P. robusta) in its stomach.

Other prey. Mysidacea occurred in 27 individuals, or 34.6% of brittle stars containing food (Table 3). Mysids were the second most important food group and were taken by Astrotoma at both South Georgia and Antarctic Peninsula locations. A few mysids could be identified to species. Three Astrotoma from station 89 off South Georgia contained Antarctomysis maxima. Mysid prey in Astrotoma from station 15-2 in the Lemaire Channel in-

TABLE 13. Number of Individuals in Various Life History Stages From a Total of 4 Copepods Taken From The Stomach of 1 Specimen of Astrotoma agassizii From Station 20-4, Hope Bay, April 2, 1983

Species	Developmental Stage								Totals
	VI		V		IV		V	IV	
	F	M	F	M	F	M	Unsexed	Unsexed	
<u>Euchaeta antarctica</u>	0	0	1	2	0	0	3
<u>Metridia gerlachei</u>	1	0	0	0	0	0	1

Three dots indicate not applicable.

cluded *Antarctomysis ohlinii*, *A. maxima*, *Antarctomysis* sp., and *Mysidetes dimorpha*. Both adult and juvenile mysids were present in the stomach samples.

Chaetognaths occurred in eight *Astrotoma*, or 10.2% of those containing food (Table 3). In seven of these instances we tentatively identified the prey as *Eukrohnia* sp. Chaetognaths were taken by *Astrotoma* at all three general locations, South Georgia, Lemaire Channel, and Hope Bay.

Euphausiids were taken by seven *Astrotoma*, or 8.9% of the feeding individuals. Krill occurred in a few brittle stars from both South Georgia and Antarctic Peninsula sites. All krill that could be identified were juvenile *Euphausia superba*.

One individual unidentified ostracode was found in the stomach of an *Astrotoma* from station 8-2, Lemaire Channel. Ostracodes are common benthic inhabitants of the Antarctic shelf. The absence of benthic ostracodes in *Astrotoma* stomachs supports our view that this brittle star derives its food primarily from the water column.

One unidentified gammaridean amphipod occurred in a brittle star from station 90a, South Georgia. No other amphipods were found in *Astrotoma* stomachs. Mortensen [1936] reported a probable hyperiid amphipod (a pelagic group) from a specimen of *A. agassizii* taken by the *Discovery* expedition.

Unidentified crustacean remains occurred in 20 *Astrotoma* stomachs (25.6% of sample) and generally consisted of tiny fragments of exoskeleton which could not be further characterized. This material did support the general conclusion that crustacean prey are the primary food taken by *Astrotoma*.

Unidentified organic material occurred in eight *Astrotoma* (10.2% of sample). In some instances we believe that this may have been derived from crustacean fecal pellets, but no specific analysis was attempted.

Feeding behavior. *Astrotoma agassizii* occurs on a variety of substrates but generally climbs up on stones or sponges, hydrocorals, gorgonians, or other organisms projecting above the seafloor (Figure 2). Its long arms are highly flexible (see morphological discussion below) and can be produced into complicated loops, twists, sinuous forms, and tight coils (Figures 1A, 2, 5C). The extensive vertical flexibility of the arms, normally associated with euryalids, is coupled in *Astrotoma* with considerable lateral flexibility as well [Dearborn, 1977]. Generally, one or two arms are used to cling to the substrate, while the others are extended. Ventrally directed spines, and probably girdle hooklets as well (see below), are used together with arm coils to assure a firm grip on the support surface.

Remaining arms extend outwards and can be coiled, curled, or extended independently

(Figure 2). Photographic evidence and observations by one of us (K.C.E.) of living *Astrotoma* in large aquaria at Palmer station suggest that individual prey may be captured primarily by initial contact with long, flexible podia, followed by immediate response from the flexible, distal portions of the arms, which produce tight coils around each prey item. Ventrally oriented hooked arm spines and girdle hooklets may also be involved in initially securing the prey and subsequently transferring it to the mouth by periodic coiling and action of podia. We rely here on the brief observations of K. C. Edwards. We were not successful in photographing the podia in action during feeding or in obtaining SEM preparations of extended podia. Wolfe [1982] suggests that in the multiarmed basket star *Astrophyton muricatum*, planktonic prey are captured by girdle hooks and that the podia do not actually capture food but act in a sensory manner. We cannot as yet, however, discount the podia as prey-capturing organs in *Astrotoma*. Living *Astrotoma* produce mucus which occurs on both disc and arms. The possible role of this mucus in feeding is not understood at present.

Morphology

The morphology and anatomy of *Astrotoma agassizii* have been described to varying degrees by Lyman [1875], Fedotov [1927], Mortensen [1936], Fell [1961], Cherbonnier [1962], and Bernasconi [1965]. Briefer comments on morphology and discussions of nomenclature and taxonomic affinities occur in a number of papers cited by Koehler [1923], Dearborn [1977], and the above-mentioned authors.

We will describe and illustrate in photographic detail the external morphology of *A. agassizii*, especially in relation to movement and feeding.

Disc. *Astrotoma agassizii* (Figures 1 and 2) is a large euryalid in which the disc diameter may exceed 60 mm. The most obvious features of the aboral disc surface (Figure 1B) are 10 prominent radial shields raised above the general disc surface and the concave interradii disc margins. Each radial shield is long, extending from the lateral arm base nearly to the center of the disc (Figures 1A and 1B). The aboral surface is thick, leathery, and finely granulated, especially in older specimens. Occasionally, the upper surfaces of the radial shields contain a few larger, elongate granules in large individuals, although these never approach the status of true spines. Because of the thick dermis, no aboral plates other than the radial shields are evident even in dried specimens.

The oral disc surface (Figure 1C) is also covered by a thick dermis with numerous granules. The oral surfaces of large, dried individuals show many small, squarish plates

