

SPERMATOPHORES OF SIX EASTERN NORTH AMERICAN PYRAMIDELLID GASTROPODS AND THEIR SYSTEMATIC SIGNIFICANCE (WITH THE NEW GENUS *BOONEA*)¹

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The intrafamilial systematics of the Pyramidellidae, one of the largest families of marine gastropods and noteworthy phylogenetically in combining prosobranch and opisthobranch traits, has so far been based on shell characters exclusively. These ectoparasites lack radulae, so even radular characters are missing. This paper, on one aspect of sexual biology, gives the first results of a study determining the relevance of biological characters in the systematics of the east North American odostomioid pyramidellids.

So far as is known, all the Pyramidellidae are simultaneous hermaphrodites. All the British pyramidellids studied by Fretter and Graham (1949, 1962) and by Fretter (1951) apparently transfer spermatozoa directly from one animal to another with an invaginable penis. Mentioning only penial copulation, Fretter (1953) also published a paper on "the transference of sperm from male to female prosobranch, with reference, also, to the pyramidellids." Fretter and Graham were not concerned with lower category systematics, and it is not possible to determine in which genus and species they observed certain things. Maas (1964) observed something of systematic interest not mentioned earlier: that the penises of five species of European pyramidellids are cuticularized and hooked or denticulate in species-specific ways. According to Brandt (1968, p. 278), a brackish water "*Chrysallida*" in Thailand has a penis carrying "two stalked appendages."

One could conclude from the literature summarized above that penial copulation is a familial trait of pyramidellids, but this is not the case. Höisaeter (1965) discovered in Norway that "*Chrysallida*" *obtusa* (Brown) [1827] [= "*C.*" (*Parthenina*) *interstincta* (J. Adams, 1797)] produces spermatophores of a characteristic shape, attached to the shell in a constant position. Höisaeter did not understand how these spermatophores function and he did not determine whether there still is a penis. In 1966, Dr. Alan J. Kohn sent me a photomicrograph (still unpublished) of some spermatophores that had been attached to the shells of an as yet unidentified "*Odostomia*" from near Friday Harbor, Washington. I noted the discovery of spermatophores in three east North American species of "*Odostomia*" (Robertson, 1967), and later briefly commented on their systematic significance (Robertson, 1968).

The present paper describes and illustrates the spermatophores of six east North American odostomioid species and shows how some of them vary in appearance and yet how each definitely is species-specific in structure. There are also three species-specific positions that the spermatophores assume on the animals (compare Figs.

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30, 44, and 76). A new genus is named in the systematic section, and the paper concludes with discussion of the implications for supraspecific systematics.

The commonest inshore east North American "*Odostomia*" species (all those treated here) are not congeneric with true *Odostomia* of Europe. For reasons given in the section on Generic Relationships of east North American odostomioids, in the two Tables and in the Discussion, the species studied here are grouped in the genera *Boonea* (new) and *Fargoa* Bartsch, 1955. Spermatophore differences helped lead to these conclusions. No definitive systematic treatment of each species is intended here, but taxonomic notes are included to clarify identities and past suppositions about interspecific relationships.

Neither by dissection nor by histology has it been possible so far to determine whether the genital ducts of the American species are as in the British species studied by Fretter and Graham. There are, however, definite differences between the genitalia of the European and American species (Table I, differences 4 and 5). Only once was an extended penis seen in any of the six species. The observations were made on a *Boonea impressa* from Texas which was about to extrude a spermatophore. A short, wide penial papilla was projecting from beneath the mentum to the right of center, and the white spermatophore could be seen inside in transparency. The animal was disturbed during observation, the penial papilla withdrew, and the spermatophore disappeared into the body posteriorly. Presumably, the spermatophore would otherwise have emerged from a pore at the tip of the penial papilla. Dissection of a *B. bisuturalis* confirmed the presence of a penial papilla (at least in *Boonea*). The papilla was withdrawn and not inverted. Its lumen presumably is where spermatophores are formed. The female pore ("genital aperture" of Fretter and Graham?) is on the neck in *Boonea*, but in *Fargoa* it is on the right side of the foot, posterolateral to the right side of the mentum (Figs. 74-76, fp). Spermatozoa somehow are attracted to or drawn into the female pore.

MATERIALS AND METHODS

Most of the observations reported in this paper were made at the Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, and the Duke University Marine Laboratory, Beaufort, North Carolina. Some data from northwest Florida and Texas are also included. There are some indications of intraspecific geographic variation in the spermatophores of several of the species. The exact localities and hosts are therefore noted for each species.

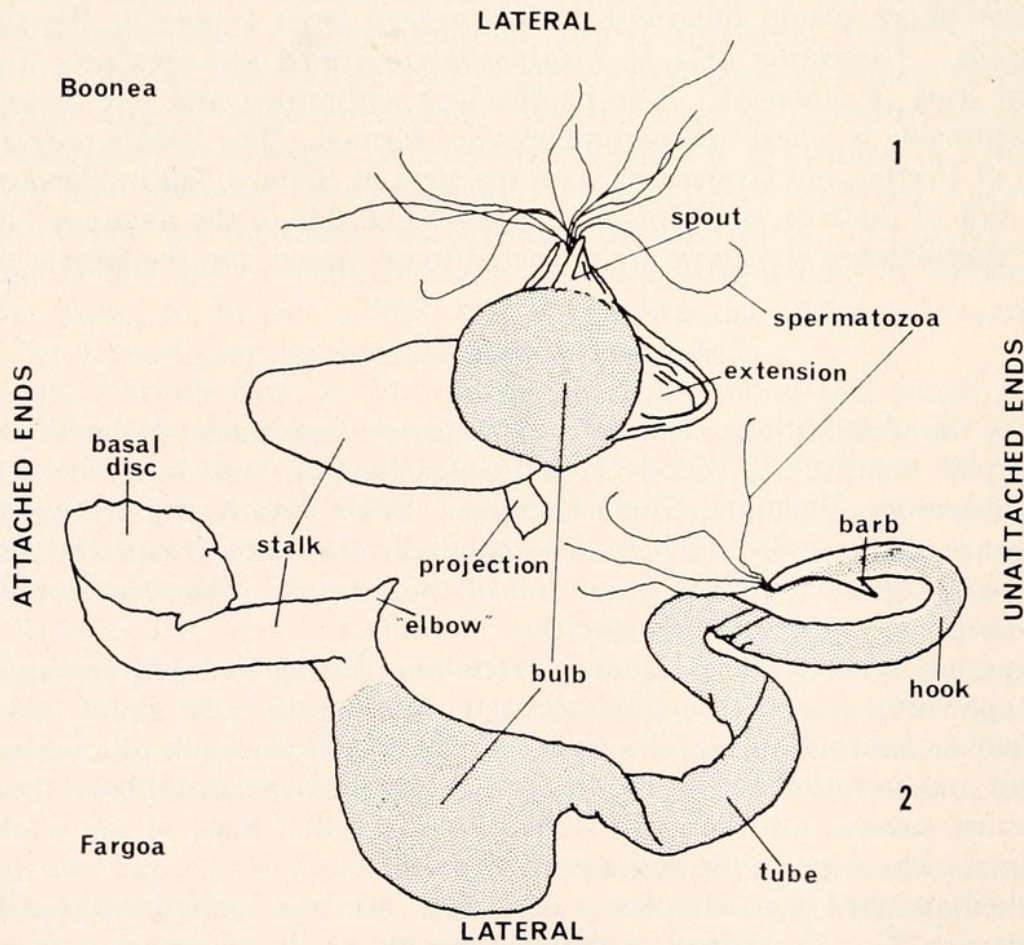
The spermatophores were obtained preceding, during and (surprisingly) soon after the spawning season. In Massachusetts this seems to be about mid-June to mid-September for the four species there, but in North Carolina this varies among five species and from locality to locality. The dates of spermatophore occurrences and spawning seasons are therefore recorded. Note that most of my work on the living animals was done in the summer months.

The shell-attached spermatophores of *Fargoa* are best located with a dissecting microscope at $\times 50$. The spermatozoa in the freshly produced spermatophores make these a characteristic pale pink. The spermatophores are easily seen on the right sides of the animals. Removal of a fresh spermatophore from a shell is difficult because it is so firmly attached. However, after several days the spermatophores

break or automatically loosen and drop off, and they then can be found on the bottom of the container. By then, though, the remaining spermatozoa are heavily infested with bacteria and protozoans. The spermatophores illustrated here without emerging spermatozoa were not fresh.

The spermatophores in the mantle cavities of *Boonea* can be seen when the bodies are extended far out of the shell (Figs. 30, 44), but once seen in this way they are difficult to remove undamaged. To loosen them I put a large sample (preferably 50 or more) of newly collected adult animals in a lidded jar about half full of sea water, and then shook the jar violently. This dislodged some of the spermatophores, and when the water was poured out and swirled in a circular bowl most of the spermatophores settled near the center. They could then be pipetted out individually onto microscope slides.

All drawings of spermatophores in this paper are based on photographs taken with a compound microscope. Even when a spermatophore was obviously bent or folded it is shown here as seen. A problem with the uncultured spermatophores is that they are so soft that they are squashed and distorted by cover slips. A feature such as the lateral spout of *Boonea seminuda* shows only if the plane of the squash is right. Series of drawings of randomly selected spermatophores show the real and apparent morphological variation within and between populations of



FIGURES 1-2. Representative spermatophores of *Boonea* (Fig. 1) and *Fargoa* (Fig. 2), showing the terminology used here. No homologies are implied by the orientations and terminological identities. Stippling shows the location of spermatozoa in the bulbs and the tube.

TABLE I

Differences between European and eastern North American odostomioids.

