

A COMPARATIVE STUDY OF SELECTED SKELETAL
STRUCTURES IN THE SEASTARS *ASTERIAS FORBESI*
(DESOR), *A. VULGARIS* VERRILL, AND
A. RUBENS L., WITH A DISCUSSION
OF POSSIBLE RELATIONSHIPS

E. K. Worley and David R. Franz

Abstract.—Morphological structures from the congeneric North Atlantic seastars, *Asterias forbesi* (Desor), *A. vulgaris* Verrill, and *A. rubens* L., were measured and compared. Significant differences in size and/or shape were found between *A. forbesi* and *A. vulgaris* in the following structures: ventral pedicellariae, adambulacral spines, oral spines, the madreporite, skeletal ossicles, and the shape of the arms. Slight but insignificant differences in size, but not shape of these structures was shown between *A. vulgaris* and the few samples of *A. rubens* examined.

The firmer, more rounded, less tapering shape of the arms in *A. forbesi* was attributed to the shape of the ossicles and their long processes which form junctions directly, or by one plate, with adjacent processes throughout the length of the arm. In the more flaccid, tapering arms of *A. vulgaris* (and *A. rubens*) short, blunt ossicle processes connect with adjacent processes by several plates in the proximal dorsolateral region forming a more open meshwork and more flaccid skeleton. The uniformly small size of these plates throughout the length of the arms in young *A. vulgaris* may account for the less tapered conditions sometimes found in small specimens causing them to resemble the shape of the *A. forbesi* arms. Furthermore, variation in size and number of these plates is suggested to be associated with the production of morphs in *A. vulgaris* and *A. rubens*. The *forbesi*-like animals from the Maine population were therefore diagnosed as local morphological variations of the variable species *A. vulgaris*, and not hybrids.

Earlier ideas and hypotheses concerning the relationships and origins of the three *Asterias* species are summarized and evaluated; and an hypothesis is formulated to account for the origin of all *Asterias* species from a common North Pacific ancestor.

The two seastars, *Asterias forbesi* and *Asterias vulgaris* of the Northwestern Atlantic coast show many similarities in ecology and morphology. Both species, however, exhibit phenotypic variability within and among populations which has resulted in problems of identification, especially in those coastal regions where the two species are sympatric. While there are no comparative studies to ascertain the differences between the species from the extremes of their ranges or from the region of overlap on the continental shelf of the Middle Atlantic Bight (MAB), the taxonomic traits tabulated by Aldrich (1956) are generally accepted as diagnostic (Schopf and Murphy 1973; Walker 1974) for all areas.

While isolated and local populations of *A. forbesi* or *A. forbesi*-like animals may occur in various shallow embayments along the Maine coast (C. Towle,

pers. comm.), *A. forbesi* is distributed more or less continuously from Casco Bay, Maine to North Carolina, and may occur south to Florida, although rare south of 20°N (Franz *et al.* 1981). It has been collected over the entire breadth of the continental shelf between Cape Hatteras (North Carolina) and Cape Cod (Massachusetts), except north of 40°N, where it is confined to the inner shelf, on the Nantucket Shoals and Cape Cod Bay. In the SW Gulf of Maine (Isle of Shoals) *A. forbesi* is restricted to depths of 10 m or less (Hulburt 1980), and is generally absent from the subtidal zone of the Gulf of Maine. On the shelf south of Cape Cod, *A. forbesi* occurs most frequently at depths <30 m. *Asterias vulgaris* is uncommon or *absent* from the inshore waters (<20 m) of the Middle Atlantic Bight (MAB) but occurs in the deeper, colder waters as far south as Cape Hatteras. Between Cape Cod and Cape Hatteras, both species co-occur in a broad zone of overlap on the continental shelf. North of Cape Cod, *A. forbesi* is rapidly replaced by *A. vulgaris* which occurs commonly on Georges Bank and the continental shelf of the Gulf of Maine, northward to the Gulf of St. Lawrence.

Asterias rubens which is widely distributed along the northeast Atlantic coast, resembles *A. vulgaris* morphologically, hence, they have been considered to be closely related species (Coe 1912; Fisher 1930; Nesis 1961) and even identical (Clark 1923; Tortonese 1963). In this paper, we examine inter- and intraspecific variability in selected skeletal features of all three species in order to evaluate the potential usefulness of measurable skeletal characters in taxonomic evaluation, and to gain insight into the possible relationships and origins of the Atlantic species of *Asterias*.

Materials and Methods

Asterias forbesi and *A. vulgaris* used in this study were collected along the northwestern Atlantic Continental Shelf and from the coastal shores of Maine and Long Island, New York. Specimens (105) were hand picked from the low intertidal shores of Muscongus Bay, Chamberlain, Maine, in August 1978 and 1979. Other inshore animals (46) were obtained by SCUBA at Shoreham, Long Island Sound, in December 1978, and from East Rockaway Inlet (50 animals), Far Rockaway, New York (southwestern Long Island) in September 1978 and December 1979. Specimens from the northwestern Atlantic Continental Shelf were collected, using an otter trawl, by the National Marine Fisheries Service during the Ground Fish Survey (Del. II Cruise 78-1, Jan–Feb 1978; Del. II Cruise 79-01 and Alb. IV Cruise 79-04, Jan–Mar 1979). The Gulf of Maine region (42°02'–44°37') included 25 stations ranging in depth from 35–348 m, and yielded 97 specimens. Between Cape Cod and Cape Hatteras (42°00'–35°58'), the Middle Atlantic Bight (MAB), 1450 specimens of *Asterias* spp. were obtained from 177 stations ranging in depth from 9–220 m. Many of the stations in both the Gulf of Maine and the Middle Atlantic Bight yielded only one or two specimens of a species and the size range from many stations was very narrow. In order to make valid comparisons between the species, measurements of the traits selected for study were based on animals within the same size range ($R = 4\text{--}9$ cm). Since the magnitude of size variability of these characters in a species was found to be no greater between stations of a region than between members of the same population, data from all populations of a species from a given geographic area were pooled.

For comparison, studies were made on formalin-preserved specimens (25) of *Asterias rubens* collected from St. Andrews, Scotland, and a small number of museum specimens (alcohol preserved) from Northwest Iceland (10) and south-west Greenland (18).

Observations on living starfish were made only on those collected from Muscongus Bay and Rockaway Beach. Material supplied by the Ground Fish Survey in 1979 was frozen immediately on collection and brought to the laboratory in this condition. All other specimens were preserved in formalin when collected and later studied in the laboratory.

Four morphological features which are usually considered of diagnostic value for *Asterias* spp. (Coe 1912; Mortensen 1927; Aldrich 1956; Gray *et al.* 1968) were selected for measurement and comparison: the shape of the rays; the size and shape of the madreporite; the size and shape of the straight (major) pedicellariae; and the structure of the skeleton, including the ossicles and the size and shape of the adambulacral and oral spines.

Gross measurements were made with Vernier calipers on the middle arm of the trivium. Body radius (R) measured from the center of the disc to the tip of the arm, was used for size comparisons between individuals of the same and different populations and species. Tapering of the rays was calculated from the ratio (a/b) between the diameter of the arm at the base (a) and the diameter measured 1 cm from the tip (b). Thus, more tapered rays exhibit higher a/b ratios than blunt, parallel-sided rays.

Spines, straight pedicellariae, and the madreporite were removed from at least 10 animals from each region and measured with a calibrated Wild Dissecting Scope. Spines and pedicellariae were selected at random from the proximal third of the arms, and each recorded value, based on the measurement of the calcareous skeleton, represents the average of a minimum of 10 samples per animal.

After removal of podia and internal organs, animals were skeletonized by placing one or more arms or the entire specimen, depending on size, in undiluted commercial Clorox (sodium hypochlorite) for 10–25 minutes, or until the soft outer covering was dissolved. Skeletons were washed in several changes of water and dried at room temperature.

Color variations were noted and compared in live and frozen specimens only, but no detailed studies were made. Preserved material showed color loss and could not be considered reliable for comparisons.

Observations

Shape of arms.—The a/b ratios, measured on animals over a size range of R = 2–8 cm, from MAB populations of *A. forbesi* and *A. vulgaris* were weakly correlated with body size (R), but the degree of tapering was greater in all sizes of *A. vulgaris* (Table 1). The a/b ratios from Shoreham and Rockaway Beach populations of *A. forbesi* were not significantly correlated with body size and had similar mean a/b ratios (Shoreham \bar{x} = 2.23; Rockaway Beach \bar{x} = 2.16). *Asterias vulgaris* from Muscongus Bay likewise showed no statistically significant correlation between a/b and R, and had essentially the same a/b mean value (\bar{x} = 2.13) as that of the two shallow, coastal water populations of *A. forbesi*. In shape, therefore, small *A. vulgaris* from Muscongus Bay resembled *A. forbesi* of comparable size.

Table 1.—Correlation between body size (R) and shape of the ray (ratio a/b).