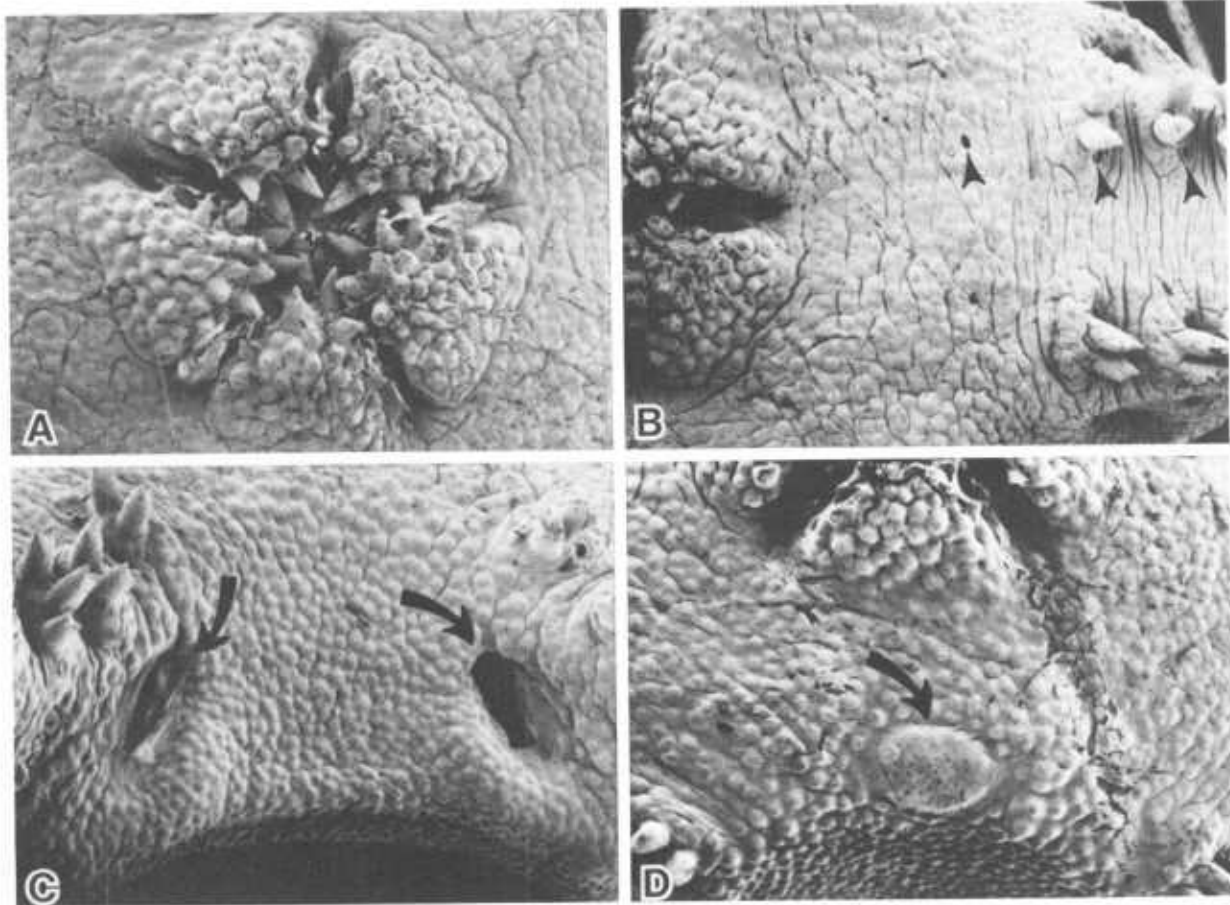


Fig. 4. SEM micrographs of oral surface of disc of small specimen (DD = 10.4 mm), x19. (A) Mouth frame. Several small siliceous sponge spicules are partially embedded in mucus near the mouth. (B) Arm base. Tentacle pores in upper series indicated by arrow heads. (C) Interradius and genital slits (arrows). (D) Interradius and madreporite (arrow).

beneath the surface. These plates are generally not evident in small specimens.

The mouth (Figures 1C and 4A) is relatively small in relation to disc size. Each of five jaws supports multiple rows of tooth papillae and a number of prominent oral papillae. Larger specimens generally have greater numbers of oral papillae.

The genital slits (Figure 4C) are small, generally about two arm segments in length. The outer edges of the genital slits bear a number of large granules.

The madreporite (Figure 4D) is large. Numerous pores can be seen in the madreporites of dried specimens, and with careful observation they may even be visible in living specimens. Large individuals of *Astrotoma* often, but not always, exhibit a prominent fleshy ridge bridging the interradii on an arc just distal to the madreporite (compare Figure 1C with Figures 4B-4D).

Arms. The arms of *A. agassizii* are un-

branched, extremely long, and highly flexible, especially in the vertical plane, resulting in the ability to form tight coils (Figures 1A and 2). Arm length in largest specimens can exceed 700 mm. Like other euryalids, *A. agassizii* is able to coil its arms vertically because of the streptospondylous articulation of its vertebral ossicles. Each vertebral ossicle bears two hourglass-shaped articulating surfaces, one on either end, oriented at 90° to each other. Meshing the distal surface of one vertebral ossicle with the proximal surface of the next allows the arm to coil upon itself vertically. Arms are also capable of a great deal of lateral flexibility. Each arm tapers rapidly along its length and becomes extremely narrow at the distal tip. Because they are small and fragile, arm tips frequently break and regenerate.

Proximally, arms are covered with small granules similar to those on the disc, but

more distally the arms become gradually smoother. No well-defined dorsal, lateral, or ventral arm plates are externally evident. Between each arm joint is a prominent double row of movable, highly modified spines or girdle hooklets, alternately arranged in opposite directions. Each row forms a loop or band extending around the lateral and upper surfaces of the arm (Figures 5A and 5C). The number of girdle hooklets in each band is primarily a function of position on the arm. Loops at the arm base contain many hooklets, while those near the arm tip contain few (compare Figures 5A, 5C, and 5E). Rows of functional girdle hooklets are found over the entire arm length, in contrast to the condition in *Astrophyton muricatum*, a basket star, in which girdle hooklets (therein termed hooks) are generally absent for the first several arm branchings [Wolfe, 1982].

Larger arm spines are restricted to the ventral (oral) rather than lateral portions of the arm, and spine morphology and arrangement vary along the length of the arm. Spines near the arm base (Figure 5B) are generally arranged in groups of three or four. These spines are blunt and peglike. Along the middle portion of the arm (Figures 5C and 5D), spines are usually arranged in pairs and have a slight paddle shape. Finally, spines near and at the arm tip (Figures 5E and 5F) are single and distinctly paddle shaped. Spine variation along the arm is probably associated with relative prey capture potential of the different regions of the arm.

From about the middle to the tip of each arm, each group of arm spines has a pair of hooklets associated with it (Figure 6). These form the lower end of a band of girdle hooklets and are slightly removed from the other hooklets and oriented differently. This pair of arm hooklets, as well as the associated arm spines, are all borne by a ventrolateral arm plate and are morphologically arm spines. Although the number of paddle-shaped arm spines decreases from two to one beginning with the middle of the arm to its tip, the number of arm spines modified into these hooklets appears to remain constant at two (compare Figures 6A and 6B, with Figures 6C and 6D). All girdle hooklets and ventrolateral arm hooklets have a distinct hook shape, while the medial arm spines' paddle shape is caused by a fleshy bridge over the hooked ossicle (Figure 6).

Tentacle pores and tube feet are present to the end of the arm (Figures 4B, 5B, 5D, and 5F). The first pair of tentacle pores (Figure 4B) lacks a spine, but all other tentacle pores are associated with two to three arm spines proximally (Figures 4B, 5B, and 5D), four to five spines in the midarm region, and two reduced to one distally (Figures 5D and

5F). Each tentacle pore consists of a rounded opening with a flexible, fleshy rim or collar (Figure 5D), within which the long extensible podia can be withdrawn. At the arm base, tentacle pores occur adjacent and medial to the arm spines (Figure 4B) but become distal to the median arm spine farther out the arm (Figure 5D). No tentacle scales are present.

