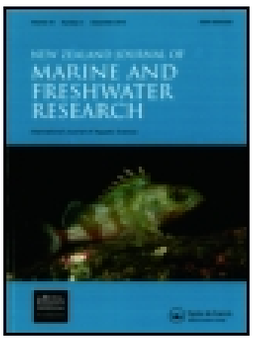

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Reproductive biology of *Arthritica crassiformis* and *A. bifurca*, two commensal bivalve molluscs (Leptonacea)

PAUL CHANLEY* and MATOIRA CHANLEY*

Fisheries Research Division, Ministry of Agriculture and Fisheries, P.O. Box 19062, Wellington, New Zealand

Arthritica crassiformis Powell and *A. bifurca* (Webster) are functional hermaphrodites. Specimens of both species were isolated and maintained in individual plastic containers until they produced two broods of larvae. *A. crassiformis* produced an average of 7.75 larvae per day, with brood sizes of 245–3120 larvae and 11–21 days between broods. *A. bifurca* produced an average of 8.56 larvae per day, with brood sizes of 5–5016 larvae and 8½ to 20 days between broods. Larger clams of both species produced more larvae than did smaller clams. Larvae were incubated for about 1 week and were usually released at one time although releases continued for as much as 3 days. *A. crassiformis* larvae averaged 150 μm in length at release. The hinge increased from 80 to 105 μm in length and was without discernible hinge teeth. A low, rounded umbo appeared at lengths of 175–200 μm and larvae set at 235–270 μm. *A. bifurca* larvae averaged 124 μm in length at release. The hinge line increased from 76 to 89 μm and was without teeth. A low, rounded umbo appeared at 150–169 μm and larvae set at 243–275 μm.

KEYWORDS: Commensal bivalves, *Arthritica* spp., Reproductive biology, Brooding patterns, Larval stages, Larval morphology, Development, Settlement.

INTRODUCTION

Many leptonacean (Erycinacea) bivalve molluscs are small clams which live in association with other invertebrates (Boss 1965). Some species are hermaphroditic or capable of self-fertilisation (Oldfield 1964, Franz 1973). Gage (1968) reported "spermatids, enclosed in elongate sac, opening into the supra-branchial space in the mantle cavity" in *Mysella cuneata;* whether this represents a true hermaphroditic condition or a modified male is unknown. Extreme modification, probably parasitic in nature, has been reported by Jenner & McCrary (1968) in the male of *Montacuta percompressa* that is found within the mantle cavity of the female. The male of *M. floridana* has also been found living within the mantle cavity of the female (Dr C. Jenner, pers. comm.).

In most leptonacean species that have been studied the larvae are incubated briefly, to the straight-hinge stage, and then undergo a relatively long planktonic existence (Chanley & Chanley 1970).

Arthritica crassiformis is a small white clam (Fig. 1) that lives commensally with the rock-boring pholadid *Barnea similis* in soft rock near the low tide line throughout the North Island, New Zealand. *A. crassiformis* reaches a maximum length of 5.4 mm (Ponder 1965), but specimens of 4 mm or less are more usual. It is most frequently attached to *B. similis* by byssus threads, especially to the thicker periostracum bordering of the shell. Several may be found on each host, with the densest concentrations on the ventral surface just posterior to the pedal gape (Morton 1973). *A. crassiformis* incubates several hundred larvae 109–150 μm in length (Ponder 1965, Booth 1979). Booth found larvae in 10% of adults collected in January and May 1972 in the Bay of Islands and described these larvae.

A. bifurca (Fig. 2) is of a similar size to *A. crassiformis* and is widely distributed in New Zealand waters. It may live commensally around the outer surface of the head end of the tube worm *Pectinaria australis* (Wear 1966) or it may be free-living (Ponder 1965, Booth 1979). Booth found that 15–35% of adult *A. bifurca* collected throughout the year were incubating larvae, but this dropped to 5–10% during the spring months; incubated larvae were 110–130 μm long. He described these larvae and tentatively identified the late stage larvae of this species from plankton samples. The late stage larval hinge lacked a true provinculum but did have "feebly developed serrations".