<i>Odostomia</i> , <i>sensu stricto</i> , and " <i>Chrysallida</i> " of Europe	
1.	Protoconchs either with $2\frac{1}{2}$ + tilted heterostrophic whorls (planktotrophic species) or with ca. 1 untilted whorl (lecithotrophic species) [Thorson, 1946, pp. 199–212, figs. 115–124].
2.	Operculum with several internal tooth-like processes (Fretter and Graham, 1949, p. 495).
3.	Excurrent siphon reduced or lacking (confirmation desirable) [Fretter and Graham, 1949, p. 527].
4.	Penial sperm transfer (except in " <i>Chrysallida</i> " <i>interstincta</i> , which has shell-attached spermatophores); penis invaginable, "whip-like" (Fretter, 1953, p. 220; Høisaeter, 1965).
5.	Genital opening on the inner half of the mantle cavity floor, with a ciliated tract running anteriad beneath the right tentacle to the opening of the penial sheath beneath the mentum (Fretter and Graham, 1949, pp. 498–499).
6.	Pigmented mantle organ of adult brown-orange, pink (Fretter and Graham, 1949, p. 500), or orange-red (Ankel, 1959, p. 4, fig. 2).
<i>Boonea</i> and <i>Fargoa</i> of eastern North America	
1.	Protoconchs either with ca. $1\frac{1}{2}$ tilted heterostrophic whorls or with ca. 1 untilted whorl (all planktotrophic except Texas <i>B. impressa</i>).
2.	Operculum without internal processes.
3.	Excurrent siphon well-developed (Fig. 30, es).
4.	Sperm transferred in spermatophores; penis a short, uninvaginable papilla (<i>Fargoa</i> ?).
5.	Female pore (genital opening?) on neck (<i>Boonea</i>) or posterolateral to right side of mentum (<i>Fargoa</i>); no ciliated tract.
6.	Pigmented mantle organ of adult yellow with a little brown, or dark brick red (<i>F. bartschi</i> only).

the three *Boonea* species. All drawings of isolated spermatophores are adjusted to the same scale to facilitate size comparisons.

Terminology adopted here is shown diagrammatically in Figures 1 and 2. Excepting Figure 1, all the illustrations show the attached end to the right in the three *Boonea* species and to the left in the three *Fargoa* species, *i.e.*, as they would be seen from the right *in situ* on the upright animals. "Stalks" refer to a solid structure at the attachment end; "bulbs" and "tubes" (shown stippled) contain spermatozoa.

Measurements, which can be determined from the illustrations, were made of all the spermatophores that were studied: total lengths, maximum bulb diameters, and stalk, tube and extension lengths. Ranges, means, standard deviations and variances were then determined. Most features measured were found to be so variable that further note is taken here only where there appear to be statistical differences.

GENERIC RELATIONSHIPS

The east American species have usually been grouped in the genus *Odostomia* Fleming, 1813, on the basis of shell characters. Table I shows that there are some profound biological differences between the eastern and western Atlantic species, and that they have been wrongly considered congeneric. Alternative generic names for the American species are difficult to find. All the prior subgeneric and generic assignments of the six species treated below were made on the assumption that conchological similarity is sufficient evidence of a relationship with an odostomioid

TABLE II

Differences between two genera of eastern North American odostomioids.

<i>Boonea</i>	
1. Adult shell >4 mm long.	
2. Protoconch with 1½ whorls, clearly heterostrophic, greatly tilted (Wells and Wells, 1961, Fig. 7).	
3. Front end of foot truncate.	
4. Median groove on under side of foot reaches posterior end (Figs. 30, 44).	
5. Female (genital?) pore on neck.	
6. Spermatophore small, stalked but not tubular, stuck in mantle cavity.	
7. Massed, fresh spermatozoa faintly greyish white.	
8. Spermatozoan head in a lax spiral.*	
9. Fully everted proboscis about 1 to 1½ times shell length.	
10. Digestive gland cream or pale brown speckled with dark grey.	
11. Parasitic on mollusks, with host preferences but no specificity; populations can be dense.	
12. Shell sculpture: noded (<i>B. seminuda</i>), spirally grooved or smooth (<i>B. bisuturalis</i>), spirally grooved (<i>B. impressa</i>).	
<i>Fargoa</i>	
1. Shell <4 mm long.	
2. Protoconch with ca. 1 whorl, slightly heterostrophic, untilted (Wells and Wells, 1961, figs. 3, 5).	
3. Front end of foot medially cleft (Figs. 74–76).	
4. Median pore or groove near posterior end of under side of foot does not reach posterior end.	
5. Female (genital?) pore posterolateral to right side of mentum.	
6. Spermatophore large, tubular towards unattached end, attached to last whorl of shell.	
7. Massed, fresh spermatozoa pale pink.	
8. Spermatozoan head linear or ovately triangular.*	
9. Fully everted proboscis about twice shell length (<i>F. bushiana</i> ?).	
10. Digestive gland brownish grey or black.	
11. Host-specific to <i>Hydroides</i> (serpulid polychaetes) [host of <i>F. bushiana</i> unknown]; populations always sparse.	
12. Shell sculpture: noded (<i>F. dianthophila</i>), noded and spirally grooved (<i>F. bushiana</i>), smooth (<i>F. bartschi</i>).	

* Great variation within one species (Höisaeter, 1965, p. 65, fig. 2b-f) was not observed.

generic type-species. This assumption becomes questionable in view of the conchological convergences and divergences shown below—even in sympatric species. Understanding of evolutionary relationships is not helped by assignment of an east American species to a taxon with a type-species that is widely allopatric and unknown biologically. Thus, I have excluded further consideration of such taxa.

Table II shows that there are major biological differences between two groups of east North American odostomioids. The concept of *Fargoa* Bartsch, 1955, can be extended to cover one group. For the other, a new genus has to be named. For the first time in pyramidellid systematics, non-conchological characters are used (except for shell size and protoconchs).

SYSTEMATIC TREATMENT

Boonea Robertson, new genus

Type-species. *Jaminia seminuda* C. B. Adams, 1839.

Species also included. *Turritella bisuturalis* Say, 1822; *T. impressa* Say, 1822.

Etymology. Named for Constance (Mrs. Hollis Q.) Boone of Houston, Texas,

who for many years has been sending me both living and preserved mollusks. Gender feminine.

Differentiae. Differences from *Odostomia*, *sensu stricto* are given in Table I and from *Fargoa* in Table II. Shell sculpture is various (Figs. 3–5).

Boonea seminuda (C. B. Adams, 1839)

Shell. Fig. 3.

Taxonomy of species. Synonyms include "*Odostomia*" *willisi* Bartsch, 1909 (p. 99, pl. 13, fig. 42) and "*O.*" *toyatani* Henderson and Bartsch, 1914.

Prior generic assignments. "*Odostomia*" *seminuda* has usually been classified in the subgenus *Chrysallida* Carpenter, 1857 (Bartsch, 1909, p. 97; Wells and Wells, 1961, pp. 149–150; Abbott, 1974, p. 292). *Chrysallida* was ranked as a genus by Thiele (1929, p. 232), Brandt (1968, pp. 277–278), van Aartsen (1977) and La-Follette (1977), among others. The type-species of *Chrysallida*, *Odostomia torrita* Dall and Bartsch, 1909, of West Mexico, has stronger axial sculpture than any species treated here, and is unknown biologically. "*O.*" *seminuda* was placed by Odé (1968) in the subgenus (or genus) *Menestho* Möller, 1842, the type-species of which, *M. albula* (Fabricius, 1780) of the northern North Atlantic, is without the columellar plica present in all six species treated here, and is unknown biologically.

Geographic range. Prince Edward Island, Canada, to Texas. Recorded from Rio Grande do Sul, Brazil by Rios (1975, p. 143), but Brazilian specimens loaned me by Rios are probably another species. West Indian records are also dubious.

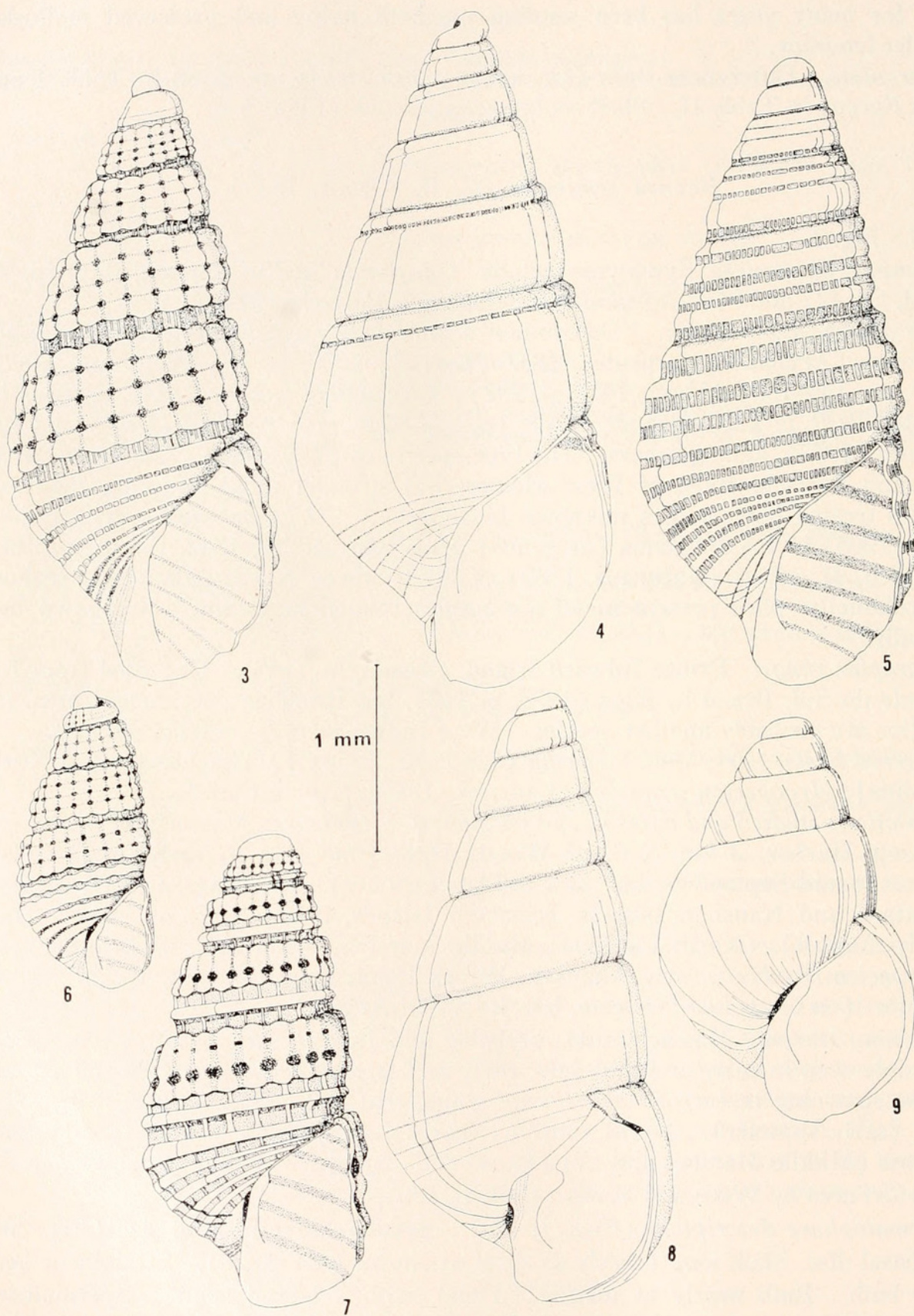
Preferred hosts. *Crepidula fornicata* (Linnaeus, 1758) [Massachusetts and North Carolina]; *Argopecten irradians* (Lamarck, 1819) [North Carolina].