Girdle hooklets are arranged in two alternating rows extending around the arm at each joint. Hooklets of the proximal row of each pair point distally, and those of the distal row point proximally, in alternating series (Figure 7A).

Each hooklet consists of a single strongly recurved ossicle (Figure 7B). The hooklet ossicle is very solid and has relatively few pores. The basal portion of the hooklet forms a prominent articulating boss with sculpturing for the attachment of ligaments and muscles.

Hooklets are supported by rectangular girdle ossicles, each of which bears articulating surfaces for eight hooklets (Figure 7C). Each girdle ossicle bears a smaller number of hooklets near the arm tip. Each ossicle is curved (Figure 7C), and collectively, they form the curvature of the arm surface. They are extremely porous, with the exception of the hooklet articulating surfaces, which are smooth and have reduced numbers of pores.

Two sets of muscles comprise the musculature of each girdle hooklet. The first consists of a large medial muscle band (Figure 8A) which inserts under the head of the girdle hooklet boss and extends over the articulating surface of the girdle ossicle to originate on the porous surface beyond the articulation. The second muscle set consists of a pair of muscle bands on either side of the joint (Figure 8B). These muscles insert on the porous edge and top of the boss on the hooklet base and extend to either side of the articulation to originate at the sides and rear of the articulating surface. Figure 8C shows the orientation of both the hooklet and the girdle ossicle with the musculature removed. Contraction of these two sets of muscles serves to rotate the hooklet to a vertical position over the articulation surface of the girdle ossicle and to lock the hooklet erect.

Arm plates (Figure 9C) of *A. agassizii*, which carry arm hooklets and spines, are small and located ventrolaterally, unlike the more lateral configuration present in most ophiurid ophiuroids. They are longer than tall and slightly convex in shape. Most bear several arm spines of two types on their distal ends. Laterally, each arm plate generally bears the two arm hooklets identical in appearance and articulation to girdle hooklets (Figures 9A and 9B). These two spines are aligned with, and form the ventral terminus

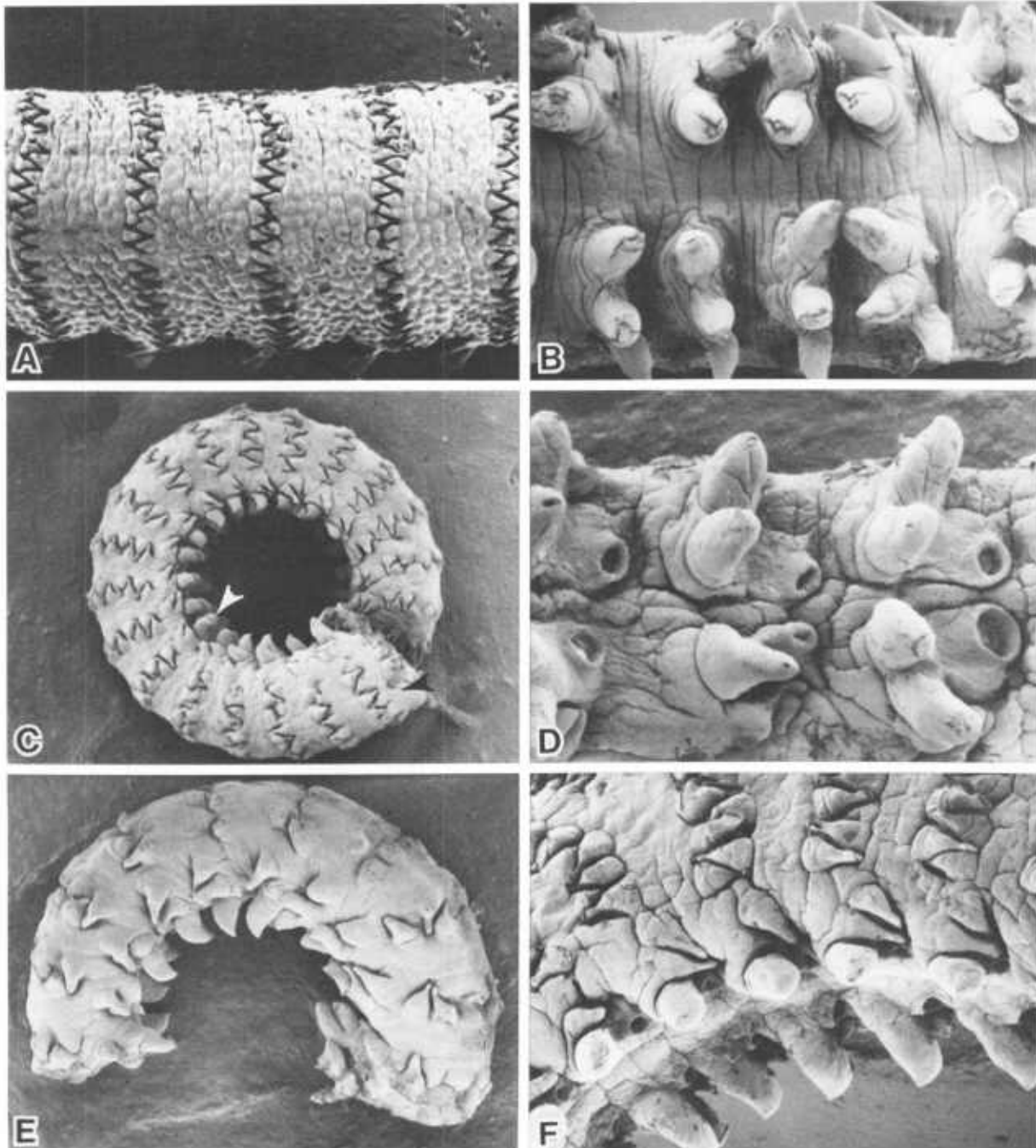


Fig. 5. Various arm sections. (A) Dorsal (aboral) surface near arm base showing rows of girdle hooklets, x20. (B) Ventral (oral) surface near arm base. Note triplets of large peglike arm spines, x19. (C) Section near middle of arm showing paired arm spines (arrow), x16. (D) Ventral view of section near middle of arm. Arm spines arranged in pairs but at this point only beginning to take on the paddle shape characteristic of more distal spines. Note prominent tentacle pores, x67. (E) Lateral view of section near arm tip. Arm spines mostly single and paddle shaped, x38. (F) Lateroventral view of section near arm tip showing lateral girdle hooklets and ventral, unpaired, paddle-shaped arm spines, x40.