Population	<i>Asterias forbesi</i>			<i>Asterias vulgaris</i>			<i>Asterias rubens</i>		
	Rockaway	MAB	Shoreham	Gulf of Maine	MAB	Muscongus Bay	St. Andrews	NW Iceland	
a/b ratio range	1.7 to 2.5	1.2 to 3.3	1.0 to 3.4		2.0 to 5.0	1.1 to 3.3	1.7 to 6.2	1.7 to 3.1	
$\bar{x} \pm s$	2.16 \pm 0.28	2.32 \pm 0.47	2.23 \pm 0.47		3.52 \pm 0.39	2.13 \pm 0.39	3.195 \pm 1.008	2.39 \pm 0.46	
r	-0.082	0.506	0.219		0.502	-0.175	0.613	0.741	
P	NS	0.01	NS		0.01	NS	0.01	0.01	
N	21	55	45		47	50	23	18	
Slope	—	0.190	—		0.187	—	0.365	0.375	
Intercept	—	1.254	—		2.273	—	1.189	0.678	

Asterias rubens, in the range of $R = 2\text{--}9$ cm, from the St. Andrews and West Greenland populations exhibited statistically significant positive correlation between R and a/b ratios. The slopes for these populations were distinctly steeper than for MAB *A. vulgaris* of comparable size (Table 1).

Madreporite.—Madreporites from a wide range of animal sizes were measured, but only data from specimens of $R = 5\text{--}9$ cm were used for comparison of the diameter (size) and height (convexity) between the species. Few *A. forbesi* from the Shoreham and Rockaway Beach populations were under 4 cm and none of the *A. vulgaris* from Muscongus Bay or available specimens of *A. rubens* were over 9 cm. Within this size range, there was little intrapopulation variability in either size or convexity of the madreporites in any species.

The average diameter of the madreporites from animals of comparable size from the three populations of *A. forbesi* studied was $\bar{x} = 4.13$ mm, which was greater than diameters from populations of *A. vulgaris* ($\bar{x} = 3.30$ mm) or *A. rubens* ($\bar{x} = 2.82$ mm), a variation hardly perceptible to the naked eye (Table 2).

The height (convexity) of the madreporites showed no significant correlation with body size (R) within any populations. *Asterias forbesi* from all regions had slightly higher (more convex) madreporites ($\bar{x} = 1.18$ mm) than *A. vulgaris* ($\bar{x} = 0.76$ mm) and *A. rubens* ($\bar{x} = 0.80$ mm) from all populations (Table 2).

Pedicellariae.—Dorsal: Numerous dorsal, straight (major) pedicellariae of the short, rounded type (Coe 1912) were distributed over the abactinal surface between the dorsal spines in *A. forbesi* from all populations. These pedicellariae ranged in size from 0.33–0.49 mm (Table 2), with little size difference between the population.

Narrow, pointed major pedicellariae (Coe 1912) were the usual dorsal type in both *A. vulgaris* and *A. rubens*, but both broad and pointed forms were sometimes found together. In both species, major pedicellariae were always less numerous and more widely distributed than in *A. forbesi*. Dorsal pedicellariae from animals of comparable size from populations of *A. vulgaris* from the Gulf of Maine (0.47–0.63 mm) and the MAB (0.58–0.72 mm), and from the samples of *A. rubens* from Northwest Iceland (0.44–0.88 mm) were longer than those of *A. forbesi* (Table 2). On the other hand, the range of length of the dorsal pedicellariae (0.29–0.41 mm) in the Muscongus Bay population of *A. vulgaris* was shorter than in *A. forbesi*, but comparable to the range found in the St. Andrews specimens (0.31–0.47 mm) of *A. rubens* (Table 2). There was no correlation between length of the dorsal pedicellariae and body size (R) in any population (Table 3).

Ventral: All ventral, straight pedicellariae were longer than the dorsal pedicellariae. However, in all three species, we selected for study only the major pedicellariae from both the inner and outer adambulacral spines of the proximal region of the arm. Each spine usually carried from one to eight major pedicellariae on the outer surface of the distal half. The number and size of the pedicellariae gradually decreased distally in the arm.

In *A. forbesi*, the major pedicellariae were broad and blunt. Comparing the pedicellariae from animals of comparable size, the differences in mean length were statistically insignificant between those from subtidal populations (Rockaway Beach $\bar{x} = 0.54$ mm; Shoreham $\bar{x} = 0.50$ mm) and those from deeper (15–60 m) MAB stations ($\bar{x} = 49$ mm) (Table 2). In no population was there a significant correlation between body radius (R) and length of the pedicellariae (Table 3).

Table 2.—Size of skeletal structure, based on animals in size range R = 5–9 cm, except NW Iceland population which ranged from R = 4–9.5 cm.

Population	<i>Asterias forbesi</i>			<i>Asterias vulgaris</i>			<i>Asterias rubens</i>	
	Rockaway	MAB	Shoreham	Gulf of Maine	MAB	Muscogus Bay	St. Andrews	NW Iceland
Madreporite (diameter)								
Range (mm)	3.32–4.98	3.32–4.56	3.82–4.98	2.90–4.15	3.32–4.15	4.29–4.15	2.49–4.15	1.41–2.90
$\bar{x} \pm s$	4.15 \pm 0.5	4.03 \pm 0.3	4.29 \pm 0.3	3.17 \pm 0.4	3.56 \pm 0.3	3.18 \pm 0.4	3.42 \pm 0.5	2.26 \pm 0.4
n	5	14	9	8	5	15	9	6
Madreporite (height)								
Range (mm)	0.83–1.24	0.83–1.24	0.83–1.66	0.66–0.83	0.66–1.00	0.41–1.24	0.41–1.66	0.41–0.83
$\bar{x} \pm s$	1.15 \pm 0.1	1.15 \pm 0.2	1.24 \pm 0.3	0.78 \pm 0.07	0.79 \pm 0.1	0.73 \pm 0.2	0.93 \pm 0.3	0.67 \pm 0.14
n	5	14	9	8	5	15	9	6
Dorsal Pedicellaria								
Range (mm)	0.39–0.46	0.33–0.49	0.37–0.46	0.47–0.63	0.58–0.73	0.29–0.41	0.31–0.47	0.44–0.88
$\bar{x} \pm s$	0.41 \pm 0.037	0.40 \pm 0.46	0.412 \pm 0.27	0.54 \pm 0.041	0.54 \pm 0.034	0.37 \pm 0.046	0.41 \pm 0.047	0.55 \pm 0.06
n	6	6	6	17	5	6	10	6
Ventral Pedicellaria								
Range (mm)	0.41–0.62	0.37–0.88	0.42–0.60	0.55–0.88	0.58–0.73	0.47–0.65	0.48–0.70	0.66–0.89
$\bar{x} \pm s$	0.54 \pm 0.07	0.49 \pm 0.18	0.50 \pm 0.06	0.68 \pm 0.08	0.67 \pm 0.06	0.59 \pm 0.06	0.60 \pm 0.06	0.77 \pm 0.07
n	6	6	6	17	5	6	10	6
Outer Adambulacra								
Range (mm)	2.67–3.73	1.93–2.89	1.58–2.89	1.33–2.93	1.87–2.78	1.97–2.54	1.60–2.51	1.83–2.82
$\bar{x} \pm s$	2.94 \pm 0.04	2.49 \pm 0.03	2.43 \pm 0.05	2.31 \pm 0.5	2.38 \pm 0.3	2.20 \pm 0.2	2.16 \pm 0.3	2.34 \pm 0.3
n	6	6	6	17	6	6	10	6
Inner Adambulacra								
Range (mm)	2.47–3.28	1.88–2.94	1.97–3.33	1.47–2.89	2.09–2.58	1.99–2.77	1.88–2.44	1.58–2.49
$\bar{x} \pm s$	2.82 \pm 0.3	2.42 \pm 0.4	2.76 \pm 0.5	2.29 \pm 0.5	2.34 \pm 0.2	2.33 \pm 0.3	2.27 \pm 0.2	2.08 \pm 0.3
n	6	6	6	17	6	6	10	6
Outer Orals								
Range (mm)	3.48–3.79	2.24–4.23	2.56–3.79	2.49–4.56	2.90–3.79	2.49–2.98	2.49–3.73	1.58–4.98
$\bar{x} \pm s$	3.70 \pm 0.1	3.16 \pm 0.7	3.24 \pm 0.5	3.21 \pm 0.6	3.39 \pm 0.4	2.82 \pm 0.3	2.99 \pm 0.3	3.25 \pm 1.1
n	6	6	6	15	5	6	10	6
Inner Orals								
Range (mm)	2.20–3.13	1.16–3.11	1.76–3.30	0.83–2.82	1.16–2.36	1.00–2.55	0.96–1.93	1.16–2.32
$\bar{x} \pm s$	2.68 \pm 0.3	2.36 \pm 0.7	2.38 \pm 0.5	1.73 \pm 0.6	1.55 \pm 0.5	1.62 \pm 0.5	1.35 \pm 0.3	1.85 \pm 0.6
n	6	6	6	15	5	5	10	6

Table 3.—Correlation between body size (R) and structure.