The present study was part of a programme to rear larvae from known parents of as many New Zealand species of bivalve molluscs as possible and to describe all developmental stages. While maintaining brood stocks of *A. crassiformis* and *A. bifurca,* observations were made on frequency of spawning, incubation period, and fecundity.

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*Present address: *Proyecto Hatchery, Fundacion Chile, Avda. Santa Maria 06500, Santiago, Chile*

MATERIALS AND METHODS

Specimens of *A. crassiformis* Powell were collected from rock-boring pholads and their burrows in soft rock at Plimmerton, on the Pauatahanui Inlet, on 27 October 1977. Most were associated with *Barnea similis*, but contrary to the reports of Ponder (1965) and Morton (1973) a few were found associated with another pholadid, *Pholadidea spathulata*.

A. bifurca (Webster) were collected from the beach at Petone, Wellington Harbour, on 10 November 1977. They were associated with the marine tube-worm *Pectinaria australis*. Both species were brought to the Fisheries Research Division Shellfish Hatchery at Mahanga Bay, Wellington, and kept separate from their hosts. Between 50 and 100 of each were kept at 15.5–19.0°C, in shallow polyethylene dishes containing sea water filtered at 1 μm. In addition, 14 *A. crassiformis* and 12 *A. bifurca* were isolated and individually maintained in clear 100-ml plastic jars at 18–20°C. The water was changed and the larvae were removed and counted daily. Adults were fed enough cultured unicellular algae to discolour the water after every water change; *Pavlova lutheri, Isochrysis galbana, Tetraselmis suecica,* and *Skeletonema costatum* were used to feed both larvae and adults. Clams were preserved for histological study at various intervals after release of larvae.

Larvae were collected and cultured separately at 18–20°C in 1-L beakers at densities of up to 15 per ml. Larvae were cultured in 1 μm filtered sea water which was changed daily by pouring it through a 75-μm nylon screen. After the water was changed, larvae were fed sufficient cultured algae to discolour the water. Samples of larvae at all stages of development were fixed in a sea water solution of 5% formalin, 5% sugar, and 15% Tris, and preserved in a sea water solution of 5% formalin, 10% propylene glycol, and 1% propylene phenoxitol, buffered to pH 8 with sodium glycerophosphate (Turner 1976). Larval measurements were made with a filar micrometer.

TERMINOLOGY

The following is an expanded version of the terminology used by Chanley & Andrews (1971) and is illustrated in Fig. 3.

TOTAL LENGTH. The maximum anteroposterior dimension (usually roughly parallel to the dorsal margin of the shell).

TOTAL HEIGHT. The maximum dorsoventral dimension (roughly perpendicular to the length).

DEPTH. The maximum left–right dimension.

HINGE LINE LENGTH. The maximum straight distance of the dorsal margin. In intact larvae this is measurable only before development of the umbo. The term is used to describe the measurable straight dorsal margin, whether it be prodissoconch I or a combination of prodissoconchs I and II.

SHOULDER HEIGHT. The maximum distance to the dorsal margin from a line extending from the extreme anterior margin to the extreme posterior margin. In straight-hinge larvae this will usually be to or near one end of the hinge line. In umbo larvae this axis will extend to the maximum dorsal extension of the umbo.