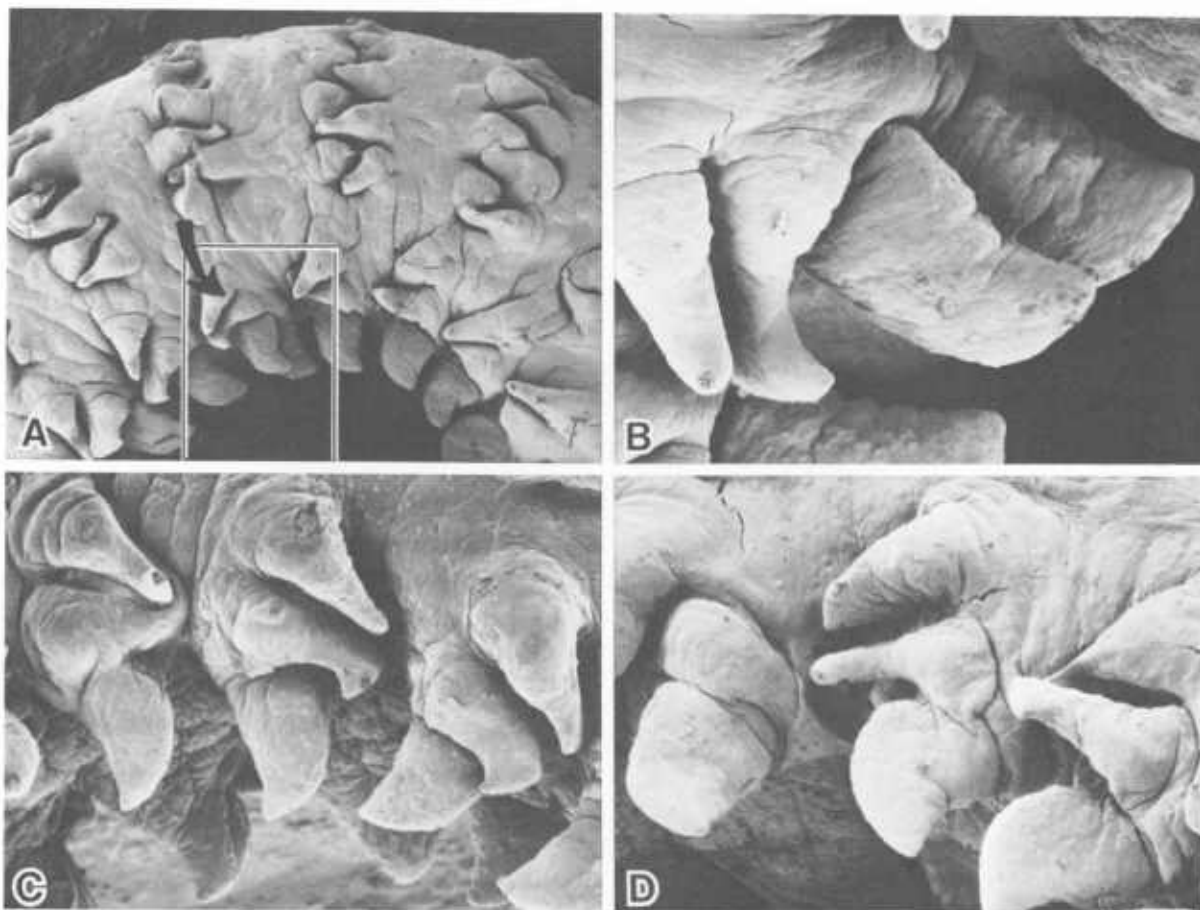


Fig. 6. Arms. (A) Lateral view of section about two-thirds out toward arm tip showing paired hooklike arm spines (arrow) above the fleshy paddle-shaped ventral spines, x49. (B) Enlargement of portion of area enclosed in Figure 6A, showing difference between hooked arm spines (left) and more ventral paddle-shaped arm spines (right). The hooked arm spines are similar in appearance to girdle hooklets, x216. (C) Spines along outer third of arm. Ventral paddle-shaped arm spines are no longer paired, but hooked arm spines generally remain paired throughout arm length, x105. (D) Spines at arm tip, x147.

of, the row of girdle hooklets. Lateral arm plates located near the arm base may not always have these spines.

Medial to the two arm hooklets are from one to several more typical arm spines (Figures 9A and 9B). The number of these spines ranges from three (occasionally four) at the arm base to one at the arm tip.

The articulation surfaces of these two spine types are distinctly different (Figure 9C). As noted above, the hookletlike arm spines have articulations similar to those of the girdle hooklets and probably operate in a similar manner. The medial arm spines, on the other hand, have articulating surfaces that are greatly reduced. They lack the well-developed smooth surface and thickened base of the ossicles which support the hooklets. This disparity in articulation morphology suggests that the medial arm spines prob-

ably are less mobile than the more lateral hooklets.

Cleaned medial arm spines vary from arm base to arm tip (Figures 10A-10F). Spines located at the arm base are blunt, thickened, and peglike (Figure 10A). No hook is evident, although the slight cleft often observed in these spines is its morphological equivalent. The ossicle is essentially porous throughout. The overall size of the arm spines becomes reduced along the arm distally (Figures 10B-10E). The distal end of each spine thickens and takes on an increasingly hooked shape. Medial arm spines at the arm tip (Figure 10F) are short and have a strongly hooked extremity. The porous ossicle base is reduced, and most of the spine shaft is solid, much like the girdle hooklets.

The hooked portions of the medial arm spines, unlike girdle hooklets and ventrolat-