Populations studied and dates of spermatophore occurrence: Massachusetts: N. end Quissett Harbor, 3 km N.E. of Woods Hole (mid-July to early August, late August to mid-September, and mid- and late October). Northwest Gutter, between Uncatena and Naushon Islands, Elizabeth Islands, 3 km S.W. of Woods Hole (early August). North Carolina: Middle Marshes, 5 km S.E. of Beaufort (on *Argopecten irradians*, early August); Wreck Point, Cape Lookout, 16 km S.E. of Beaufort (on *Crepidula fornicata*, late July, mid-August).

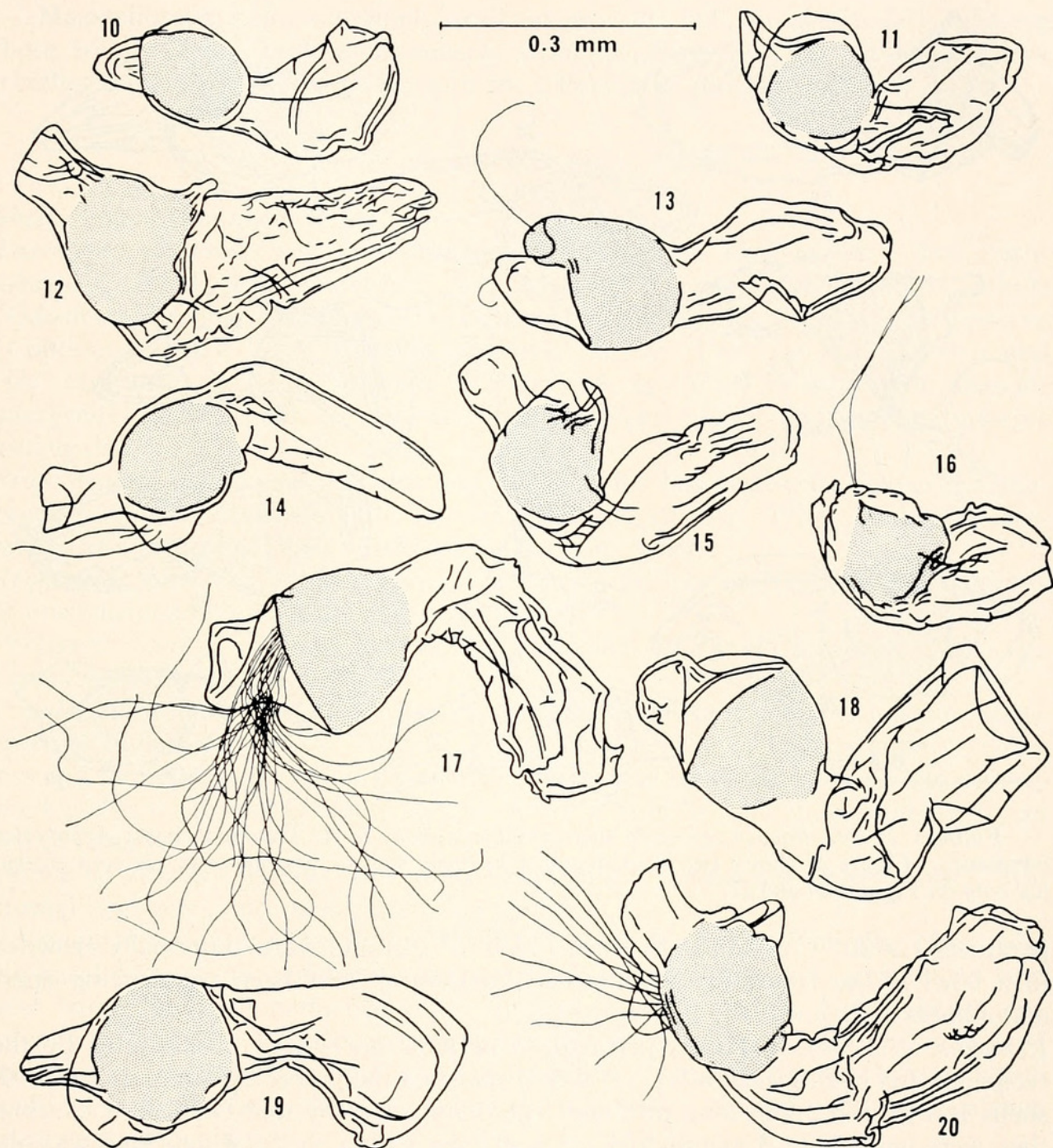
Spawning season. Massachusetts: probably mid-June to early October, but spawn was only seen in early and mid-July, early and late September, and early October. Those spawning in early October were young that had settled earlier in the same year (early summer). North Carolina: early July (Middle Marshes) and early August (Middle Marshes and Cape Lookout). Spawn was seen in January in the Beaufort area by Wells and Wells (1961, p. 156).

Spermatophore description (Figs. 10–29). Small relative to shell size (Fig. 30). No basal disc. Stalk long (rarely as short as shown on Fig. 29). Straight or bent near bulb. Bulb nearly at unattached end, with a lateral spout. Spermatozoa emerge from slit on spout. Extension beyond bulb prominent (rarely as short as shown on Fig. 16), sometimes distinguished with difficulty from spout (e.g. Fig. 17). Nowhere cuticularized. Massed, fresh spermatozoa faintly greyish white.

Transfer. This was not seen, but it probably occurs when the animals cluster and



FIGURES 3-9. Shells. 3. *Boonea seminuda*, North Carolina. 4. *B. bisuturalis*, Massachusetts. 5. *B. impressa*, Texas. 6. *Fargoa dianthophila*, North Carolina. 7. *F. bushiana*, North Carolina. 8. *F. bartschi*, Massachusetts (holotype). 9. *F. gibbosa*, Texas. The three species of *Boonea* (shown not full-grown) attain much larger sizes than the four species of *Fargoa*. Note that the two genera are not distinguishable by the conchological features shown here (the protoconchs differ). Drawings by Faith A. Pittman.

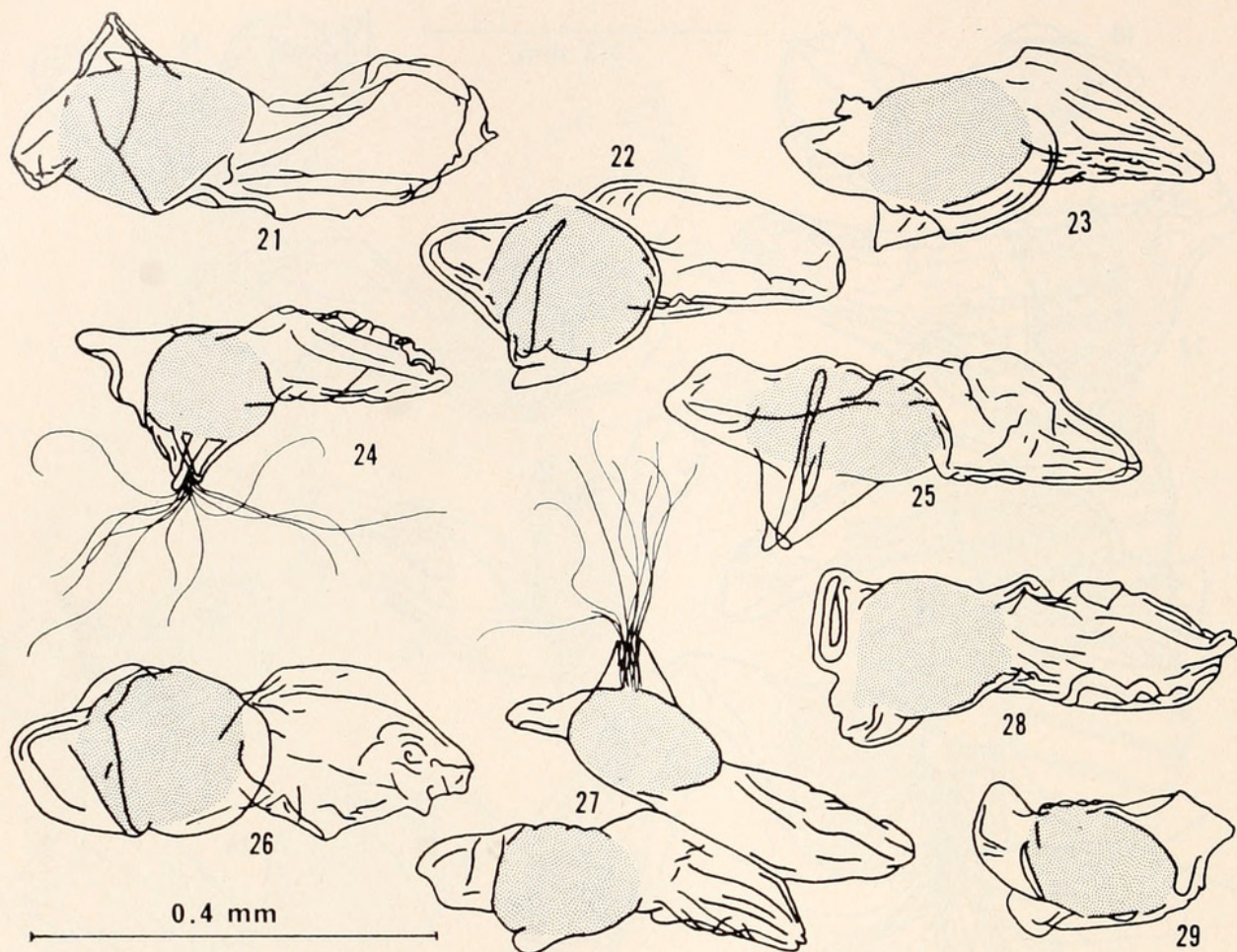


FIGURES 10-20. *Boonea seminuda* spermatophores from Massachusetts (host: *Crepidula fornicata*). Spermatozoa are seen emerging only on Figures 13, 14, 16, 17, and 20.

crawl over each other. As in *B. bisuturalis*, the spermatophores probably are positioned by the mentum and the front end of the foot.