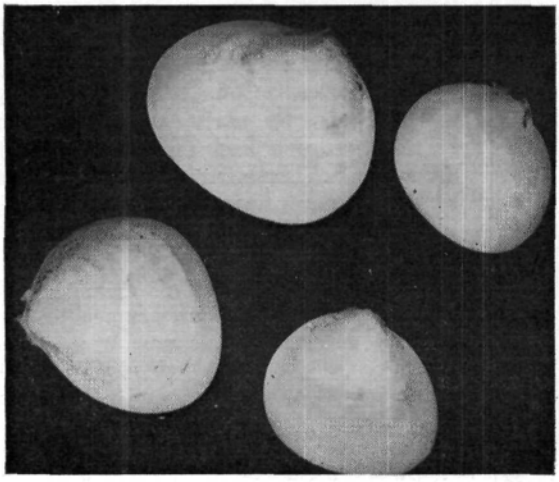


Fig. 1. Adult *Arthritica crassiformis*. Natural size 3.0–4.5 mm.

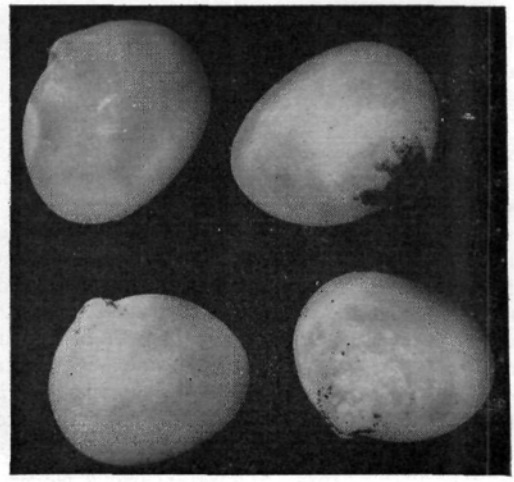


Fig. 2. Adult *Arthritica bifurca*. Natural size 3.0–4.0 mm.