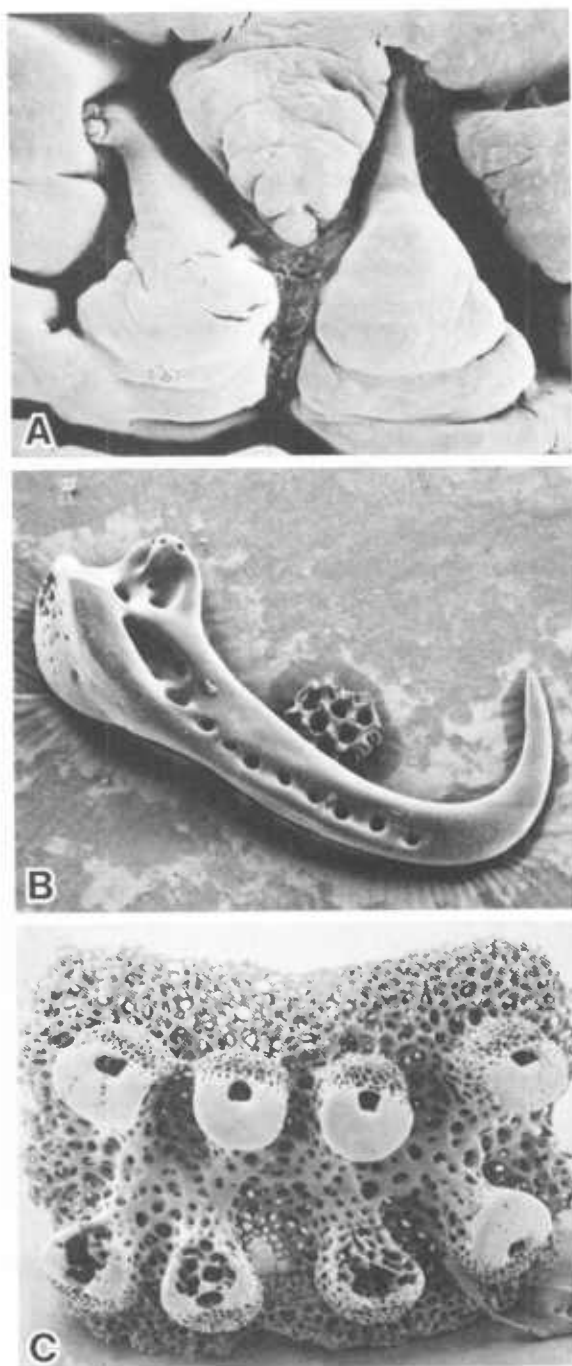


Fig. 7. Girdle hooklets. (A) Retracted hooklets on dorsal surface of arm near base, x196. Tips of hooklets are strongly curved. In this view the central hooklet lacks a hooklet tip. This may represent regeneration or developmental abnormality. (B) Cleaned girdle hooklet. Note strongly recurved tip (right) and bosses at base (left), x250. (C) Single girdle ossicle bearing eight bosses for articulation with girdle hooklets, x125. Multiple girdle ossicles support each complete row of girdle hooklets.

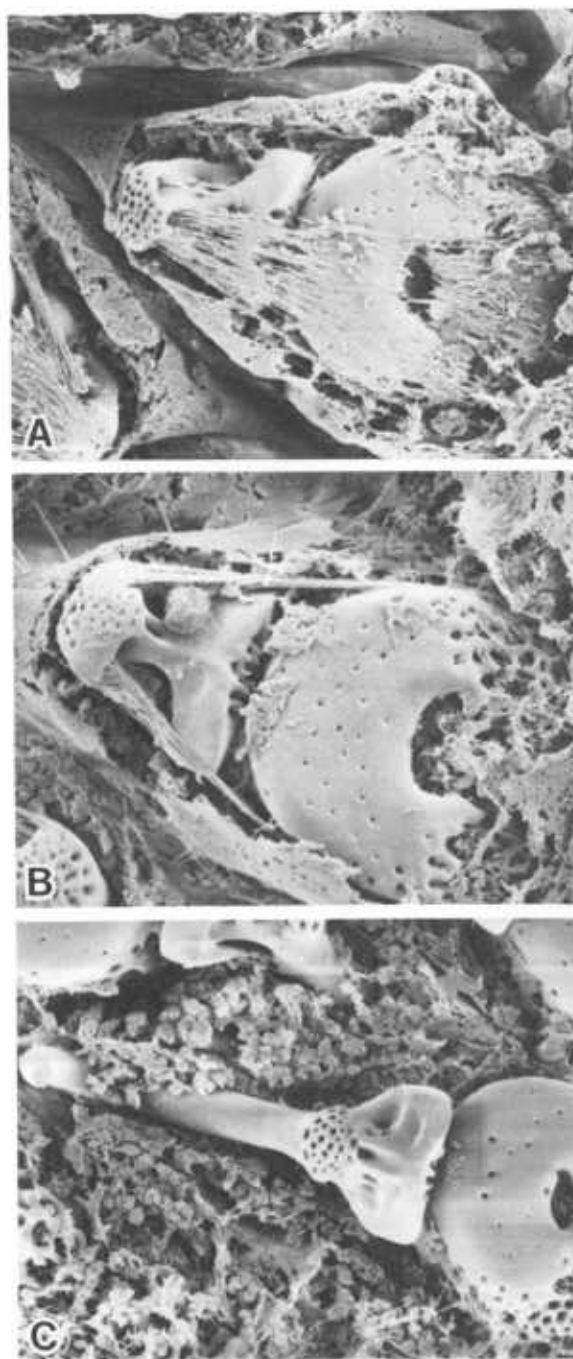
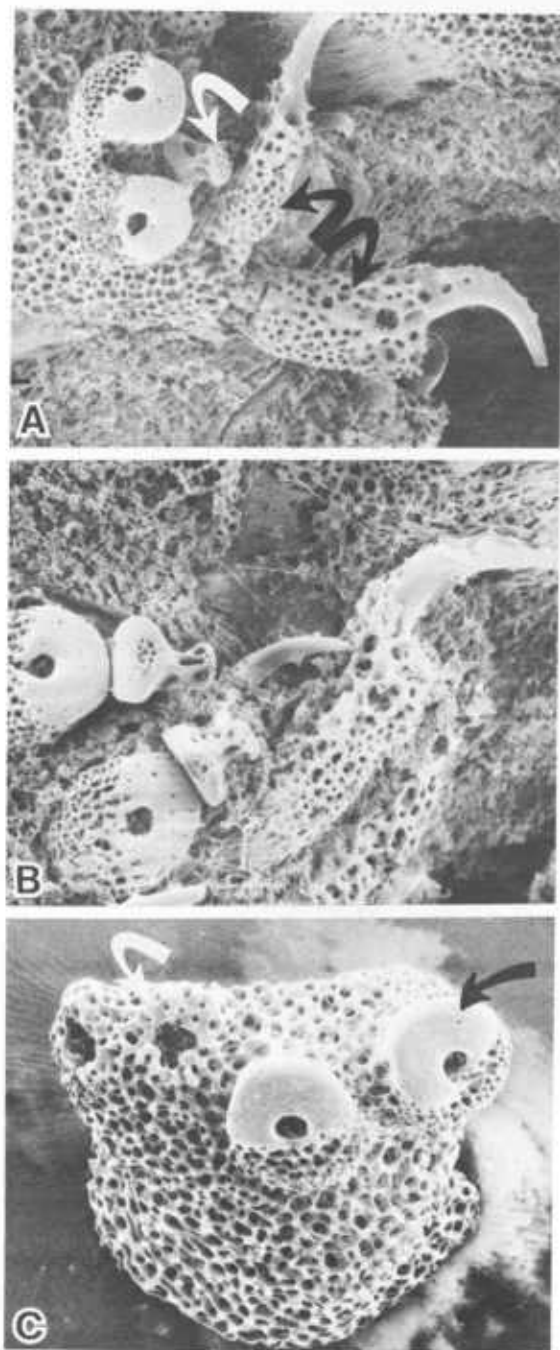


Fig. 8. Hooklet articulations from which soft tissue has been partially digested away. (A) Medial muscle fibers control elevation of girdle hooklet, x390. (B) Lateral muscle fibers control angle of girdle hooklet and aid in hooklet elevation, x415. (C) Hooklet articulation from which musculature has been cleaned to show relative orientation of hooklet and basal ossicle in retracted position, x385. Note that the hooklet rolls up and over a smooth articulating surface to become erect.



eral arm hooklets, are always bridged by a thin web of translucent tissue in the living animal (Figure 6). Thus although the girdle hooklets and arm hooklets exhibit a true hook shape in life, the medial arm spines, because of this web, appear peglike at the arm base or paddlelike on the outer tip of the arm. The function of the webbing of the medial arm spines is not currently understood. The tissue may contain secretory cells and aid in mucus secretion, retention of prey following capture, or both.