	<i>Asterias forbesi</i>			<i>Asterias vulgaris</i>			<i>Asterias rubens</i>		
	Rockaway	MAB	Shoreham	Gulf of Maine	MAB	Muscongus Bay	St. Andrews	W. Greenland	NW Iceland
Range (R) (cm)	6.5–10.0	2.8–8.9	3.8–10.0	2.3–12.5	3.7–13.5	4.2–10.4	2.2–8.9	3.1–6.0	2.0–9.5
Dorsal Pedicellaria									
Structure range (mm)	0.35–0.48	0.32–0.49	3.5–0.46	0.41–0.67	0.47–0.77	0.29–0.49	0.23–0.47	0.33–0.50	1.7–4.8
N	10	10	10	32	10	14	17	10	8
r	0.243	0.465	0.320	0.561	0.816	0.258	0.439	0.758	0.796
P	NS	NS	NS	0.01	0.01	NS 0.05	NS 0.05	0.05	0.05
Slope	—	—	—	0.010	0.022	0.006	—	0.056	0.299
Intercept	—	—	—	0.482	0.412	0.349	—	0.668	1.00
Ventral Pedicellaria									
Structure range (mm)	0.41–0.64	0.36–0.48	0.42–0.60	0.50–0.88	0.55–0.74	0.41–0.68	0.39–0.70	0.55–0.75	0.40–0.63
N	10	10	10	32	10	14	18	18	8
r	0.097	0.554	0.298	0.545	0.650	0.536	0.702	0.296	0.468
P	NS	NS	NS	0.01	0.05	0.05	0.01	NS	NS
Slope	—	—	—	0.017	0.017	0.185	0.034	—	—
Intercept	—	—	—	0.570	0.528	0.452	0.367	—	—
Outer Adambulacral Spine									
Structure range (mm)	2.71–3.75	1.69–2.89	1.58–2.89	1.14–3.90	1.50–4.01	1.73–3.48	0.93–2.51	1.41–1.99	1.49–2.66
N	10	10	10	32	10	14	18	18	8
r	0.708	0.958	0.901	0.830	0.907	0.942	0.792	–0.231	0.856
P	0.05	0.01	0.01	0.01	0.01	0.01	0.01	NS	0.01
Slope	0.193	0.702	0.195	0.179	0.207	0.881	0.204	—	0.151
Intercept	1.408	1.047	0.823	1.11	0.967	0.753	0.741	—	1.26

Table 3.—Continued.

	<i>Asterias forbesi</i>			<i>Asterias vulgaris</i>			<i>Asterias rubens</i>		
	Rockaway	MAB	Shoreham	Gulf of Maine	MAB	Muscongus Bay	St. Andrews	W. Greenland	NW Iceland
Inner Adambulacral Spine									
Structure range (mm)	2.47–3.48	1.70–2.94	1.66–3.33	1.17–4.32	1.56–4.02	1.56–3.76	1.22–2.51	1.21–1.99	1.41–2.49
N	10	10	10	32	10	14	18	18	8
r	0.569	0.913	0.974	0.828	0.949	0.942	0.841	0.231	0.948
P	NS	0.01	0.01	0.01	0.01	0.01	0.01	NS	0.01
Slope	—	0.191	0.762	0.197	0.218	0.881	0.207	—	0.135
Intercept	—	1.067	0.617	1.01	0.897	0.653	0.787	—	1.16
Outer Oral Spine									
Structure range (mm)	3.48–4.92	2.24–4.23	2.34–3.94	1.08–5.67	1.99–4.15	2.49–4.40	1.24–3.73	1.41–2.90	1.49–4.98
N	10	10	10	28	10	14	18	10	8
r	0.772	0.256	0.913	0.563	0.750	0.712	0.789	0.881	0.964
P	0.01	NS	0.01	0.01	0.05	0.01	0.01	0.01	0.01
Slope	0.251	—	0.215	0.180	0.170	0.240	0.277	0.451	0.430
Intercept	1.812	—	1.627	1.749	2.07	1.51	1.008	0.100	0.355
Inner Oral Spine									
Structure range (mm)	2.20–3.88	1.16–3.11	1.77–3.30	0.75–3.30	1.16–3.24	1.00–2.82	0.75–1.93	0.83–1.41	0.50–2.90
N	10	10	10	29	10	12	18	9	8
r	0.459	0.501	0.818	0.708	0.863	0.696	0.699	0.733	0.936
P	NS	NS	0.01	0.01	0.01	0.05	0.01	0.05	0.01
Slope	—	—	0.172	0.176	0.199	0.196	0.128	0.150	0.261
Intercept	—	—	1.158	0.462	0.266	0.706	0.447	0.428	0.068

The major ventral pedicellariae in *A. vulgaris* and *A. rubens* were longer and more pointed than those of *A. forbesi* (Table 2). Variation in the mean length of the pedicellariae did not differ significantly between populations of *A. vulgaris* (Gulf of Maine \bar{x} = 0.68 mm; MAB \bar{x} = 0.67 mm; Muscongus Bay \bar{x} = 0.59 mm) and *A. rubens* (St. Andrews \bar{x} = 0.60 mm; N.W. Iceland \bar{x} = 0.77 mm) (Table 2). A weak but significant correlation with body radius (R) was noted in all populations of *A. vulgaris*, but only in the St. Andrews population of *A. rubens* (Table 3).

Skeleton and spines.—The main divisions of the *Asterias* skeleton (ambulacral, actinal, marginal, dorsolateral, carinal) are based on the principal longitudinal rows of inbricated ossicles, rigidly held together throughout life, except in the dorsolateral region where there is a loose, irregular connection between ossicles which forms an open meshwork. Details of ossicle morphology have not been adequately described in *Asterias* and a standard terminology has not been established. Consequently, many of the terms used in this study to describe skeletal structures follow those presented by Turner and Dearborn (1972) for the mud-star *Ctenodiscus crispatus*, in addition to those employed for *A. amurensis* (Fisher, 1930) and for *A. forbesi* and *A. vulgaris* by Hyman (1955).

Ossicle designates the large, calcarious structures which make up the basic rigid framework of the skeleton (Fig. 1A). Ossicles are typically quadrilateral, except in the dorsolateral region where 2–6 sided forms are found. They regularly have one or more *pustules*, mound-like elevations or *bosses*, with a central depression, the *spine pit*, for the attachment of the spine (Fig. 1A). A projection, or *process* from each side of the ossicle forms a suture or junction with a process from an adjacent ossicle either directly, by overlapping or underlapping, or indirectly by one or more narrow, bar-like, overlapping *plates*. These are flattened, calcareous structures, smaller than ossicles and usually without processes, pustules, or spines (Fig. 1B). Connections between the ossicles are called *arches* (Hyman 1955). Longitudinal rows of parallel arches were designated *channels* by Fisher (1930). In the spaces between the arches, the *fenestrae* (Hyman 1955), a membrane stretched between the walls of the arches, is perforated by a regularly arranged ring of a fairly specific number of openings for the papulae (Fig. 1B).

Actinolateral ossicles.—In all three species of *Asterias*, the actinolaterals usually do not overlap but form a row along the outer edge of the adambulacral ossicles (Figs. 2–4). Each actinolateral forms sutures internally with two or three underlying adambulacral ossicles. The actinolaterals are small, dorsoventrally thickened and have short, blunt anterior and posterior processes. In *A. forbesi* the dorsal (abactinal) process of each ossicle is elongated and forms a suture directly with the elongated ventral (actinal) process of the adjacent inferomarginal ossicle to form a small, round arch, within which the fenestra membrane bears a single ring of 4–6 openings (Fig. 1B). This row of arches forms the actinal channel of Fisher (1930).

In *A. vulgaris*, and *A. rubens*, the dorsal processes of the actinolateral ossicles are short and connect with the short, blunt ventral processes of adjacent inferomarginal ossicles by single plates, each of which may bear a spine in the proximal part of the arm (Figs. 3, 4). The arches thus formed are dorsoventrally oblong, larger than those in *A. forbesi*, and the membrane within the fenestra has a ring of 5–8 openings.