Position. Fairly deep in the mantle cavity, consistently stuck on the right-side of the rear of the neck, with the attached ends anteriad (Fig. 30). The spermatophores can occur in clusters of up to three or more (stuck together?)

Frequency. On October 27, 1977, I selected at random ten large animals from a large series collected the day before near Woods Hole. Six animals lacked spermatophores in their mantle cavities, but three had one each, and one had three clustered. The animals had been separated from their hosts, were at higher tem-



FIGURES. 21-29. *Boonea seminuda* spermatophores from North Carolina (host: *Argopecten irradians*). Figure 27 shows two stuck together by their stalks. Spermatozoa are seen emerging only on Figures 24 and 27.

peratures ($> 20^{\circ} \text{C.}$) than in the field (15° – 17°C.) and were abnormally crowded in a bowl in the laboratory. They may, therefore, have been transferring spermatophores at an unusually high rate.

Remarks. At Woods Hole, spermatozoa perhaps are stored over winter by the recipients (as in *B. bisuturalis*). Animals spawned the preceding summer and with shells less than 3.2 mm long produced spermatophores by mid-October, *i.e.*, when they were only about 3 months old. A specimen with a shell 2.4 mm long was observed to extrude a spermatophore bulb end first, indicating maturity even at this small size.

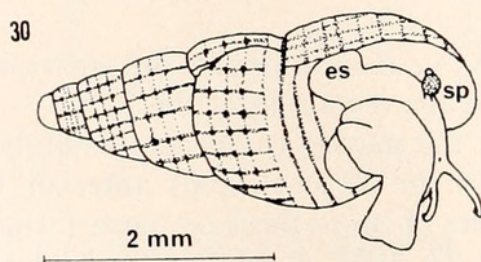


FIGURE 30. *Boonea seminuda* with a spermatophore (sp) on the neck. Note the excurrent siphon (es). From a photograph.

Massachusetts stalks commonly are bent near the bulb (Figs. 10–20), whereas those from North Carolina are nearly straight (Figs. 21–29). It is uncertain whether this difference correlates with the different locality or host.

Boonea bisuturalis (Say, 1822)

Shell. Fig. 4 (nominate form).

Taxonomy of species and shell variation. Some of the shell variation was documented by A. H. Scheltema (1965, Fig. 1A–C). Synonyms and variants include “*Odostomia*” *trifida* (Totten, 1834) [Bartsch, 1909, pl. 13, fig. 46], “*O.*” *exigua* (Couthouy, 1838), “*O.*” *trifida bedequensis* Bartsch, 1909 (pl. 13, fig. 49), and “*O.*” *bisuturalis ovalensis* Bartsch, 1909 (pl. 14, fig. 57). Possibly hybridizes or intergrades clinally with *B. impressa*, but as shown below, their spermatophores usually differ.

Prior generic assignment. “*Odostomia*” *bisuturalis* has been classified in the subgenus *Menestho* (Bartsch, 1909, p. 106; Abbott, 1974, p. 295). *Menestho* was ranked as a genus by Thiele (1929, p. 234), among others.

Geographic range. New Brunswick, Canada, to vicinity of New York (erroneous or unconfirmed reports from farther south).

Preferred hosts. Various, but include *Littorina littorea* (Linnaeus, 1758) and *Crassostrea virginica* (Gmelin, 1791).

Populations studied and dates of spermatophore occurrence. Massachusetts: shore opposite Flume Pond, S. of Gunning Point, 4 km N.N.E. of Woods Hole [grooveless and multigrooved (*trifida*) forms with nominate form] (late June, late July to late October). N. end Quissett Harbor, 3 km N.E. of Woods Hole (mid-April and late October).

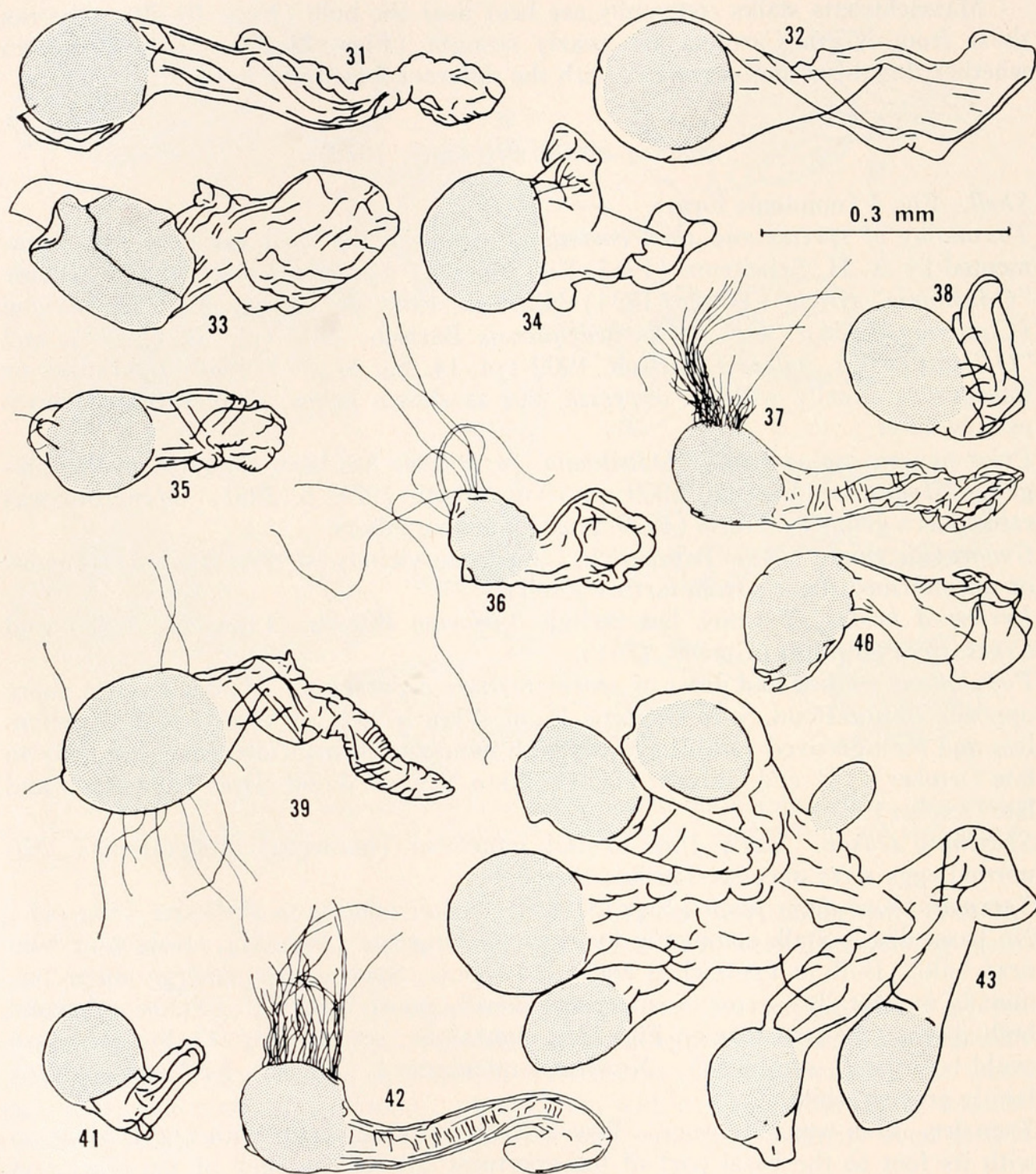
Spawning season. Early June to mid-September (numerous observations). Abnormal eggs were once seen in late September.

Spermatophore description (Figs. 31–43). Small relative to shell size (Fig. 44). No basal disc. Stalk commonly long, rarely bifurcate (Fig. 34), straight or bent near bulb. Bulb at unattached end. No spout. Spermatozoa emerge either terminally or laterally; sector of emergence usually poorly defined. Extension beyond bulb absent (the structure on Fig. 33 is anomalous; see also Fig. 43, lowest, which could be from *B. seminuda*). Nowhere cuticularized. Massed, fresh spermatozoa faintly greyish white.

Transfer. This was seen once. Two animals were adjacent, with one holding on with its foot to the basal part of the apertural side of the shell of the other. A spermatophore was first seen in transparency through the right side of the rear of the mentum. The spermatophore then was extruded bulb end first. With the aid of the anterior part of the mentum, the spermatophore was moved from beneath the mentum to the mantle cavity of the recipient, in which there already were two spermatophores.

Animals with shells 5.5 and 5.8 mm long were seen to release two fresh spermatophores from their excurrent siphons. Perhaps these spermatophores had not been properly stuck to the mantle wall.

Position. Deep in the mantle cavity, consistently stuck on the dorsal mantle wall to the left of the excurrent siphon, usually about half way between the siphon and the



FIGURES 31-43. *Boonea bisuturalis* spermatophores from Massachusetts. Figure 43 shows seven stuck together by their stalks. Spermatozoa are seen emerging only on Figures 35-37, 39 and 42.

anterior end of the mantle cavity; attached ends anteriad (Fig. 44). The spermatophores occur singly or in clusters of up to seven or more (Fig. 43), the stalks stuck together.

My 1967 statement about placement was erroneous, being based on spermatophores that were not fresh and had become stuck elsewhere.

Frequency. Out of ten large animals selected for study, three lacked spermatophores in their mantle cavities, two had one each, three had two each, one had four, and one had about five clustered (same date and circumstances as for *B. seminuda*, in which there were fewer spermatophores).

Remarks. At Woods Hole, spermatozoa probably are stored over winter by the recipients (compare dates of spermatophore occurrence with spawning season; I assume that the winter is too severe for spermatophores to be produced during that season). Animals spawned the preceding summer and with shells less than 3.5 mm long produced spermatophores by mid-October, *i.e.*, when they were only about three months old.

Stalk length is usually greater than in the closely related species (or geographic race?) *B. impressa*.

Boonea impressa (Say, 1822)

Shell. Fig. 5.

Taxonomy of species. Synonyms include "*Odostomia* (*Menestho*)" *beauforti* Jacot, 1921. See under *B. bisuturalis* regarding the distinctness of that species.

Prior generic assignment. "*Odostomia*" *impressa* has been classified in the subgenus *Menestho* (Bartsch, 1909, p. 103; Abbott, 1974, p. 294). *Menestho* was ranked as a genus by Thiele (1929, p. 234), among others.

Geographic range. Doubtfully Massachusetts; New Jersey to Quintana Roo, Mexico.

Preferred host: *Crassostrea virginica*.