Tissue Preparation

The distinctive nature of the several spine types (girdle hooklets, arm hooklets, and medial arm spines) present in *A. agassizii* underscores the importance of proper preparation techniques for the interpretation of functional morphology. Figure 11 illustrates this point. An arm segment prepared according to the methods outlined here is shown in Figure 11A. The distinct difference between the appearance of the medial arm spines (black arrow) and the girdle hooklets (white arrow) is apparent. The spine tips are covered by fleshy tissue. There is a lack of obvious shrinkage and cracking of the epidermis. Comparison with fresh specimens of *A. agassizii* indicates to us that Figure 11A accurately reflects the appearance of these structures in the living organism.

In contrast, the arm sections illustrated in Figures 11B and 11C were prepared by more conventional methods, with no hardening step and with the usual ethanol dehydration series before critical point drying. Extensive shrinkage is evident. In each case the tissue appears tight, with numerous tears and cracks. In particular, shrinkage of tissue

Fig. 9. Arm plates and arm spine articulations after partial cleaning with sodium hypochlorite. (A) Two arm spines (black arrows) and one remaining hooklet spine (white arrow) attached to ventrolateral arm plate, x155. Although all are morphologically arm spines, structural differences suggest functional variations between inner and outer pairs. (B) Plate with all four spines intact, x195. Note the erectile nature of the outer modified arm hooklets, which is identical to that of girdle hooklets. The larger, unmodified arm spines are more rigidly mounted, without clear evidence of a joint surface, suggesting more limited capability for movement. (C) Isolated ventrolateral arm plate, x200. The prominent flattened articulating surfaces (black arrow) are hooklet spine articulations. The arm spine joints (white arrows) show no apparent provisions for movement.

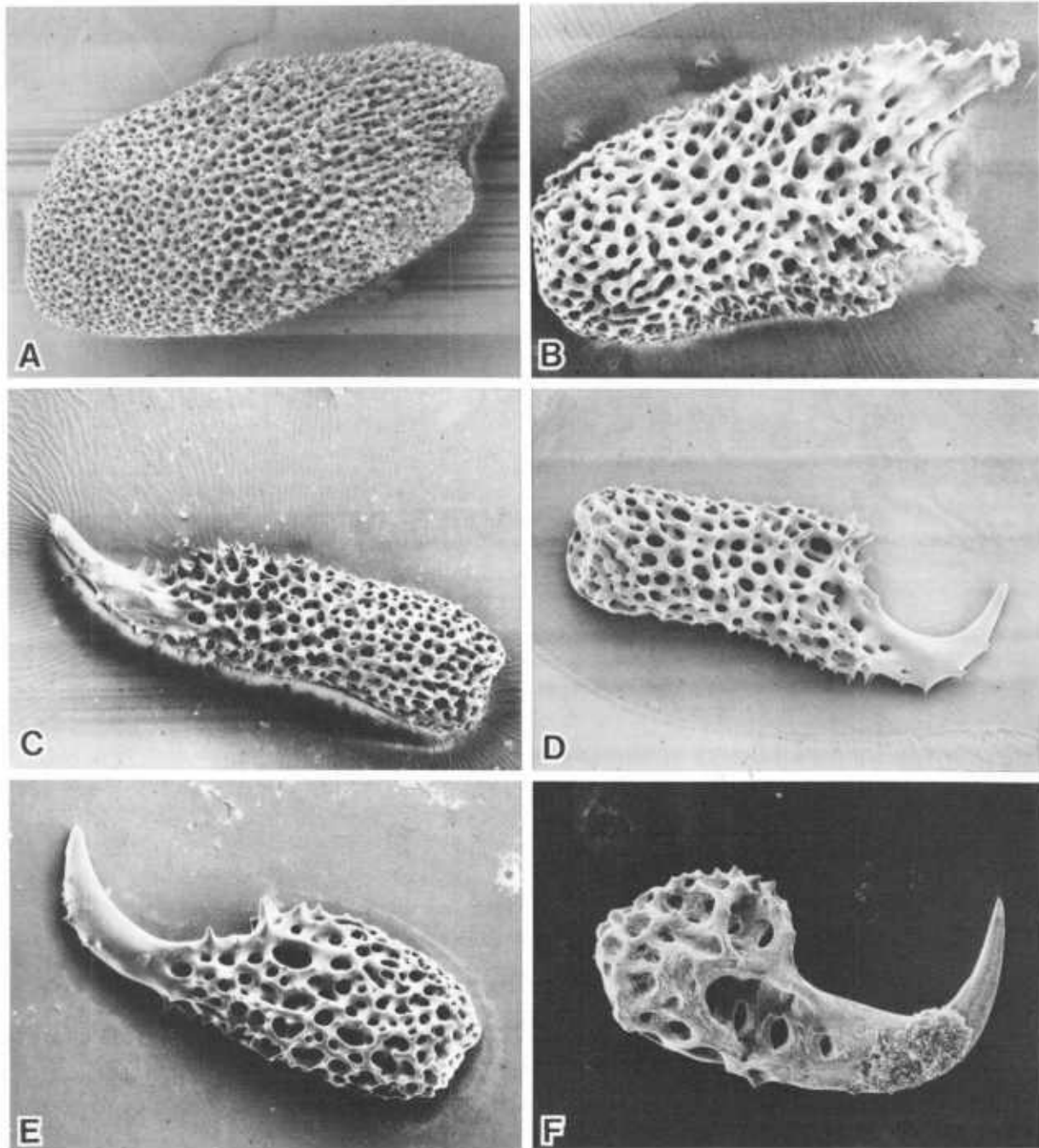


Fig. 10. Series of cleaned arm spines from arm base (A) to arm tip (F). (A) x95, (B) x210, (C) x145, (D) x210, (E) x210, (F) x402. Note transition from blunt peg-shaped spines near arm base to smaller, hooked spines near arm tip. This transition corresponds to the presumed increase in prey-capturing ability of the arm toward the flexible tip.

has exposed the tips of the medial arm spine hooks (Figures 11B and 11C, black arrows), as well as creating tears in the tissue covering the girdle hooklets. In this case, shrinkage

due to poor preparation may produce a false impression of the hooklike nature of the arm spines and thus possibly affect interpretation of prey capture mechanisms.

General Feeding Considerations

Hendler and Miller [1984] point out that because species with simple arms occur in all four families of the Euryalina, and species with branching arms occur in only two families, it is important to determine if behavior is allied more to arm morphology or phylogenetic affinities. They review in detail the behavior of species with branched arms and compare these data with their findings on *Asteroporpa annulata*, the only unbranched species studied until now. Although we have been able to categorize the diet of *Astrotooma agassizii* and describe morphological features, we cannot provide data from direct in situ examination for comparison with the behavioral observations of Hendler and Miller [1984] on *Asteroporpa*. Direct observation of feeding was not possible in either study. The mechanics of feeding in euryalids with simple arms remains to be determined.