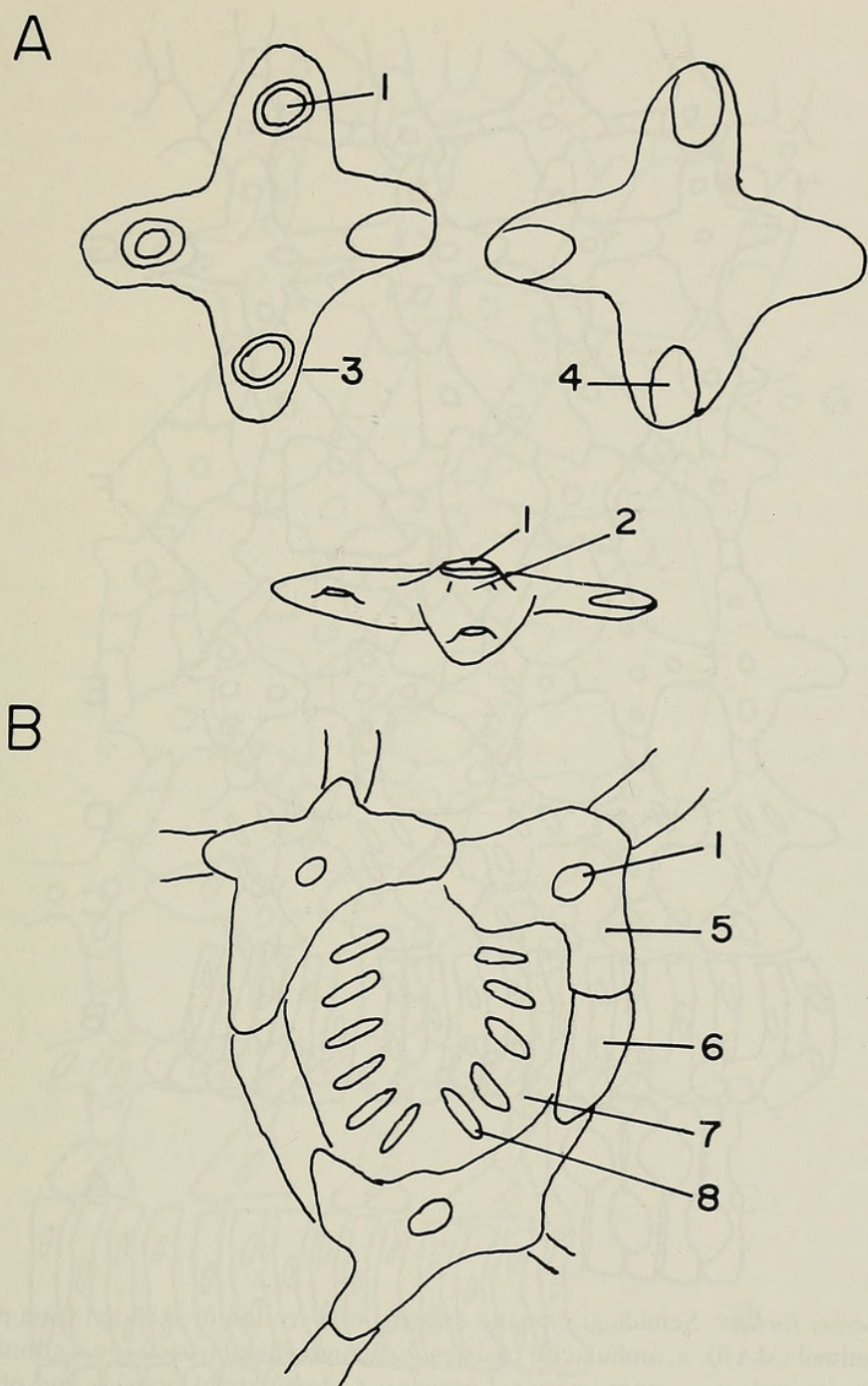


Fig. 1. *Asterias forbesi*. A, Diagrammatic views of a typical dorsolateral ossicle: outside (above left), inside (above right), side view (center). B, Diagram of a typical arch: 1, spine pit; 2, pustula; 3, process; 4, articulation depression; 5, ossicle; 6, plate; 7, membrane in fenestra; 8, opening for papula.

Inferomarginal ossicles.—The inferomarginal ossicles in all three species of *Asterias* form a prominent longitudinal row of large, closely imbricated, quadrilateral ossicles dorsal to the actinolaterals on the ventral (actinal) side of the animal. Each ossicle bears 3–4 pustules with slit-shaped, obliquely arranged spine pits, the most posterior of which lies nearest the ambulacral groove (Figs. 2–4). In *A. forbesi*, the dorsal (abactinal) processes of the interomarginal ossicles are elongated and pointed. Each articulates either directly, or by a single plate, with the ventral (actinal) process of the adjacent superomarginal ossicle (Fig. 2), thus forming a row of rounded arches, designated the intermarginal channel by Fisher

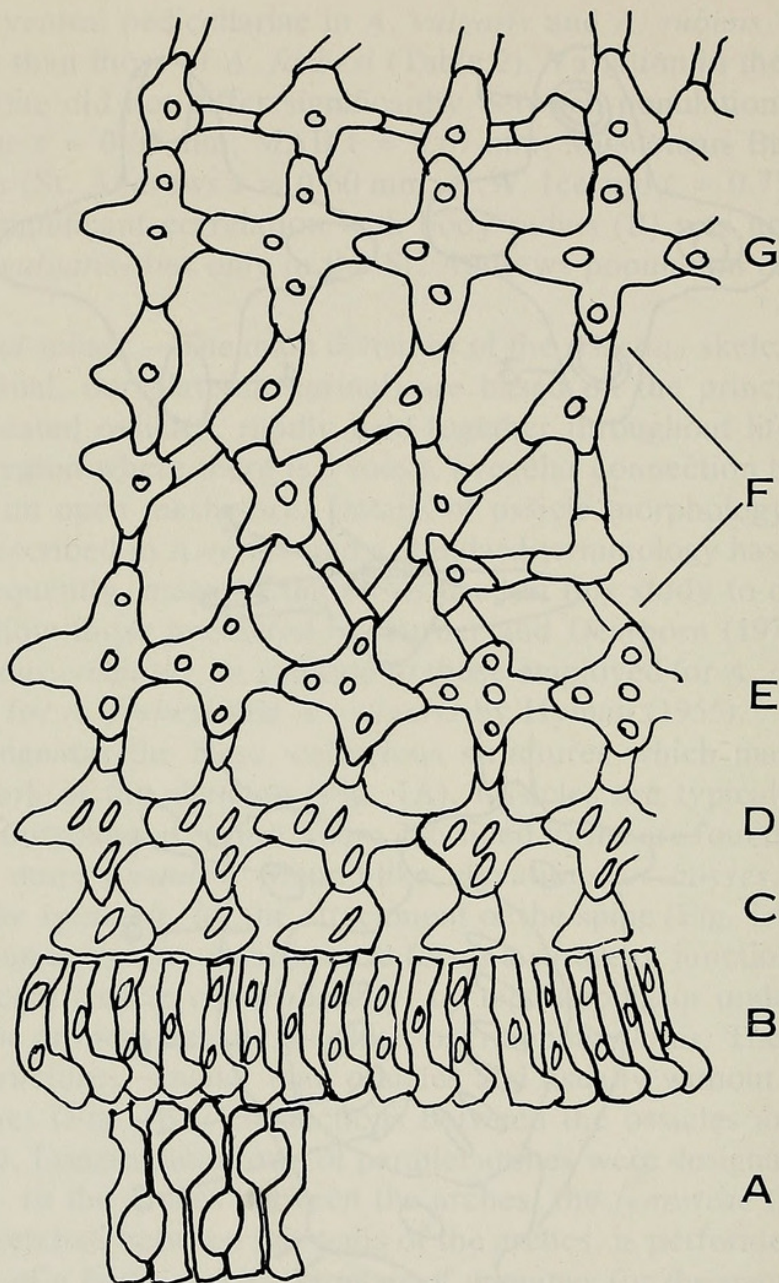


Fig. 2. *Asterias forbesi*. Semidiagrammatic drawing of a section of skeleton from proximal region of left side of animal (MAB). a, ambulacral ossicles; b, adambulacral ossicles; c, actinolateral ossicles; d, inferomarginal ossicles; e, superomarginal ossicles; f, dorsolateral ossicles and plates; g, carinal ridge. $\times 3$.

(1930). The membrane within each fenestra contains an elongated ring of 8–10 openings.

In *A. vulgaris* and *A. rubens*, the dorsal processes of the inferomarginal ossicles are short and blunt and connect with the ventral processes of the superomarginals by at least one plate, thus forming oval arches which are larger than those of *A. forbesi*, especially in large animals (Figs. 3, 4). The membrane within each fenestra may have as many as 16–18 openings arranged in an elongated ring.

Superomarginal ossicles.—The superomarginal ossicles in all three species of *Asterias* form a strong, prominent longitudinal overlapping row along each margin (ambitus) of the ray dorsal to the inferomarginals (Figs. 2–4). Each ossicle has a