Populations studied and dates of spermatophore occurrence. North Carolina: opposite Pivers Island, Beaufort (mid-August and mid-November). W. side Banks Channel, Wrightsville Beach, 14 km E.S.E. of Wilmington (mid- and late May). N.W. Florida: Dixon Bay, Wakulla County (early November). Texas: off 61st St., Offats Bayou, inlet of Galveston West Bay (mid-November, late December, early January, late February, early March and late April).

Spawning season. North Carolina: spawn seen late May and mid August. Wells (1959, p. 141) observed spawn in early May to mid-September in the Beaufort area. Texas: spawn seen late November to late December, and early March to early April.

Spermatophore description (Figs. 45–67). Very small or small relative to shell size. No basal disc. Stalk usually short and bent, uncommonly with lateral projection

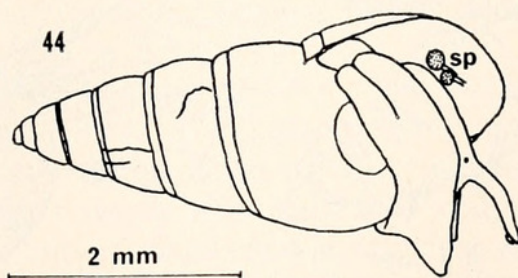
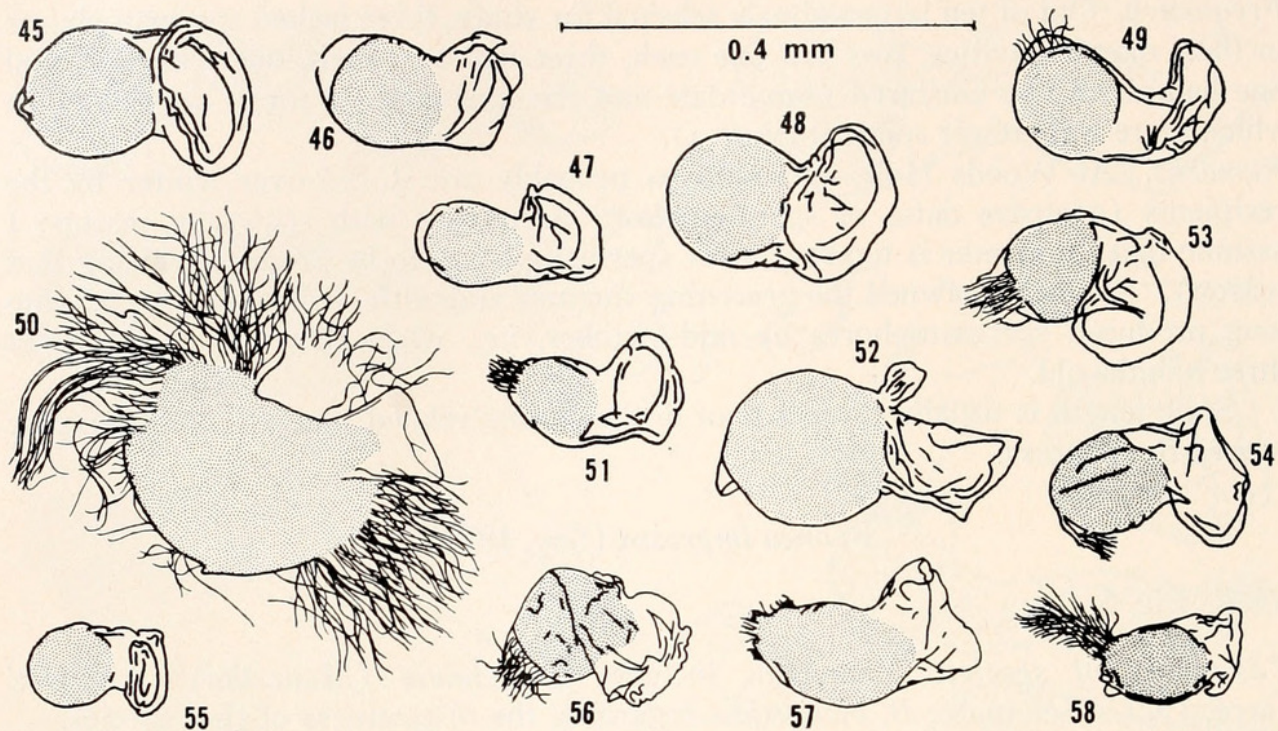
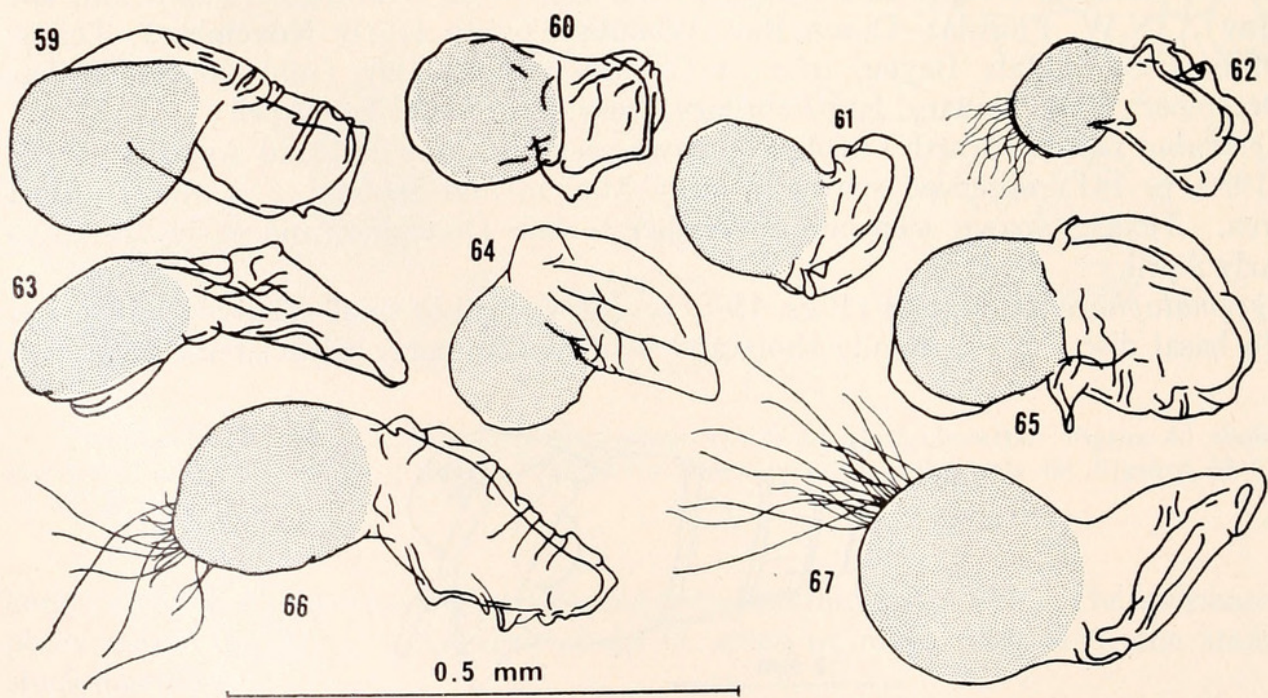


FIGURE 44. *Boonea bisuturalis* with two spermatophores (sp) on the dorsal mantle wall. From a photograph.



FIGURES 45-58. *Boonea impressa* spermatophores from North Carolina (Figs. 45-55) and N.W. Florida (Figs. 56-58). Figure 50 was squashed more than the others. Spermatozoa are seen emerging only on Figures 49-51, 53, 54, 56-58.

(Figs. 52, 65). Bulb at unattached end. No spout. Spermatozoa emerge either terminally or laterally; sector of emergence usually poorly defined. Extension beyond bulb absent. Nowhere cuticularized. Massed, fresh spermatozoa faintly greyish white.



FIGURES 59-67. *Boonea impressa* spermatophores from Texas. Spermatozoa are seen emerging only on Figures 62, 66, and 67.

Transfer. Not seen; comments under *B. seminuda* apply.

Position. Deep in the mantle cavity, consistently stuck on the dorsal mantle wall to the left of the excurrent siphon, usually about half way between the siphon and the anterior end of the mantle cavity; attached ends are antieriad. The spermatophores occur singly (four observations) or in clusters of up to four (one observation) or more; up to two were seen stuck together by their stalks.

Remarks. The North Carolina and N.W. Florida spermatophores (Figs. 45–58) are smaller than the ones from Texas (Figs. 59–67). The maximum North Carolinian and Floridian bulb diameters are 80–160 μm (average of 13 measurements [excluding Fig. 41]: 114 μm); the Texan diameters are 120–215 μm (average of nine measurements: 170 μm). Some of the Texan stalks (*e.g.*, Figs. 63 and 66) approach those of *B. bisuturalis* in length. Note that in *B. impressa* the spermatophores are placed as they are in *B. bisuturalis*, not as in *B. seminuda*.

Genus *Fargoa* Bartsch (1955, p. 80)

Type-species (by original designation). *Fargoa calesi* Bartsch, 1955 ("Pliocene" or Pleistocene) = "*Odostomia*" *bushiana* Bartsch, 1909.

Species also included. "*Pyramidella* (*Sulcorinella*)" *bartschi* Winkley, 1909; "*Odostomia* (*Chrysallida*)" *dianthophila* Wells and Wells, 1961; "*Odostomia*" *gibbosa* Bush, 1909. Shell form and sculpture are various (Figs. 6–9).

Fargoa dianthophila (Wells and Wells, 1961)

Shell. Fig. 6.

Prior generic assignments. "*Odostomia*" *dianthophila* was originally classified in the subgenus *Chrysallida* (Wells and Wells, 1961, p. 152; Abbott, 1974, p. 293), but Odé (1971) placed it "in the *Menestho* group of odostomias . . . in the genus *Fargoa* of Bartsch." *Chrysallida* and *Menestho* have each been ranked as a genus (see earlier).

Geographic range. Massachusetts to Texas.