Observations by K. C. Edwards of living *Astrotooma* held in flowing seawater tanks are suggestive. They indicate that podia can be extended to at least 3 times the length of an arm spine. Podia are generally held extended in a V-shaped array, of more or less uniform length. Although we have been unable to observe feeding directly, we believe that this pattern of podial positioning may be significant in sensing prey items as well as in physical capture of the prey. We also suggest that *Astrotooma* uses these long, possibly sticky, podia in combination with hooklets and rapid, tight coiling of the extremely thin and flexible distal portions of the arms to capture and manipulate prey. Probably, mucus, the ventrolaterally oriented arm hooklets, and ventrally oriented arm spines are also involved in prey retention and movement of food to the mouth. Specific functions for these various structures in the feeding process have yet to be defined.

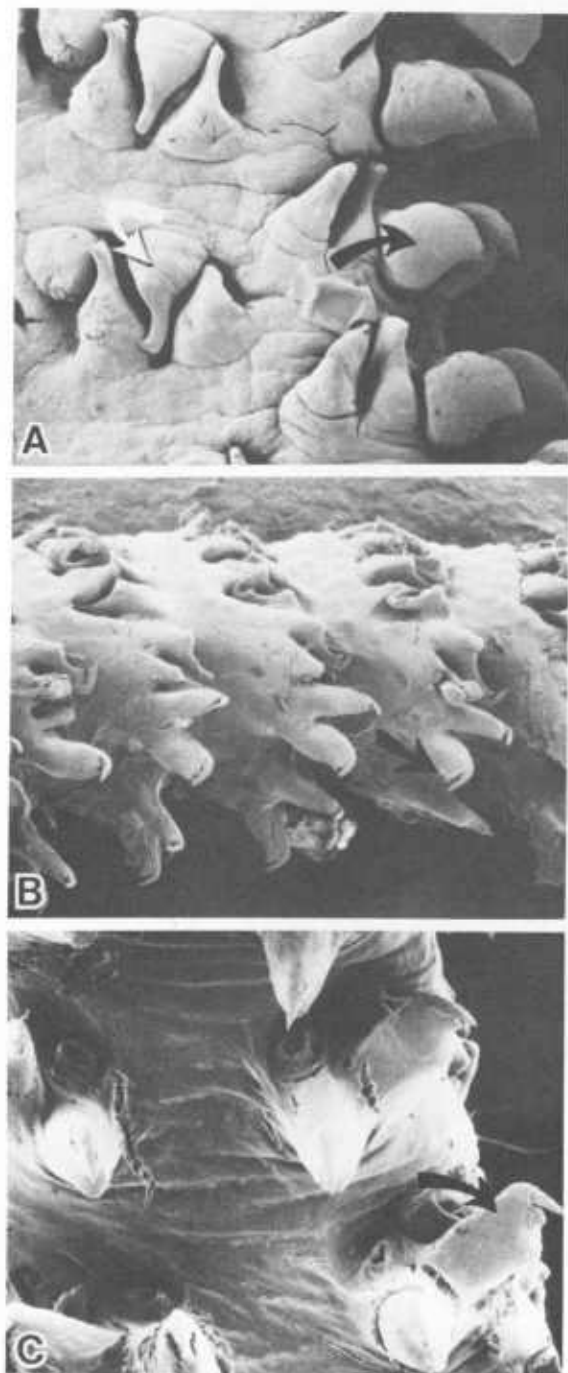


Fig. 11. Effects of tissue shrinkage on preservation and interpretation of specimens. (A) Arm section after treatment to harden specimen and prevent shrinkage, x74. Arm spines (black arrow) are distinctly paddle shaped when fleshed and show little hooking. Girdle hooklets (white arrow), on the other hand, are distinctly hook shaped even after proper hardening. (B) Arm section not properly hardened before processing, x53. Effects of shrinkage are evident and misleading. Note that paddles of tissue bridging the arm spines have torn away, creating a naked hook not present in life. Flesh over the girdle hooklets is similarly shrunken. (C) Oral view of untreated arm section, x68. Note tissue of arm spines (black arrow) is greatly shrunken, permitting the tips of spines to be unnaturally exposed.

The prey of both Asteropora annulata [Hendler and Miller, 1984] and Astrotoma agassizii [Dearborn et al., this study] is dominated by copepods. These are the only species of simple-armed euryalids for which any such data are available. Asteropora prey included smaller planktonic copepods, many less than 2 mm: Oncaea, Corycaeus, Lubbockia, Macrosetella, and Candacia. Other prey included veligers and pelagic ostracodes [Hendler and Miller, 1984]. In our study, Astrotoma has consumed much larger calanoid copepods, also associated with the water column rather than the substrate. We assume that smaller prey items such as adult or juvenile copepods are available but are not captured by the brittle star. We believe the critical conclusion here is that Astrotoma, and probably other euryalids, are transferring carbon from the water column to the benthos by selective predation.

Several important questions arise from this conclusion about A. agassizii. Are copepods (and other zooplankton) alive or dead when captured by the euryalid brittle stars? Are there biological processes that sort living copepods, or hydrological processes that sort living and dead copepods, which could affect the animals available for brittle star capture relative to a more diverse fauna immediately near or in the 50-100 m of water above the brittle star? Do euryalids select copepods alive or dead? Do they collect copepods randomly? Some answers will depend upon studies of the population structure of copepods in the water column and near the bottom at the time of feeding. Such information is unavailable for this study and has been inferred for only a few species of calanoids. Questions involving brittle star behavior ultimately should be answered by direct observations. However, we will present here several suggestions which may help narrow the field of inquiry.

Extrapolation from the status of copepods in the stomachs of brittle stars to their condition immediately prior to capture is difficult. It is impossible to differentiate deterioration following death before capture from that caused by brittle star digestion. However, if all copepods are dead before capture, especially if they died near the surface, chances of observing specimens in good condition from brittle star stomachs are negligible. If the copepods are alive immediately before ingestion, chances are better that some animals that were recently captured will be in good condition in brittle star stomachs. A number of such animals in good condition--individuals of Drepanopus forcipatus, Calanoides acutus, and Euchaeta antarctica--were encountered in several brittle star stomachs, suggesting that these copepods are taken alive. In addition, if copepods are dead before capture, some should

eventually sink to the substrate, where they would be consumed by animals feeding along the substrate. Very few Antarctic studies address this problem. However, an examination by Fratt and Dearborn [1984] of the stomach contents of 2475 specimens of Ophionotus victoriae, a large ophiurid brittle star abundant along the Antarctic Peninsula, some of which were taken at identical sites as Astrotoma, showed that copepods occurred in only 0.3% of individuals containing food and these were primarily of benthic origin. No large pelagic species were represented. Ophionotus victoriae uses various feeding methods, but not suspension feeding like Astrotoma. It has a catholic diet which includes members of at least 13 phyla [Fratt and Dearborn, 1984]. If large numbers of dead pelagic copepods were on the substrate, it seems reasonable to assume that O. victoriae would have eaten them.