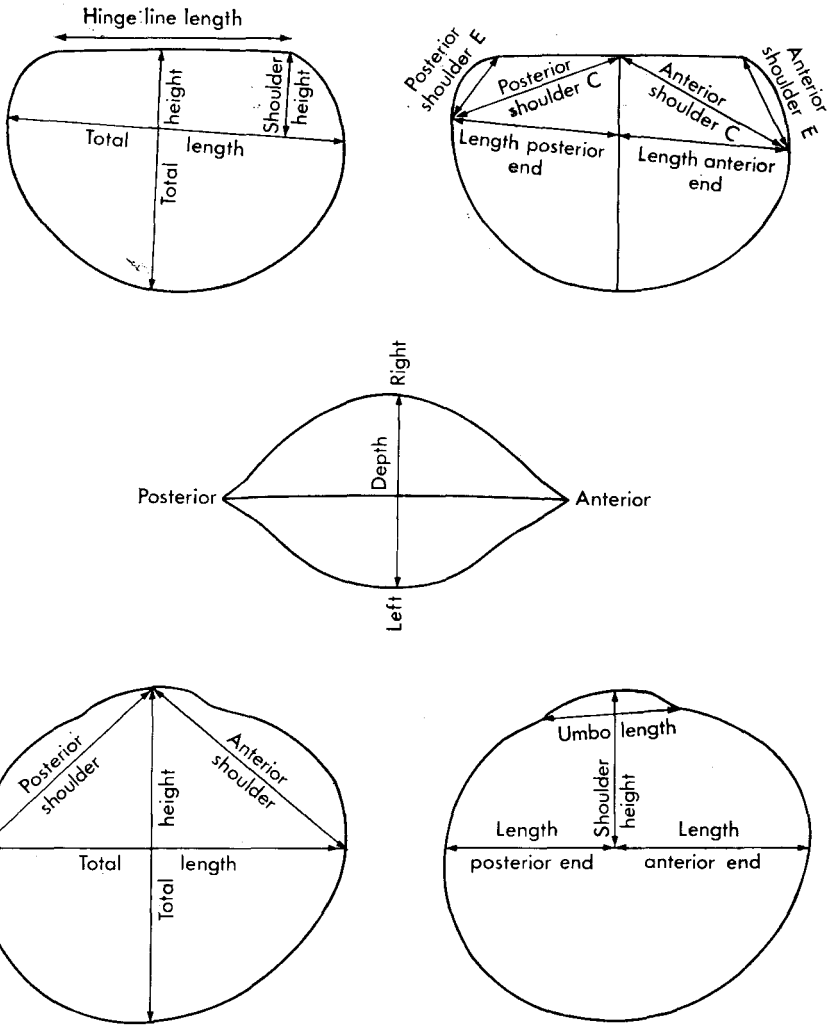


Fig. 3. Terminology used in describing larvae of *Arthritica crassiformis* and *A. bifurca*. Larval outline used in the illustration is that of *Choromytilus chorus*.

SHOULDER LENGTH C. In straight-hinge larvae the maximum straight line distance from the extreme anterior margin to the centre of the hinge line (anterior shoulder) and the maximum straight line distance from the extreme posterior margin to the centre of the hinge line (posterior shoulder). In umbo larvae the maximum straight line distance from the maximum dorsal extension of the umbo to the extreme anterior and posterior margins respectively.

SHOULDER LENGTH E. This dimension (measurable only in straight-hinge larvae) is the maximum straight line length from the extreme anterior margin to the anterior end of the hinge line (anterior shoulder) and from the extreme posterior margin to the posterior end of the hinge line (posterior shoulder).

LENGTH ANTERIOR END. The distance from the anterior extremity of the shell to a line drawn from the middle of the umbo or straight-hinge line to the extreme ventral margin of the shell.

LENGTH POSTERIOR END. The total length less the length of the anterior end.

UMBO LENGTH. The distance between the anterior and posterior points where the umbo extends above the remainder of the dorsal margin of the shell. This dimension is measurable in the 'knobby' type of umbo where the separation of umbo from the dorsal margin is clear, but is usually not measurable for other umbo types. Occasionally it can be measured when a minor protuberance extends above the dorsal margin with umbones otherwise shaped as 'round', angular', or 'broadly round'.

UMBO. The swollen dorsal protuberance of the shell. (See Chanley & Andrews (1971) for umbo shapes.)

RESULTS

REPRODUCTIVE BEHAVIOUR OF ISOLATED CLAMS

Arthritica crassiformis. Some of the adults of this species released larvae within 24 h of isolation; all had released some larvae by the 16th day of isolation. Also by the 16th day, some of the isolated clams had begun to release a second batch of larvae (Table 1). By the 36th day all but one clam had released two batches of larvae; this clam was also atypical in that it produced only 245 larvae on the one occasion it did release larvae. The other adults released from 424 to 3120 larvae at a time. Total larvae produced in two broods ranged from 1028 to 5182 per clam. Larger clams tended to produce more larvae than smaller clams. The eight largest clams, 3.3–4.6 mm long after their second release of larvae, had released an average of 1922 larvae per release. The six smallest clams ranged from 2.2 to 3.2 mm long and released an average of 866 larvae per batch. Clams often released larvae over a 2–3-day period. The time between batches of larvae ranged from 11 to 24 days, but most often the second brood of larvae was released 13–14 days after the first.

A. crassiformis ranged from 2.0 to 4.3 mm (average 3.1 mm) in length at the beginning of the experiment. After their second batch of larvae, clams ranged from 2.2 to 4.6 mm in length (average 3.3 mm). These figures indicate that experimental conditions did permit the growth of clams but they cannot be used to assess growth rate as the time from the start of the experiment to preservation of clams after the release of the second batch of larvae varied from 17 to 32 days.

Arthritica bifurca. Clams began releasing larvae within 1 day of being placed in isolation. All 12 had released larvae by the 14th day of isolation, by which time some of the clams had begun to release their second batch of larvae (Table 2). By the 31st day, 9 of the 12 had released a second batch of larvae, but the other 3 had not done so after 35–37 days and were preserved. One of these may have lost its second batch of eggs when the first larvae were released as many eggs were found in the container with the adult and the larvae. Another clam discharged some eggs with larvae on one occasion.