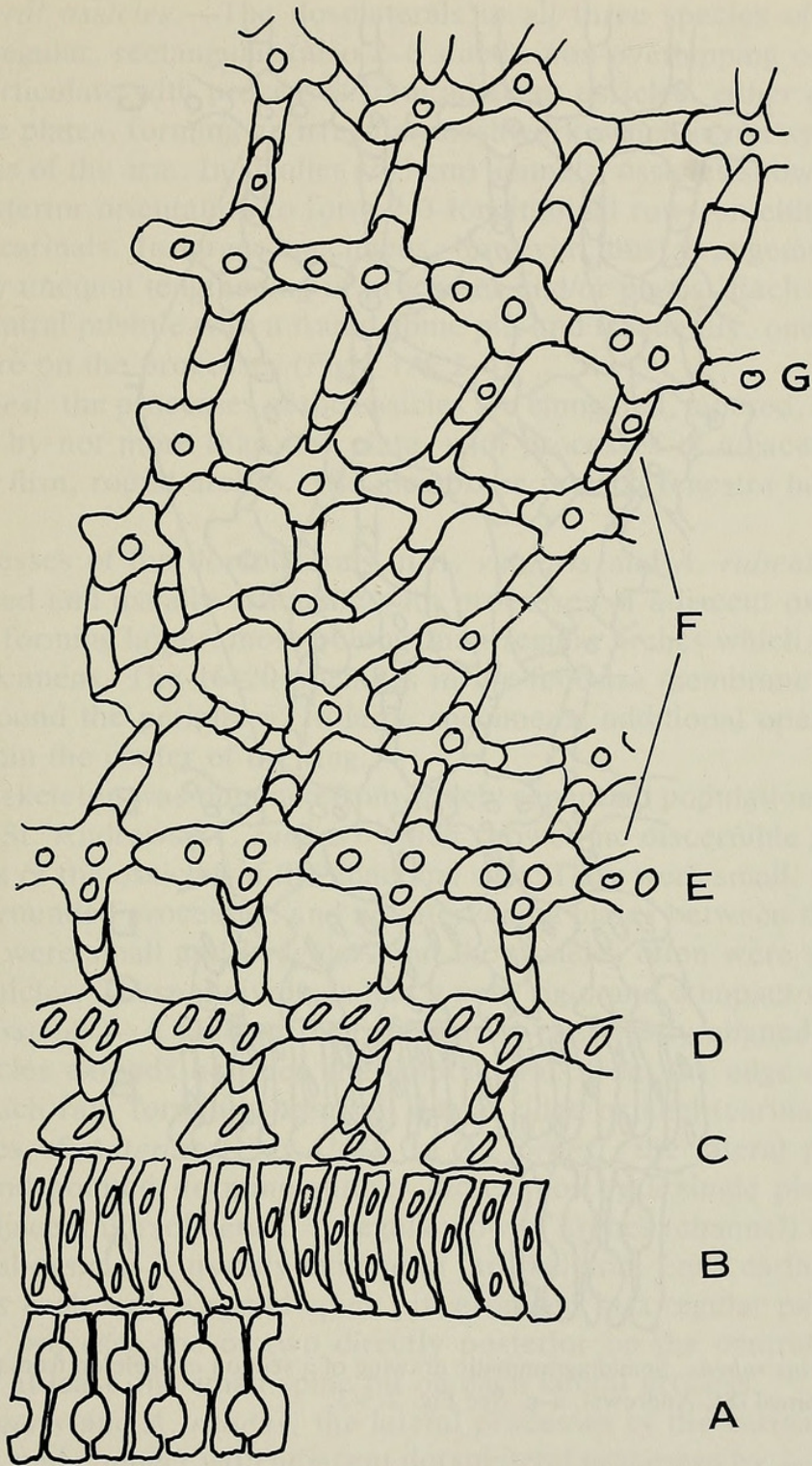


Fig. 3. *Asterias vulgaris*. Semidiagrammatic drawing of a section of skeleton from proximal region of left side of animal (MAB). a-g. See Fig. 2. $\times 3$.

short anterior process which overlaps a longer posterior process of the preceding ossicle, a ventral (actinal) process which forms a suture with a dorsal (abactinal) process forming a junction, either directly or indirectly by one or more plates with an actinal process of the adjacent dorsolateral ossicle.

In *A. forbesi*, the superomarginal ossicles are smaller and flatter than the inferomarginals. Each ossicle has 3-5 round spine pits, one on the anterior process,

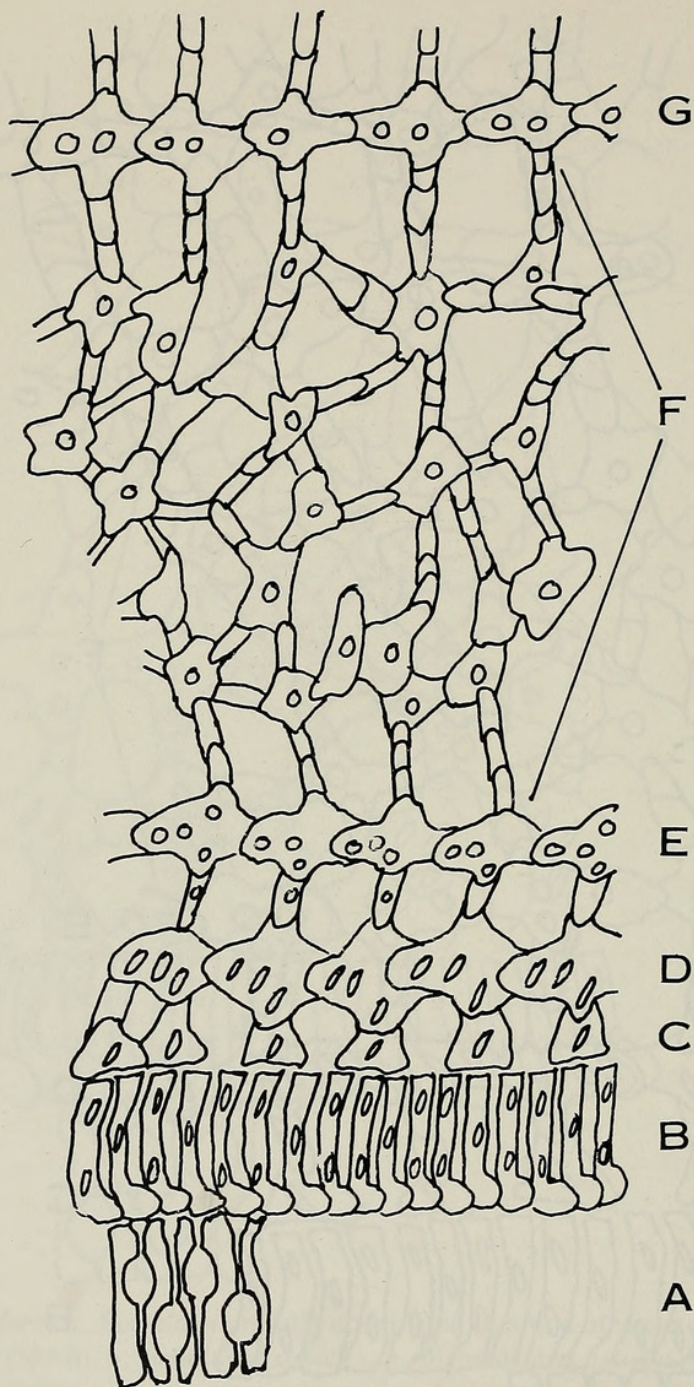


Fig. 4. *Asterias rubens*. Semidiagrammatic drawing of a section of skeleton from proximal region of left side of animal (St. Andrews). a-g. See Fig. 2. $\times 3$.

one or two on the central boss, and one on each lateral process. Both of the lateral processes are elongated and articulate directly, or by a single short plate, with adjacent processes, thus forming two rows of arches. Each fenestra membrane contains 16–20 openings which are scattered throughout the entire area.

The anterior and posterior processes of the superomarginals in *A. vulgaris* and *A. rubens* are elongated, but the lateral processes are short and blunt (Figs. 3, 4). Each ossicle has three round spine pits, two on the central boss and one on the actinal process. Articulation with the adjacent dosolateral ossicles is by 1–3 elongated plates forming a row of large arches. The 16–20 openings in each fenestra membrane are arranged in a ring along the periphery of the arch.

Dorsolateral ossicles.—The dorsolaterals in all three species of *Asterias* are typically irregular, rectangular (also 2–6 sided), non-overlapping ossicles whose processes articulate with processes from adjacent ossicles, either directly or by one or more plates, forming an irregular meshwork which is not symmetrical on the two sides of the arm. In smaller (2–3 cm) animals, ossicles show more regular anterior-posterior orientation to form 2–3 longitudinal rows on either side of the mid-dorsal carinals. In larger specimens, however, this arrangement is usually obscured by unequal lengthening of processes and/or plates. Each ossicle has at least one central pustule with a round spine pit, and frequently, one or two small spine pits are on the processes (Figs. 1A, 2–4).

In *A. forbesi*, the processes of the ossicles are elongated, tapered, and articulate directly, or by not more than one plate, with processes of adjacent ossicles to form small, firm, round arches. The membrane in each fenestra has 8–10 openings.

The processes of the dorsolaterals in *A. vulgaris* and *A. rubens* are shorter, more rounded and usually articulate with processes of adjacent ossicles by 1–3 plates, thus forming larger, more oblong and irregular arches which are quite long in large specimens. The 16–20 openings in the fenestra membrane are arranged in a ring around the periphery. In large specimens, additional openings may be present within the center of the ring.

Rarely, a skeleton was obtained from widely separated populations (Shoreham, *A. forbesi*; St. Andrews, *A. rubens*) which showed no discernible pattern in the arrangement of the ossicles of the abactinal side. They were small, nearly square with short, rounded processes, and no intervening plates between the processes. The arches were small and irregular, and the ossicles often were superimposed on other ossicles. These individuals had a very rigid and compact skeleton.

Carinal ossicles.—A median row of anterior-posteriorly aligned, overlapping carinal ossicles extends between the dorsolaterals from the edge of the disc to the tip of each ray, forming a central, dorsal ridge or keel (carinal ridge) in all three species of *Asterias* (Figs. 2–4). In *A. forbesi*, the lateral processes are elongated and pointed, forming sutures directly or by a single plate, with processes of adjacent dorsolaterals. A regular row of arches (channel) on either side of the carinal ossicles is usually evident in the skeleton. Each carinal ossicle has 3–4 pustules each with a round spine pit, arranged in a regular pattern; one on the anterior process, one or two directly posterior on the central body of the ossicle, and at least one small spine pit on each lateral process.

In *A. vulgaris* and *A. rubens*, the lateral processes of the carinal ossicles are short, blunt, and connect with adjacent dorsolateral processes by 2–3 overlapping plates forming a distinct row of arches on either side of the carinal ossicles. Each ossicle has one or two pustules, one in front of the other along the median ridge of the ossicle. This arrangement results in a more or less straight, single row of spines along the median dorsal ridge of the arm (the carinal ridge).

Adambulacral spines.—The adambulacral spines in the proximal region of the arms in all three species of *Asterias* were more or less regularly arranged in the typical *Asterias* alternating 1-2-1-2 etc. pattern (Mortensen 1929) forming three rows, an inner series along the edge of the ambulacral groove, a middle, and an outer row. Only spines from the inner and outer rows were measured and compared (Fig. 5A, B).