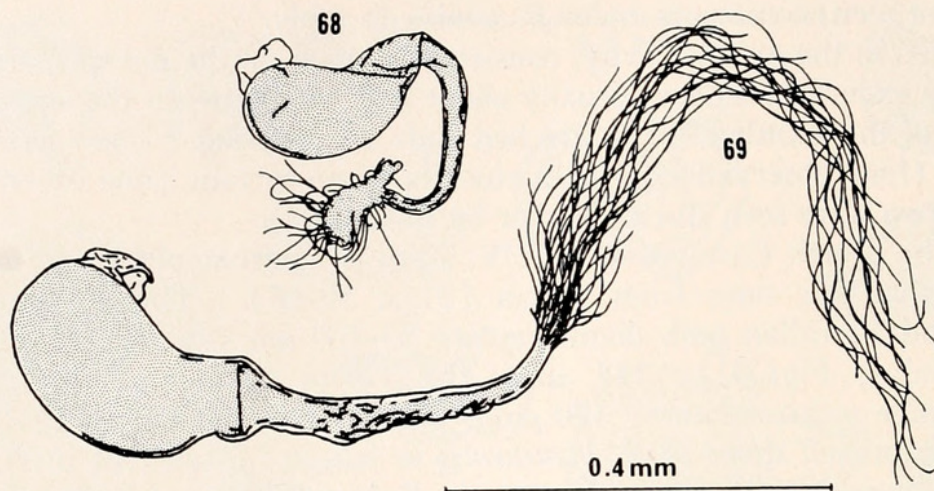
Preferred hosts. *Hydroides dianthus* (Verrill, 1873) [Massachusetts] and this and other *Hydroides* spp. [North Carolina to Gulf of Mexico].

Populations studied and dates of spermatophore occurrence. Massachusetts: shore opposite Flume Pond, S. of Gunning Point, 4 km N.N.E. of Woods Hole (mid-July to early August, mid- and late September, and mid-October). North Carolina: opposite Pivers Island, Beaufort (early July).

Spawning season. Massachusetts: spawn seen in mid- and late July and mid-August. North Carolina: probably spawns in late May to July in the Beaufort area (Wells and Wells, 1961, p. 156).

Spermatophore description. (Figs. 68–69). Very large relative to shell size (would not fit in mantle cavity). Basal disc present. Stalk at attached end short, with no "elbow". Bulb moderately large, swollen, without (Fig. 68) or with (Fig. 69) a secondary swelling towards the unattached end, merging with long, fairly narrow tube. Nowhere cuticularized, and unattached end not hooked or barbed. Spermatozoa emerge terminally. Massed, fresh spermatozoa pale pink.

Transfer. This was seen once. The donor crawled methodically over the shell of the recipient, probing with its mentum. The donor then assumed the position



FIGURES 68–69. *Fargoa dianthophila* spermatophores from Massachusetts. Spermatozoa are seen emerging from both.

shown in Figure 70 while holding the basal disc of the spermatophore against the shell with the front end of the foot for about two minutes.

Position. Attached to the shell; basal disc on the apertural side of the last whorl, posterior and to the right of the posterior end of the aperture; unattached end anteriad, on the right side of the body, adjacent to, and then inserted deep in the female pore. One spermatophore is normally placed at a time, but one animal was seen with two spermatophores inserted in the female pore; one of them was attached also to the shell.

Remarks. These spermatophores closely resemble those of “*Chrysallida*” *interstincta* described and illustrated by Høisaeter (1965), differing only in having a

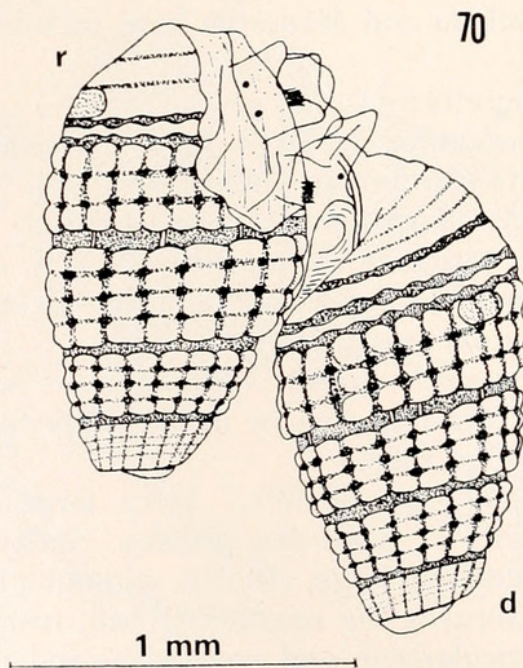


FIGURE 70. *Fargoa dianthophila*: positions assumed during spermatophore transfer, with the donor (d) on the shell of the recipient (r). It is difficult to see what happens. Drawing by Faith A. Pittman.

more inflated bulb and a narrower tube. Their positions on the shells are identical, but this is probably true of all the shell-attached pyramidellid spermatophores.

Fargoa bushiana Bartsch, 1909

Shell. Fig. 7.

Taxonomy of species. *F. bushiana* has commonly been known as "*Odostomia*" *dux* Dall and Bartsch (1906, p. 350, pl. 17, fig. 4; type-locality: Japan), since Wells and Wells (1961, pp. 150–151) argued that the type-locality was wrong. However, they did not see the type or other specimens identified by Dall and Bartsch, and Saurin (1962, p. 250; Saurin, 1959, pl. 5, fig. 17) recorded a range extension of "*Miralda*" *dux* to Viet Nam and the Gulf of Thailand. There could be convergence between odostomioid shells from east America and the Far East, and I prefer to use a name definitely pertaining to the American species—even though it was poorly illustrated by Bartsch (1909, pl. 13, fig. 44). Synonyms include *F. calesi* Bartsch, 1955 (type-species of *Fargoa*) and *F. archeri* Bartsch, 1955. "*Odostomia bushiana* Jeffreys, 1884" of Bush (1909, p. 482) is *Turbonilla bushiana* Verrill, 1882, synonymized by Jeffreys (1884, p. 357) with an "*Odostomia*" (actually a *Turbonilla*).

Prior generic assignments. "*Odostomia*" *bushiana* has usually been classified in the subgenus *Chrysallida* (Wells and Wells, 1961, p. 150; Abbott, 1974, p. 293), and *Chrysallida* has also been ranked as a genus (see earlier). The species has also been placed in the subgenus (or genus) *Menestho* (Odé, 1968) and in the genus *Miralda* A. Adams, 1863 (Odé and Speers, 1972, p. 9, fig. 4). *M. diadema* (A. Adams, 1860), the type-species of *Miralda*, is from Japan and is unknown biologically.

Geographic range. Massachusetts to São Paulo, Brazil (Rios, 1975, p. 143). Brazilian specimens loaned me by Rios are definitely this species.

Host(s). Unknown.

Population studied and date of spermatophore occurrence. North Carolina: Wreck Point, Cape Lookout, 16 km S.E. of Beaufort (mid-August).

Spawning season. Unknown.

Spermatophore description (Fig. 71). Very large relative to shell size (would not fit in mantle cavity). Basal disc present. Stalk fairly short, with no "elbow". Bulb fairly small, hardly swollen, confluent with wide and long tube towards unattached end. Terminal end of tube cuticularized, hooked, with a small barb. Spermatozoa emerge terminally. Massed, fresh spermatozoa pale pink.

Transfer. Not seen.

Position. Attached to the shell; the basal disc on the apertural side of the last whorl, posterior and to the right of the posterior end of the aperture; hooked end on the right side of the body, bent slightly to the right over the outer lip of the shell (the only misplaced spermatophore seen in any of the species?) The spermatophore was not seen hooked in the female pore, but this must occur.

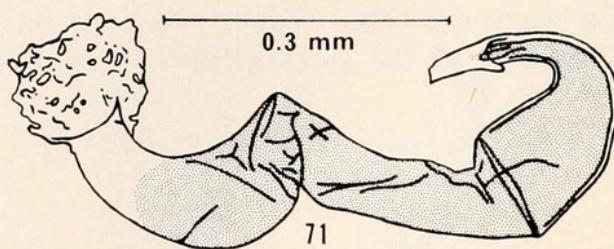


FIGURE 71. *Fargoa bushiana* spermatophore from North Carolina.

Remarks. Only one spermatophore was seen, attached to a shell only 1.4 mm long. Its unattached end is reminiscent of the cuticularized and hooked penis tips discovered by Maas (1964).

Fargoa bartschi (Winkley, 1909)

Shell. Fig. 8.

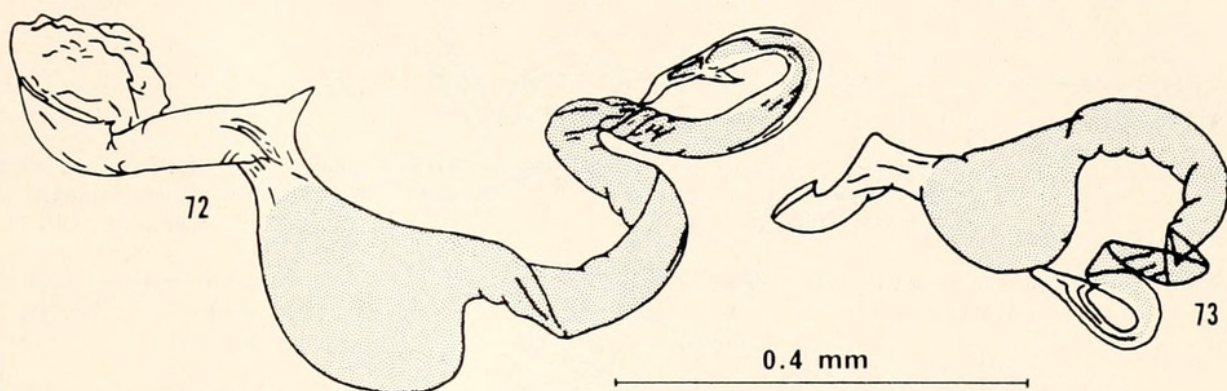
Taxonomy of species. This little-known species has been known as "*Odostomia*" *modesta* [*Chemnitzia modesta* Stimpson, 1851 not *C. modesta* Orbigny, 1842] and "*O.*" *dealbata* (Stimpson, 1851) [a *nomen dubium*]. Abbott (1974, p. 292) suggested that "*O.*" *modesta* is *O. conoidea* (Brocchi, 1814) but this European species differs. "*O.*" *modesta* of Bartsch (1909, p. 108, pl. 13, fig. 50) is "*O.*" *gibbosa* Bush, 1909 (Fig. 9). The holotype of *Pyramidella* (*Sulcorinella*) *bartschi* Winkley (1909, fig.), at the Museum of Comparative Zoölogy (no. 32810), shows that this was incorrectly described and illustrated; the outer lip is broken back and there is no deep peripheral sulcus (Fig. 8). The shell was better illustrated by Bush (1909, fig. 6). *F. bartschi* resembles the grooveless form of *B. bisuturalis* but differs in the characters shown in Table I, in having a dark, brick red, pigmented mantle organ instead of a yellow and brown one, in having a projecting excurrent siphon, and in having brown superficial spots behind the head, golden yellow spots elsewhere, and an operculum with a spiral sector that, superficially, is cream white.