Several points will be made about biological processes which may act to sort particular elements of the pelagic fauna and make these elements available to brittle stars. We will confine our attention to the three copepods dominating the stomach contents. Bayly [1982] mentions that throughout its life, Drepanopus forcipatus is confined to shallow coastal waters. Lee [1966] found this abundant species extensively along the southeastern continental shelf of South America. The life history of D. forcipatus, a presumed pelagic species, is not well known; capture of specimens by brittle stars at bottom depths greater than 100 m seems paradoxical. However, Pesta [1930] noted the striking abundance of this species in dredge hauls and suggested that it may form aggregations close to the bottom. We suspect that this biological sorting, perhaps temporally episodic, may allow the living copepods to be captured by brittle stars.

We also believe that Calanoides acutus and Euchaeta antarctica are alive when caught and that a particular biological sorting process also is operational in regulating their capture. And further selection by the brittle stars should not be ruled out. Regarding this second process, a study of the brittle star Ophiocten hastatum in the Gulf of Maine by Schoener [1971] is particularly instructive. Schoener found common pelagic copepods among the stomach contents of O. hastatum collected in late July. As in our present study, most of Schoener's copepods had deteriorated, and it was impossible to determine whether deterioration occurred before or after ingestion. However, some copepods were "exceedingly well-preserved," prompting the author to suggest that they were alive when captured. As in the present study, the captured fauna comprised a calanid, i.e., Calanus finmarchicus, 39 specimens, CV = 85%, CVI = 16%; a euchaetid, i.e., Euchaeta norvegica, 7 specimens, juveniles (probably CI-CIII) = 42%, CIV or CV

= 29%, CVI female = 29%; and a metridiid, i.e., Metridia longa, 3 specimens, all CVI female; in addition, "eggs and spermatophores probably of copepod origin were minor dietary components."

A common biological process is suggested by dominance of copepods from the same two pelagic families (Calanidae and Euchaetidae) in stomachs of different brittle stars with dissimilar feeding strategies collected in these disparate localities. Many species of the family Calanidae, including Calanoides acutus and Calanus finmarchicus, are known to undertake seasonal ontogenetic migrations. CIII, CIV, or CV animals move away from epipelagic waters of seasonally high plankton productivity and into mesopelagic waters (see Andrews [1966] for the former species; Marshall and Orr [1955], Davis [1976], Grigg and Bardwell [1982], and Hirche [1983, 1984] for the latter). For reports of other calanids with a similar strategy, see Conover [1962], Omori [1970], Fulton [1973], Binet and Suisse de Sainte-Claire [1975], Petit and Courties [1976], Petit [1982], and Miller et al. [1984]. These migrations generally are correlated with presumed adverse changes in the epipelagic waters where feeding occurs, such as cessation of upwelling-induced phytoplankton productivity for Calanoides or onset of cooler water temperatures and reduced phytoplankton productivity for Calanus s.l. Grigg and Bardwell [1982] suggest conditions unfavorable to the nauplii and early copepodids may be responsible for this strategy of Calanus finmarchicus.

In addition, in situ observations from a submersible by Alldredge et al. [1984] of Calanus pacificus californicus presumably utilizing a similar strategy indicate an extensive horizontal range and narrow vertical zone (20 m) for an aggregation of this calanid at depth (450 m) off California. Extremely high densities of CIV and CV animals ($26 \times 10^6 \text{ m}^{-3}$) occur within the aggregation. The animals appeared quiescent, supporting observations on the torpid condition of deeper, net-collected Calanus hyperboreus by Conover [1962]. Indirect and direct evidence for reduced ingestion and metabolic activity by such calanids is provided by Hirche [1983] and Alldredge et al. [1984].

At depth these densely packed calanids must be protected against continuous, severe predation. Alldredge et al. report that CIV and CV Calanus pacificus californicus at depth are found within a zone of low oxygen concentration and suggest that this strategy may provide some protection for the quiescent animals from predators below the aggregation. However, if these dense compact aggregations begin forming immediately after the calanids begin their descent from epipelagic waters, the animals may be particularly vulnerable to

large, opportunistic, pelagic predators such as euchaetids. Such a predator, Euchaeta norvegica, is known to feed on Calanus finmarchicus (see Båmstedt and Holt [1978] for details). We suggest a similar relationship for their ecological cognates, Calanoides acutus and Euchaeta antarctica, in the southern ocean.

The availability of a rich and seasonally predictable calanid prey may intensify euchaetid reproductive activity. Schoener [1971] reported unidentified detached eggs and spermatophores in Ophiocten hastatum stomachs. Calanus finmarchicus CVI females do not carry egg sacs and are seldom found bearing spermatophores [Marshall and Orr, 1955]. The reverse is true for Euchaeta norvegica [Ferrari, 1978]. In the present study, the percentages of CVI and CV males of E. antarctica are comparable to similar values for E. norvegica [Hopkins, 1982], suggesting significant mating activity by E. antarctica prior to capture. The percentage of females with spermatophores is much lower than the value reported by Hopkins. However, these structures may be easily dislodged by the brittle star during capture of the euchaetid.

We regard larval dispersal as important in determining the presence of Calanoides in shoal waters favored by Astrotoma. Following a seasonal ascent from depth, hydrographic processes may disperse some nauplii into shallower waters. Upon completing their epipelagic season, downward migrating calanids in these waters also would have to move horizontally to avoid contact with benthic substrates shallower than the depth of quiescence (below 500 m for Calanoides acutus, 800 m for Calanoides carinatus, or 450 m for Calanus pacificus californicus). Some calanids and accompanying predatory euchaetids may come into close proximity with this shallow substrate along gently sloping bottom contours or in large semienclosed basins. These copepods would provide a rich and seasonally predictable food source for benthic invertebrates capable of their exploitation, such as Ophiocten hastatum and Astrotoma agassizii.

Finally, the presence of rare CVI males of Calanoides acutus in the stomachs of Astrotoma agassizii may be explained by the following. If sex is important to the biology of Calanoides acutus, the very low percentage of CVI males from less selective net samples of the population may be misleading. Presence of CVI females and males in the population is undoubtedly seasonal. Males may occur only during descent and quiescence, with mating activity confined to the period prior to ascent. Recently molted males and females may move down through the aggregation and congregate along its deeper sections. During quiescence at depth they would be protected by CV animals from midwater predators searching

above the aggregation. However, during descent the deeper CVI animals would be easily susceptible to predation by benthic brittle stars in shallow waters, since they would be the first copepods to come into proximity with the substrate.

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