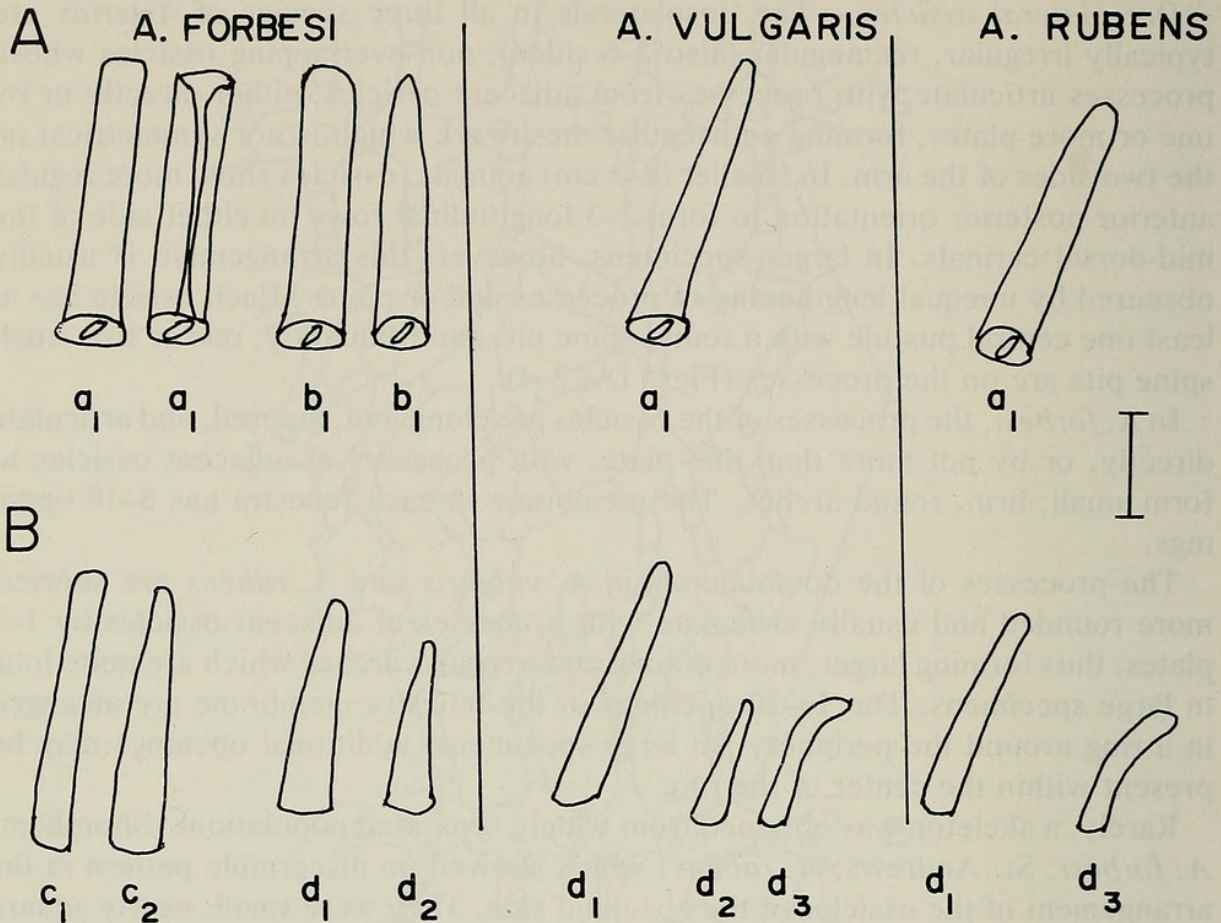


Fig. 5. Diagrammatic outer views of typical adambulacral and oral spines from *Asterias forbesi*, *A. vulgaris* and *A. rubens*. A, Adambulacral spines: a_1 , typical form of outer spines; a_2 , grooved form; b_1 , typical form of inner adambulacral spines; b_2 , pointed form. B, Oral spines: c_1 , typical outer oral spine; c_2 , pointed form; d_1 , typical inner oral spine; d_2 , pointed form; d_3 , curved form. Scale line equals 1 mm.

The length of the inner and outer adambulacral spines in *A. forbesi* was comparable in the three populations studied (Table 2), ranging between a low of 1.58 mm to a high of 3.33 mm. In all populations, both inner and outer ambulacral spines were truncate, wide, (\bar{x} = 0.66 mm) and flattened. The outer spines were frequently grooved on the outer side (Fig. 5). Thinner, more pointed spines were sometimes found among the more truncate forms.

In *A. vulgaris* and *A. rubens*, both inner and outer adambulacral spines were typically round, pointed (Fig. 5), and approximately within the same length range (1.33–2.93 mm) as those in *A. forbesi* in animals within the same size range (Table 2). The slightly narrower average width (\bar{x} = 0.5 mm) of the *A. vulgaris* spines tended to give the rows a more delicate and crowded appearance, but in animals in the same size range, there was no significant difference among the species in the actual number of spines present per row. Double-pointed as well as flat, but ungrooved, truncate spines sometimes occurred along with the pointed spines.

The adambulacral spines in all species exhibited a strong correlation with body radius (R) (Table 3). While the slope for both types of spines was steep in all populations (Table 3), the Muscongus Bay population (*A. vulgaris*) showed the steepest slope for both inner and outer adambulacral spines (Table 3).

Oral spines.—The inner and outer oral spines in *A. forbesi* were about the same length or slightly longer than the adambulacral spines (Table 2), and resembled them in shape, but were not grooved. Occasionally an animal was found with larger and more pointed oral spines. Significant correlation between length of the outer oral spines and body radius (R) was evident in the Rockaway Beach ($r = 0.772$) and Shoreham ($r = 0.913$) populations (Table 3) but not in those from the MAB ($r = 0.256$). Inner oral spines showed significant size correlation only in the Shoreham population ($r = 0.818$) (Table 3). There was no significant difference in the three populations in the mean ratio between length of inner/outer oral spines (Rockaway Beach $\bar{x} = 0.72$ mm; Shoreham $\bar{x} = 0.76$ mm; MAB $\bar{x} = 0.74$ mm).

In both *A. vulgaris* and *A. rubens*, however, there was a difference in size and shape between the inner and outer oral spines (Table 2). The inner oral spines were shorter, slightly curved, narrow, and sharply pointed while the outer oral spines were longer, straight, narrow, round, and pointed (Fig. 5C, D). Neither truncate nor grooved oral spines were found in any population. The correlation of body radius (R) and oral spine length was significant in all populations (Table 3). The mean inner/outer spine ratios in *A. vulgaris* (Gulf of Maine $\bar{x} = 0.58$; Muscongus Bay $\bar{x} = 0.54$; MAB $\bar{x} = 0.516$) were lower than those in *A. forbesi*, but not significantly different from *A. rubens* (St. Andrews $\bar{x} = 0.46$, West Greenland $\bar{x} = 0.53$; Northwest Iceland $\bar{x} = 0.54$). There was greater difference in length between the inner and outer oral spines in both *A. vulgaris* and *A. rubens* than was found in *A. forbesi*.

Color.—Color patterns and intensities in both *A. forbesi* and *A. vulgaris* showed wide variation between different stations but in each species, a distinct intrapopulation color pattern tended to predominate in a given locality (Coe 1912). In *A. vulgaris* from the MAB, the basic color of the abactinal surface was yellowish to reddish brown with varying amounts of bluish purple ranging from a narrow band along the carinal ridge to being suffused over the aboral surface from the dark purple disc to the tips of the arms, hence the name of “purple starfish.” Specimens of *A. vulgaris* from deep locations (200 m) from the Gulf of Maine were cream colored to light tan. Animals from Muscongus Bay ranged from light brown to deep reddish brown and purplish blue. Spines on animals from all locations were light yellow and not conspicuous against the pale color of the dermis.

Asterias forbesi from the MAB were reddish and abactinal markings were darker blue than those of the lighter, yellowish colored, sympatric *A. vulgaris*. Live Rockaway Beach animals were usually a uniform, deep red, but occasionally lighter forms were found. Light (white or yellowish) colored spines outlined the arms and frequently formed a definite carinal ridge. Irregular longitudinal rows of dorsolateral spines often made a distinct pattern against the dark color of the aboral surface.

Discussion

Characters that showed significant size-relationship to body radius (R) included inner and outer adambulacral spines and inner and outer oral spines in all three species; and the tapering of the arm (a/b ratio) in *A. vulgaris* (except from Muscongus Bay), and *A. rubens*.

Characters that did not show significant size relationships in any species included dorsal pedicellariae; ventral pedicellariae; madreporites.

Characters that were significantly different in size and/or shape among the species included ventral pedicellariae; inner oral spines; inner and outer adambulacral spines (shape); ossicles (shape); madreporite (shape).