Prior generic assignments. "*Odostomia*" *bartschi* has been classified in the subgenus *Odostomia* Fleming, 1813, *sensu stricto* (Abbott, 1974, p. 292, as "*O.*" *modesta*), the type-species of which, *O. plicata* (Montagu, 1803), of Europe, presumably is one of the species with penial copulation (no spermatophores) studied by Fretter and Graham (1949). The protoconch of *O. plicata* (Thorson, 1946, p. 201, fig. 115B) is unlike that of any east North American odostomioid. "*O.*" *bartschi* was also placed by Winkley (1912) in the subgenus *Evalea* A. Adams, 1860, the type-species of which, *O. (E.) elegans* A. Adams, 1860, of Japan, is unknown biologically. *Evalea* has also been classified as a "Sectio" of *Menestho* (Thiele, 1929, p. 234).

Geographic range. Massachusetts to Texas.

Preferred host. *Hydroides dianthus* [Massachusetts; previously unreported].

Populations studied and dates of spermatophore occurrence. Massachusetts: shore opposite Flume Pond, S. of Gunning Point, 4 km N.N.E. of Woods Hole (mid-June to early September). N. end Quissett Harbor, 3 km N.E. of Woods Hole



FIGURES 72-73. *Fargoa bartschi* spermatophores from Massachusetts (Fig. 72) and North Carolina (Fig. 73).

(mid-July to early August). North Carolina: Wreck Point, Cape Lookout, 16 km S.E. of Beaufort (mid-August). W. side Banks Channel, Wrightsville Beach, 14 km E.S.E. of Wilmington (mid- and late May).

Spawning season. Massachusetts: spawn seen mid-July to late August. North Carolina: spawn seen late May and mid-August.

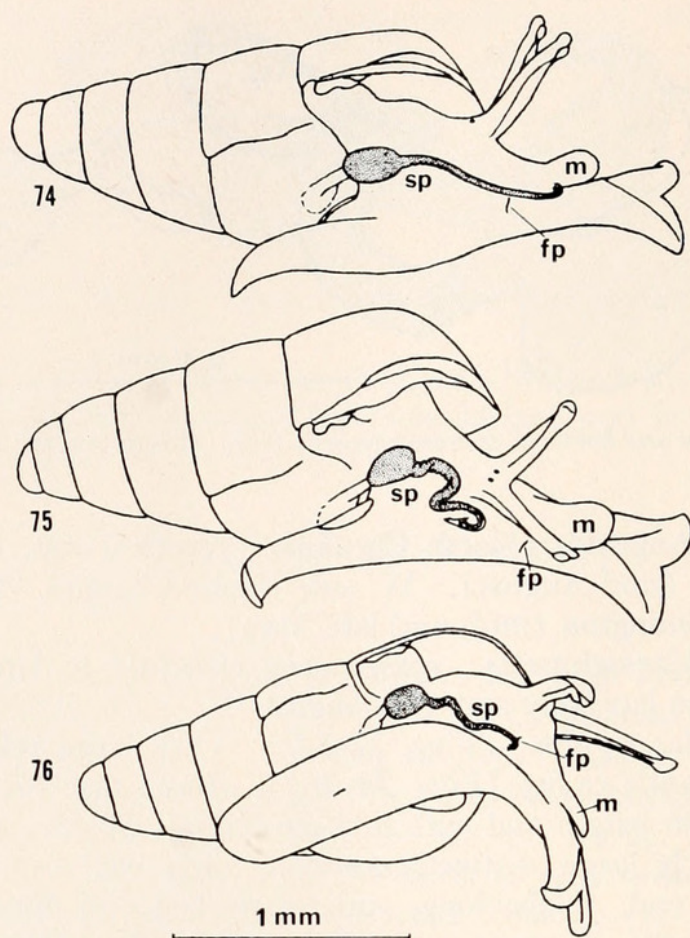
Spermatophore description. (Figs. 72-73). Very large relative to shell size (would not fit in mantle cavity [Figs. 74-76]). Basal disc present. Stalk at attached end of medium length and with a sharp lateral "elbow". Bulb on opposite side to "elbow", fairly large, distinctly swollen, fairly well demarcated from tube towards unattached end. Tube long, and unattached end cuticularized, hooked, with a fairly large barb. Spermatozoa emerge terminally. Massed, fresh spermatozoa pale pink.

Transfer. This was seen four times, once reciprocally. The donors crawled over the shells of the recipients for about five minutes or longer, with the anterior ends of the mentum and foot moving to and fro over the shell. The donors assumed the same position as seen in *F. dianthophila* (Fig. 70), with the foot wrapped around the shell of the recipient. A spermatophore was once seen emerging from beneath the eyes and under the base of the mentum, basal disc first and bulb and hooked end last. During attachment, the basal disc of the spermatophore is held against the shell with the front end of the foot for about three to ten minutes. The hooked end usually is hooked in the female pore within about one hour after transfer.

Position. Attached to the shell; basal disc on the apertural side of the last whorl, posterior and to the right of the posterior end of the aperture; hooked end anterior, on the right side of the body, adjacent to (and then hooked in) the female pore. Usually one spermatophore is placed at a time, but twice two were seen attached near together (one was $4\frac{1}{2}$ days older than the other). Sometimes the stalk breaks before the basal disc detaches, leaving one or more discs on the shell. One exceptional spermatophore remained attached to a shell for $5\frac{1}{2}$ days.

Remarks. This is the most elaborate spermatophore so far known in the Pyramidellidae. Its hooked end is reminiscent of the cuticularized and hooked penis tips discovered by Maas (1964).

The spermatophores from Massachusetts (Fig. 72) were appreciably larger than any seen from North Carolina (Fig. 73). This is because the species attains much larger sizes in Massachusetts. The longest shell observed from Massa-



FIGURES 74-76. *Fargoa bartschi* with a spermatophore (sp) attached to the shell, first (Fig. 74) with the distal end hooked under the mentum (m), then (Fig. 75) loose, and then (Fig. 76) hooked in the female pore (fp). Figure 74 may show an abnormal occurrence.

achusetts is 4.1 mm, while the longest from North Carolina is only 1.9 mm. Spermatophores from North Carolina were observed on presumably mature shells only 1.0 and 1.3 mm long.

The statement (Robertson, 1967) about self-fertilization in "*Odostomia modesta*" is probably erroneous, having been based on a single observation of a spermatophore already attached to the shell, first with the hooked end (accidentally?) under the mentum in or near the male pore (Fig. 74), then with the unattached end loose (Fig. 75), and then later with the hooked end in the female pore (Fig. 76). It is doubtful that the animal attached a spermatophore to its own shell, and transfer was later found to occur. Thus there is no good evidence of self-fertilization in the Pyramidellidae.

DISCUSSION

The three species of *Boonea* differ from two or more of the species of *Fargoa* in life style. The two genera have hosts in different phyla and they differ also in population density. It is the three species of *Fargoa* which are scarce and have large shell-attached spermatophores. These probably are transferred less frequently than the smaller mantle cavity spermatophores of *Boonea*. The more elaborate

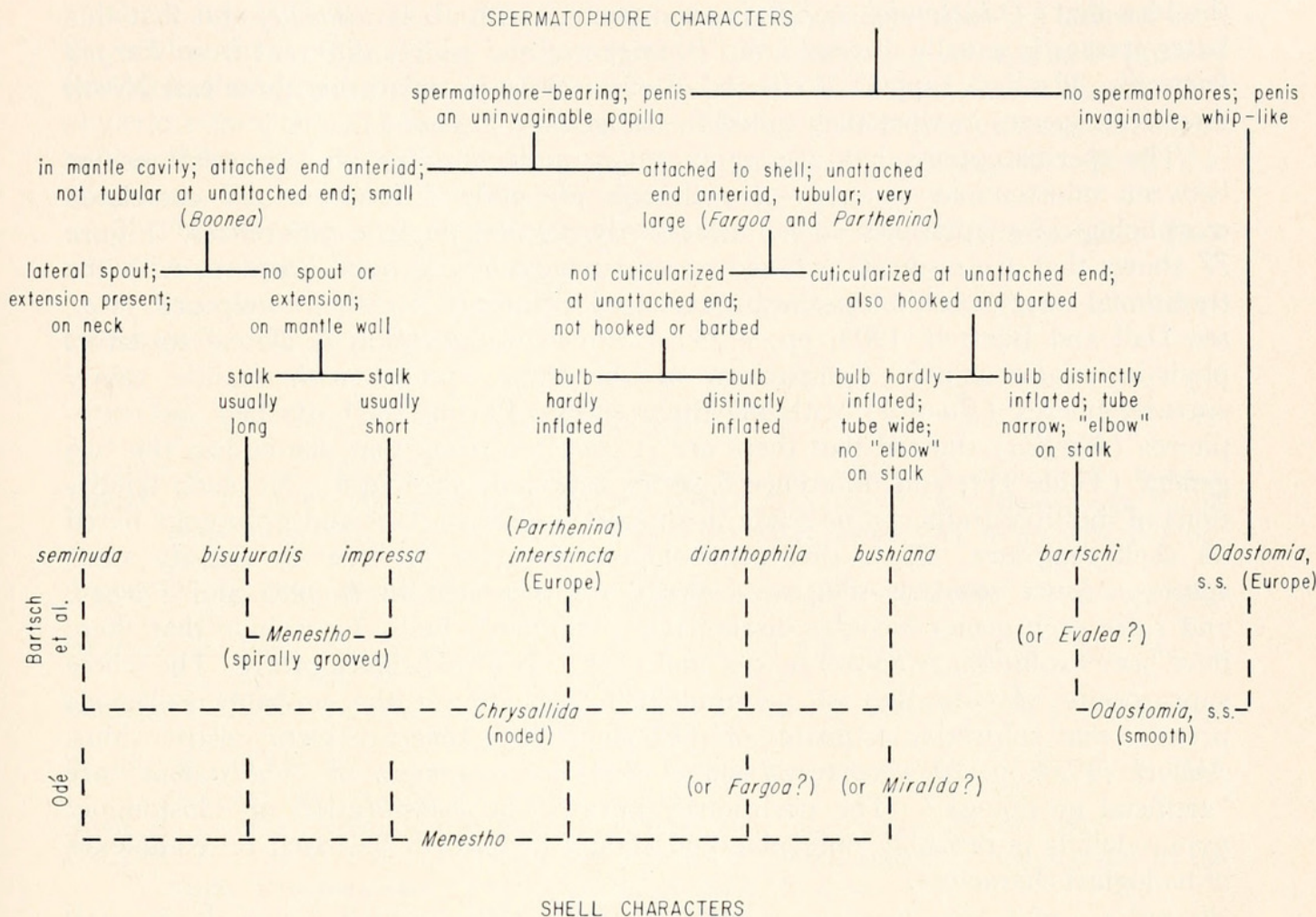


FIGURE 77. Comparison of a classification of some odostomioids based on spermatophores with two classifications (those of Bartsch and Odé) based on shell sculpture, upon which the traditional classification into subgenera or genera is primarily based. There are also sculptural similarities between the grooveless form of *B. bisuturalis* and *F. bartschi*, and *F. bushiana* is sculpturally intermediate between *B. seminuda* and *B. impressa* (see Odé, 1968). Note that the spermatophore and two shell classifications are nonconcordant. Spermatophore characters allow a more natural classification of species than shell characters.