Some of the structures which show correlation between size and body radius (R) are associated with functions which increase with growth of the animal. The adambulacral spines, for example, extend over the ambulacral canal and protect the underlying podia (Hyman 1955). As the canal widens with growth of the animal, the spines lengthen to continue coverage of the canal. The oral spines, which cover the oral region, also lengthen with increase in body size to maintain their protective function. Tapering of the arms (greater a/b ratio), on the other hand, in *A. vulgaris* and *A. rubens* increases as the animal grows due to the lengthening of the greater number of connections (plates) between the ossicles in the proximal region of the arms than in the distal portion. In *A. forbesi* where growth of the arm is more uniform throughout its length, there is less tapering (a lower a/b ratio).

Ventral and dorsal pedicellariae and the madreporite, which are not significantly size-related, serve essential functions which do not change as the animal grows. These structures attain their optimal size at an early age of the animal and do not change significantly.

Structures (ventral pedicellariae, madreporite) which show significant differences among the three species in size and/or shape have long been considered diagnostic. Coe (1912) suggested that the difference in size and shape of the major ventral pedicellariae in *A. forbesi* and *A. vulgaris* was the most reliable criterion for species identification. Comparison of measurements of these structures from widely separated populations justifies this conclusion. While the shape of the ventral pedicellariae is similar in *A. vulgaris* and *A. rubens*, there are differences in size. Ventral pedicellariae from *A. vulgaris* of Muscongus Bay have a slightly lower size range than (other) *A. vulgaris* from the Gulf of Maine or MAB. However, this range falls within that of ventral pedicellariae from the St. Andrews population of *A. rubens*, but is shorter than those of *A. rubens* from N.W. Iceland. Variations in size would therefore appear to be population related and not species specific.

The difference in the color of the madreporites in *A. forbesi* and *A. vulgaris* has usually been considered more significant for species identification than shape and size (Coe 1912; Aldrich 1956; Gray *et al.* 1968). However, the greater convexity of the structure in *A. forbesi* was described in detail by Verrill (1866). This difference in shape is slight but significant and may not be readily detected except by comparison of measurements.

Some structures which are significantly different in *A. forbesi* and *A. vulgaris* are variable and have not been listed as diagnostic. In this group are included the outer and inner adambulacral and outer and inner oral spines. Verrill (1866) and later Clark (1904) noted the predominance of blunt, grooved adambulacral spines in *A. forbesi* compared to the slender, often pointed spines of *A. vulgaris*. In the specimens available for the present study, the shape of most of the adambulacral spines of a specimen corresponded to this distinction, although both types of spines were often found together in the same animal. This situation is not an indication of hybridization, but rather the expression of a polymorphic structure (Schopf and Murphy 1975).

Clark (1904) noted that the oral spines in *A. forbesi* and *A. vulgaris* were "not peculiar." However, in the animals of the present study, the inner oral spines showed variability both in size and shape. In *A. vulgaris* and *A. rubens*, the inner oral spines were on the average shorter than the outer oral spines and usually curved, while in *A. forbesi*, the inner orals were straight and approximately equal in length to the outer orals. The difference between the lengths of the inner orals measured in *A. vulgaris* and in the few representatives of *A. rubens* available suggest that it would be interesting to evaluate the mean size of these structures between and within larger samples of both *A. vulgaris* and *A. rubens* populations. When inner oral spines of *A. vulgaris* from all areas were compared with those of the St. Andrews population only, the difference between the mean size was slightly greater in *A. vulgaris* ($\bar{x} = 1.85$ mm) than in the *A. rubens* population ($\bar{x} = 1.33$ mm) and statistically significant at the $P = 1.0$ level but not at the $P = 0.5$ level.

If the observations of Fisher (1930) on *A. amurensis*, the North Pacific species, are compared with the present results, the resemblance, especially in the adambulacral spines and the inner oral spines, to the North Atlantic species is evident. Fisher described the adambulacral spines of *A. amurensis* as long, compressed, tapered, bluntly pointed and grooved, a description resembling that for the adambulacral spines usually found in *A. forbesi*. The inner oral spines were described as curved, tapering and blunt, the shape which is comparable to that regularly found in *A. vulgaris* and *A. rubens* and infrequently in *A. forbesi*. These, and other close resemblances suggest a common ancestor for the species.

Descriptions in the literature of the skeletal structures of *Asterias* spp. are generalized and incomplete. Mortensen (1927) called the dorsal skeleton of *A. rubens* faintly developed. Verrill (1866) distinguished the skeleton of *A. forbesi* from that of *A. vulgaris* by the larger number of plates in the dorsal area which gave it a "stout" condition. In *A. vulgaris*, the lateral plates were described as separated by large spaces and were connected by plates broken into distinct pieces. Hyman (1955) recognized a basic, reticulate pattern but the diagram she presented was reproduced from Fisher (1928) and was based on Pacific forms of *Asterias*. Gray *et al.* (1968) called the skeleton of *A. forbesi* a mosaic of interlocking plates of ossicles, and that of *A. vulgaris* a network of narrow, bar-like plates forming a weak skeleton.

Basically, the skeletons of the three species of *Asterias* are equally strong and well developed, and the arrangement of the main ossicles all follow the same general pattern (Figs. 2-4). The essential differences in the skeletal structure among the species are the shape of the lateral processes (long, pointed in *A. forbesi*; short, blunt in *A. vulgaris* and *A. rubens*), and the greater number of plates between the processes in *A. vulgaris* and *A. rubens*. These differences are associated with the rigidity, shape, and tapering (a/b ratio) of the arms. In *A. vulgaris* and *A. rubens*, where the plates elongate during the growth of the animal, lateral distance between the ossicles, especially in the dorsolateral region, increases and forms the open meshwork with elongate fenestrae resulting in a more flaccid skeleton. This less rigid arrangement also gives the arms a flatter and wider appearance, especially in the proximal portion. However, in the distal part of the arms, the plates between the processes remain small or absent forming a tight, rigid meshwork and producing the tapering of the arms and an increased

a/b ratio. In *A. forbesi*, on the other hand, where the skeletal meshwork is formed by sutures between elongated processes with only one or no connecting plates, a more rounded and rigid framework results throughout the length of the arm giving a lower a/b ratio. Elongation of the several plates between processes in *A. vulgaris* and *A. rubens* may be one explanation for these species attaining a greater size than is possible in *A. forbesi* where growth of the skeleton is limited principally to elongation of the processes directly connecting the ossicles.

Local populations of *A. rubens* with rigid, straight and rounded arms have been described from several locations (N.W. Iceland, Heding 1892 museum label; Scandinavia, Masden, pers. comm.; Great Britain, Vevers 1947). These morphs may result from variations in the size and/or number of the connecting plates. Similarly, the *forbesi*-like animals from the Muscongus Bay population may be juveniles of *A. vulgaris* in which the plates in the proximal dorsolateral region have not elongated. No specimens of otherwise typical *A. forbesi* have been described as having flaccid skeletons. Hence, the invariably rigid skeleton would appear to have become a genetically fixed characteristic in *A. forbesi*.

The more frequent occurrence of a prominent carinal ridge in *A. vulgaris* and *A. rubens* than in *A. forbesi* may also be related to the greater dependence of the more flexible skeletons on a stronger, more rigid central keel for support.

Our observations, as well as those of all other workers, clearly demonstrate distinctive differences between *Asterias forbesi* and *A. vulgaris*, differences both at the morphological and structural as well as the physiological and ecological levels. These differences are clearcut in spite of marked genetic similarity (Schopf and Murphy 1975). The co-occurrence of such closely-related congeners in the shallow shelf of the N.W. Atlantic is rather remarkable, particularly in view of the overlapping ecological and spatial niches of the species, and the probable high degree of competition in areas of sympatry, and the generally low overall diversity of asteroids in the Middle-Atlantic continental shelf of the NW Atlantic. We attempt to provide a historical hypothesis to account for the co-occurrence of these species in the following section.

The specific identity of *A. vulgaris* vis-a-vis *A. rubens* is not resolved in this study; moreover, descriptive analyses of morphological characteristics probably can not produce a definitive answer. Our results indicate that populations of *A. vulgaris* from the Gulf of Maine and MAB differ from the St. Andrews population of *A. rubens* in skeletal structures such as the dorsal and ventral pedicellaria (Table 2), but that these small differences disappear in significance when the Muscongus Bay population of *A. vulgaris* and the N.W. Iceland population of *A. rubens* are included in the comparison. Thus, from a strict descriptive taxonomic viewpoint, we can provide no basis for maintaining *A. vulgaris* as distinct from *A. rubens*, even though populations of *A. vulgaris* are geographically isolated from *A. rubens*. Even assuming the questionable existence of a permanent population of *A. rubens* in S.W. Greenland, the directional flow of surface currents along the W. Greenland coast in the Davis Strait, and the absence of *Asterias* populations in Labrador, imply essentially complete geographical isolation of populations of *A. vulgaris* in the Gulf of St. Lawrence from the nearest major concentrations of *A. rubens* in Iceland.

Since the major difference between the geographical zone of *A. rubens* in the N.E. Atlantic and *A. vulgaris* in the N.W. Atlantic is the thermal environment

rather than the structure of biotic communities, we would predict that genetic differentiation would involve primarily physiological rather than morphological traits—and these have not been investigated. Until this is done, we believe that the most parsimonious approach to the question of taxonomy would be to conserve the status quo, i.e., while recognizing the very close genetic and taxonomic relationships between *A. vulgaris* and *A. rubens*, to continue to consider them as separate species until more relevant aspects of their biology can be evaluated.