Fargoa spermatophores may be adapted to fertilize rarely encountered individuals, although these animals sometimes live in pairs. *Boonea* animals commonly cluster in groups.

All the east North American odostomioids may have spermatophores. The only species of these obtained alive in the present study and in which spermatophores were not found is "*Odostomia*" *gibbosa* (Fig. 9). However, only two animals of this species were under observation at different times. My prediction is that "*O.*" *gibbosa* has a shell-attached spermatophore, since the animal has the traits of *Fargoa* in Table II. The medially cleft front end of the foot (trait 3) seems to be used in positioning shell-attached spermatophores, and the female pore is in the appropriate position (trait 5) for the unattached end to hook in.

The spermatophores of the six species described above provide useful species characters. Allowing for some shell variation (such as in *B. bisuturalis*), they confirm the conchological characterizations of the species. Spermatophores support

the idea that "*Odostomia*" *trifida* is synonymous with *B. bisuturalis*, and that this latter species is usually distinct from *B. impressa* and widely different from *Fargoa bartschi*. The data support Wells and Wells (1961) in separating three east North American species in what they called the subgenus *Chrysallida*.

The spermatophore data are significant in understanding phyletic relationships between odostomioid species—even though life style differences and correlated morphological adaptations do not necessarily parallel phyletic differences. Figure 77 shows that a classification based on spermatophores is nonconcordant with the traditional supraspecific classifications based primarily on shell sculpture (*e.g.*, see Dall and Bartsch, 1904, pp. 9–14). Which classification is closest to actual phyletic relationships? Comparison of the three species with mantle cavity spermatophores (*Boonea*) with the three species having shell-attached spermatophores (*Fargoa*) showed that there are at least ten traits that distinguish the two genera (Table II), and difference 5 seems especially profound. No such tabulations of multiple traits can be made to support the separations and groupings based on shell sculpture. Note that conchologists disagree on how to classify some species. Since similarly-sculptured shells are separated in *Boonea* and *Fargoa*, and since each group includes dissimilarly sculptured shells, I conclude that there have been evolutionary convergences and divergences in shell sculpture. The whole supraspecific classification of pyramidellids is based on the probably fallacious premise that subjective estimates of shell similarities reflect phyletic relationships. Abbott (1974, p. 291) correctly stated that the subgenera of "*Odostomia*" are "artificial groupings." The traditional supraspecific classification of odostomioid pyramidellids is probably untenable and should henceforth be based on complexes of biological characters.

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SUMMARY

1. Six east North American odostomioid species (Gastropoda: Pyramidellidae) are shown to have spermatophores that are species-specific in structure and position. The spermatophores of *Boonea seminuda*, *B. bisuturalis* and *B. impressa* are stuck in the mantle cavity; those of *Fargoa dianthophila*, *F. bushiana* and *F. bartschi* are attached to the shell in a constant position.

2. A supraspecific classification based on spermatophores does not accord with the traditional ones based on shell sculpture. By comparing all available lines of evidence, the spermatophore classification is shown to accord more closely with phyletic relationships. Shell sculpture has converged and diverged evolutionarily and is therefore unreliable in supraspecific pyramidellid systematics. With due allowances for variation it is, however, useful at the species level.

3. The new genus *Boonea* is named, based on spermatophore and other data, with "*Odostomia*" *seminuda* as type-species.

4. Reasons are given for using the name *F. bartschi* for "*O. modesta*" and *F. bushiana* for "*O. dux*" of authors.

LITERATURE CITED

- AARTSEN, J. J. VAN, 1977. European Pyramidellidae I. *Chrysallida*. *Conchiglie*, **13**: 49-64.
- ABBOTT, R. T., 1974. *American seashells; the marine Mollusca of the Atlantic and Pacific coasts of North America*. Ed. 2. Van Nostrand Reinhold Co., New York, 663 pp., 24 pls.
- ANKEL, W. E., 1959. Beobachtungen an Pyramidelliden des Gullmar-Fjordes. *Zool. Anz.* **162**: 1-21.
- BARTSCH, P., 1909. Pyramidellidae of New England and the adjacent region. *Proc. Boston Soc. Nat. Hist.*, **34**: 67-113, pls. 11-14.
- BARTSCH, P., 1955. The pyramidellid mollusks of the Pliocene deposits of North St. Petersburg, Florida. *Smithson. Misc. Collect.*, **125**(2): i-iii, 1-102, pls. 1-18.
- BRANDT, R. A. M., 1968. Description of new non-marine mollusks from Asia. *Arch. Molluskenkd.*, **98**: 213-289, pls. 8-10.
- BUSH, K. J., 1909. Notes on the family Pyramidellidae. *Am. J. Sci.*, **27**: 475-484.
- DALL, W. H., AND P. BARTSCH, 1904. Synopsis of the genera, subgenera and sections of the family Pyramidellidae. *Proc. Biol. Soc. Wash.*, **17**: 1-16.
- DALL, W. H., AND P. BARTSCH, 1906. Notes on Japanese, Indopacific, and American Pyramidellidae. *Proc. U. S. Natl. Mus.*, **30**: 321-369, pls. 17-26.
- FRETTER, V., 1951. *Turbonilla elegantissima* (Montagu), a parasitic opisthobranch. *J. Mar. Biol. Assoc. U. K.*, **30**: 37-47.
- FRETTER, V., 1953. The transference of sperm from male to female prosobranch, with reference, also, to the pyramidellids. *Proc. Linn. Soc. Lond.*, **164**: 217-224.
- FRETTER, V., AND A. GRAHAM, 1949. The structure and mode of life of the Pyramidellidae, parasitic opisthobranchs. *J. Mar. Biol. Assoc. U. K.*, **28**: 493-532.
- FRETTER, V., AND A. GRAHAM, 1962. *British prosobranch molluscs; their functional anatomy and ecology*. Ray Society, London, xvi + 755 pp.
- HÖISAETER, T., 1965. Spermatophores in *Chrysallida obtusa* (Brown) (Opisthobranchia, Pyramidellidae). *Sarsia*, **18**: 63-68.
- JEFFREYS, J. G., 1884. On the Mollusca procured during the 'Lightning' and 'Porcupine' Expeditions, 1868-70. (Part VIII.) *Proc. Zool. Soc. Lond.*, **1884**: 341-372, pls. 26-28.
- LAFOLLETTE, P. I., 1977. Inbreeding and intraspecific variation in *Chrysallida* Carpenter, 1857 (Gastropoda: Pyramidellidae). *West. Soc. Malac. Ann. Rept.*, **10**: 18-23.
- MAAS, D., 1964. Über Cuticularbildungen am Penis von Pyramidelliden. *Zool. Anz.*, **173**: 137-148.
- ODÉ, H., 1968. *Odostomia* (Menestho) *bushiana* Bartsch 1909. *Texas Conchologist*, **5**: 26-27.
- ODÉ, H., 1971. *Odostomia dianthophila* Wells and Wells, 1961. *Texas Conchologist*, **7**: 89.
- ODÉ, H., AND A. B. SPEERS, 1972. Notes concerning Texas beach shells. Superfamily Pyramidellacea. Part II. The odostomiid genera and the genus *Longchaeus*. *Texas Conchologist*, **9**: 1-17.
- RIOS, E. C., 1975. *Brazilian marine mollusks iconography*. Museu Oceanográfico, Fundação Universidade do Rio Grande, Rio Grande do Sul, 331 pp., 91 pls.
- ROBERTSON, R., 1967. The life history of *Odostomia bisuturalis*, and *Odostomia* spermatophores (Gastropoda: Pyramidellidae). *YearB. Am. Philos. Soc.*, **1966**: 368-370.

- ROBERTSON, R., 1968. Hosts, spermatophores, and the systematics of five east American species of *Odostomia*, s. l. (Pyramidellidae). *Am. Malacol. Union Inc. Annu. Rept.*, 1967 [Bull. 34]: 12-13.
- SAURIN, E., 1959. Pyramidellidae de Nha-Trang (Viêt-Nam). *Ann. Fac. Sci. Univ. Saigon*, 1959: 223-282, pls. A, 1-9.
- SAURIN, E., 1962. Pyramidellidae du Golfe de Thaïlande. *Ann. Fac. Sci. Univ. Saigon*, 1961: 231-266, 5 pls.
- SCHELTEMA, A. H., 1965. Two gastropod hosts of the pyramidellid gastropod *Odostomia bisuturalis*. *Nautilus*, 79: 7-10.
- THIELE, J., 1929. *Handbuch der systematischen Weichtierkunde*. Fischer, Jena. Band 1 (1), pp. 1-376.
- THORSON, G., 1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Øresund). *Medd. Komm. Danmarks Fisk.- Havunders.*, ser. Plankton, 4: 1-523.
- WELLS, H. W., 1959. Notes on *Odostomia impressa* (Say). *Nautilus*, 72: 140-144.
- WELLS, H. W., AND M. J. WELLS, 1961. Three species of *Odostomia* from North Carolina, with description of new species. *Nautilus*, 74: 149-157.
- WINKLEY, H. W., 1909. New England Pyramidellidae, with description of a new species. *Nautilus*. 23: 39-40.
- WINKLEY, H. W., 1912. New England notes. *Nautilus*, 26: 54-55.



Robertson, Robert. 1978. "SPERMATOPHOES OF SIX EASTERN NORTH AMERICAN PYRAMIDELLID GASTROPODS AND THEIR SYSTEMATIC SIGNIFICANCE (WITH THE NEW GENUS BOONEA)." *The Biological bulletin* 155, 360–382. <https://doi.org/10.2307/1540958>.

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