Hybridization Between *Asterias forbesi* and *Asterias vulgaris*

Hybridization between *A. forbesi* and *A. vulgaris* is often assumed to occur, and to account for the existence of individuals with external characters intermediate between typical *A. forbesi* and *A. vulgaris*. Given the genetic similarity demonstrated by Schopf and Murphy (1975), such hybridization might be expected. However, evidence for hybridization is very weak; and, to the best of our knowledge, is limited to the occurrence of morphological “intermediates.” Even the work of Ernst (1967), cited as containing experimental evidence for hybridization, contains no conclusive evidence proving that hybridization occurs under natural conditions.

After examining thousands of individuals of both species from the Middle Atlantic continental shelf, including many from the geographical zone of sympatry, we have never observed an individual which could not be assigned with confidence to one or the other species. While it is possible that hybrids may occur in shallow waters near Cape Cod, this was discounted by Clark (1923:235), who stated unequivocally that “. . . if such hybrids occur they must be very rare, for there are no authentic specimens on record or extant, as far as I know.” Moreover, sympatric populations of *A. forbesi* and *A. vulgaris* which occur in the SW Gulf of Maine (Isle of Shoals area) are distinguishable morphologically and ecologically (Hulbert 1980, pers. comm.).

The possibility that *A. forbesi*-like animals occurring in embayments along the Maine Coast may represent hybrids seems unlikely to us. Inshore populations of typical *A. forbesi* occur in the SW Gulf of Maine and south of Cape Cod, but not on Georges Bank or the inner shelf of the Gulf of Maine, where summer bottom temperatures remain below 15°C (Franz *et al.* 1981). More likely, these unique coastal populations of *A. forbesi*-like seastars are either morphological variants of *A. vulgaris* (as is the case in the Muscongus Bay intertidal population reported in this paper) or relict populations of *A. forbesi* which are retained within and restricted to shallow coastal embayments. Relict populations of oysters (*Crassostrea virginica*) occur in the Sheepscot Estuary, and McAlice (1981) has presented evidence for the existence of relict populations of other estuarine trans-hatteran invertebrates in Maine coastal estuaries. If relict populations of *A. forbesi* date from the Hypsithermal Period (7000–9000 years BP), it would not be surprising if they had undergone a degree of morphological and genetic differentiation from the main body of *A. forbesi* populations further south.

The Origin of *Asterias forbesi* and *Asterias vulgaris*

Several workers have speculated on the origins of *Asterias forbesi* and *A. vulgaris*. A. H. Clark (1923) observed that no species of *Asterias* ranged farther

south than *A. forbesi*, indicating to him the likelihood that *A. forbesi* evolved from *A. vulgaris* as a general consequence of adapting to warmer waters. No mechanism of speciation was suggested.

More recently, Schopf and Murphy (1973) postulated that *A. vulgaris* evolved from *A. forbesi* during the Pleistocene as a result of geographic isolation brought about by the emergence of Georges Bank during the last glacial episode. This land barrier effectively isolated northern populations from the remaining southern populations. Presumably, natural selection favoring individuals living in the cold and increasingly harsh environment brought about the evolution of *Asterias vulgaris*. With the submergence of this land barrier during the Holocene, the recently differentiated "semispecies" again converged to produce the partially overlapping species which presently exist.

While this hypothesis does provide for allopatric speciation and accounts for the major thermal adaptations of the species, as well as their close genetic relationship, there are several problems. The time period allocated for speciation may be too short—roughly 7000 years (the period between the minimum sea level, *ca* 15,000 years BP, to about 7000 years BP when rising sea levels would have again united the separated areas). Another, more serious, objection is presented by the severity of environmental conditions believed to have existed on the coastal shelf north of 42°N during glacial periods. While many questions remain, recent studies (McIntyre 1976) indicate that essentially arctic conditions prevailed during glacial maxima. *Asterias vulgaris* presently does not live in arctic waters. It reaches its northern limit in the Gulf of St. Lawrence, and is not found in the Strait of Belle Isle (Grainger 1966). This suggests that *A. vulgaris* could not have persisted north of 42°N, i.e., north of the land barrier, during glacial maxima. Schopf and Murphy's hypothesis also fails to account for, or explain the relationships between the NW Atlantic species and the North Pacific and NE Atlantic congeners *A. amurensis* and *A. rubens*.

Tortonese (1963) suggested that *Asterias rubens* (including, in his opinion, *A. vulgaris*), *A. forbesi* and *A. amurensis* comprise a superspecies, i.e., a set of allopatric species sharing a common ancestor which, in his opinion, was probably *A. rubens*. He further suggested that the center of dispersion was the North Atlantic, and that *A. forbesi* and *A. amurensis* differentiated from *A. rubens* (or a closely-related ancestor) following westward dispersion into the NW Atlantic (*A. forbesi*) and, either eastward dispersion across Siberia or westward through the Canadian Arctic into the North Pacific (*A. amurensis*). He provided no explanation as to how or when such dispersions may have occurred or under what conditions *A. forbesi* differentiated from sympatric *A. vulgaris*.

While agreeing with Tortonese that the species of *Asterias* comprise a superspecies (*sensu* Mayr 1963) we do not agree with his suggestion of an Atlantic origin. While an Atlantic origin of some boreal North Pacific invertebrate species is probable (Durham and MacNeil 1967), there is an emerging consensus that the amphiboreal fauna of the North Atlantic is largely derived via transarctic dispersals in the Pliocene (or, in some cases, earlier) (Durham and MacNeil 1967; Franz *et al.* 1980; Franz *et al.* 1981).

We suggest that the common ancestor of all North Pacific and North Atlantic *Asterias* probably lived in the North Pacific during the Miocene. After the opening

of the Bering Straits at the end of the Pliocene, the climate warmed and this species, or one of its descendants, migrated from the North Pacific into the North Atlantic via the Arctic, entering the North Atlantic via the straits and sounds of the Canadian Archipelago and/or Norwegian Sea (Nesis 1961).

As populations spread southward along both coasts of the North Atlantic, geographic and genetic connections were broken, possibly facilitated in the late Pliocene, by the closure of the Isthmus of Panama and the development of the Labrador Current system. These events brought about a strengthening and modification of the axis of the Gulf Stream (Berggren and Hollister 1977) and provide an explanation for environmental changes in the Atlantic which, as argued by Franz and Merrill (1980), may account for the evolution of a separate boreal fauna in the North Atlantic, as well as the ecological separation of NW Atlantic and NE Atlantic *Asterias* populations to produce *A. forbesi* and *A. rubens*.

During one or more of the extensive interglacial periods, or possibly as late as the Holocene, *A. rubens* may have extended its range westward along the island arc of the North Atlantic (Faroes, Iceland, Greenland) and via the Davis Strait to Labrador and New England, becoming partly sympatric with *A. forbesi*. During glacial maxima, *A. forbesi* would have been displaced southward (as would have *A. rubens* on the European coast). Possibly, relict populations of *A. rubens* remaining in the NW Atlantic may have been able to survive these periods in the NW Atlantic by extending their ranges southward into the Middle Atlantic Bight. Alternately, the westward range extensions of *A. rubens* into the NW Atlantic may have occurred in the Holocene. In either case, these relict populations of *A. rubens* in the NW Atlantic are now known as *A. vulgaris*.

Evidence to support this hypothesis is circumstantial. The diversity of asteroids in the North Pacific is very great, leading to the conclusion that this area marks the center of origin of the Asteridae. Since species of *Asterias* do not occur in subtropical or tropical waters, it follows that North Atlantic populations were derived from North Pacific ancestors via transarctic migration. Caenozoic migrations are thought to have occurred at least twice: the well-documented late Pliocene/early Pleistocene Beringian Transgression, 1 million years BP (Allison 1978); and a less well documented late Miocene transgression which is substantiated primarily on zoogeographic evidence (MacNeil 1965; Durham and MacNeil 1967).

Evidence for the westward range extensions of boreal invertebrates during the Pleistocene is summarized in Franz and Merrill (1980). In spite of the North Atlantic Drift, some European species have extended their ranges westward via Iceland to Greenland (Kraeuter 1974). Populations of *A. rubens* presently occur abundantly in Iceland and, at least periodically, in West Greenland (Einarsson 1948). Since *A. rubens* could not have survived in these areas during the Wisconsin glacial maximum, it follows that *A. rubens* extended its range westward during the Holocene. It seems reasonable to assume that if *A. rubens* can extend its range westward as far as West Greenland during present conditions, it may have been able to extend its range into the Davis Strait and to Labrador, and hence southward to New England, during the unusually warm conditions which prevailed during the Hypsithermal. Alternately, if the westward range extension occurred earlier, e.g., during a late interglacial, *A. rubens* may have been able to survive glacial conditions in the Middle Atlantic zone of the NW Atlantic,

based on the analysis of environmental conditions in this zone during the Wisconsin glacial maximum (McIntyre 1976). We have no basis for distinguishing between these alternatives.

Unfortunately, we are unable, at this point, to propose a definitive procedure to falsify the hypotheses discussed above. Ultimately, when taxonomic relationships within the *A. amurensis* complex are more clearly established, it may be possible to investigate evolutionary relationships among geographical groups of *Asterias* using both biochemical (isoenzyme) and morphological (cladistic) approaches.

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Biology Department, Brooklyn College/CUNY, Brooklyn, New York 11210.



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