The numbers of larvae released at one time varied considerably; the lowest counts were 5, 136, and 166 and the three largest releases were of 3205, 3517, and 5016 larvae.

The smallest number of larvae released in two batches by a single clam was 987 and the greatest 8533. As with *A. crassiformis* larger adults usually produced more larvae than smaller adults. Six that were 2.8 mm or more long at the end of the experiment had averaged 2442 larvae per release and 6 that were 2.6 mm and under averaged only 968 larvae per release. Usually a single batch of larvae was completely released on one day, but some individuals released larvae over a 2–3-day period. The time between the first and second release of larvae varied from 8 to 21 days (Table 1).

Ten of the 12 isolated *A. bifurca* adults were 2.3–3.2 mm long initially, and were 2.5–3.3 mm long after the second release of larvae. The other two were accidentally lost or broken before the final measurement. Average lengths increased by 0.1 mm during this period, indicating that growth took place during the experiment.

HISTOLOGICAL EXAMINATION

Examination revealed that *A. crassiformis* adults were hermaphroditic with no separate or parasitic

Table 1. Lengths, time in isolation, and numbers of larvae released by isolated adult *Arthritica crassiformis* (–, no data; n.c., not counted).

Length (mm) initial	Length (mm) after 2nd larval release	Days in isolation before 1st release of larvae	Days in isolation before 2nd release of larvae	Nos of larvae 1st release	Nos of larvae 2nd release	Nos of larvae Total	Days between releases
2.0	2.2	12	28–29	604	424	1028	16–17
2.3	2.4	16	27	638	571	1209	11
2.6	2.8	1–3	16–17	1504	1064	2568	13–16
2.7	–	1–3	–	245	–	245	–
2.8	2.8	16–17	29	1248	1068	2316	12–13
2.9	3.2	9	23	1296	n.c.	–	14
3.1	3.3	15	28–29	737	1211	1948	13–14
3.2	3.3	1–3	18–19	1407	1573	2980	15–18
3.3	3.3	7–8	21–23	1771	3120	4891	13–16
3.4	3.5	14–15	28–30	2707	1216	3923	13–16
3.6	3.8	9–12	24–25	2498	1317	3815	12–16
3.7	3.9	1–3	17	2330	2023	4353	14–16
3.8	4.2	12–14	36	3094	2088	5182	22–24
4.3	4.6	14–15	32	3074	579	3653	17–18

males (Fig. 4). Many individuals were incubating larvae yet had mature eggs and sperm in the gonad. Three individuals preserved 2–4 days after releasing larvae had ovaries full of eggs and testes with mature sperm, but were not incubating larvae or eggs in gill or mantle brood chambers. One individual preserved 4 days after releasing larvae was incubating fertilised eggs and another, preserved 5 days after last release of larvae, had large numbers of unfertilised eggs in brood chambers; ovaries were empty but testes were filled with mature sperm.

A. bifurca adults were also hermaphroditic with no separate parasitic male. They were often incubating larvae at the same time as they had mature eggs and sperm in the gonad. All individuals preserved more than 1 day after releasing larvae were again incubating larvae, but one specimen preserved 3 days after releasing larvae was not incubating eggs or larvae.

LARVAL DEVELOPMENT

Arthritica crassiformis (Figs 5 & 6)

STRAIGHT-HINGE LARVAE. Larvae were at the straight-hinge stage when released from the parent and were 126–165 μm (average 150 μm) long, with a depth of 40–68 μm. Larvae remained straight-hinged until 175–207 μm long; during this period height increased from 93 to 159 μm and was usually 32–42 μm less than length. Depth increased from 58 to 121 μm and was initially 70–80 μm less than length. The anterior end of the straight-hinge larvae was less pointed than the posterior end and was usually 5–20 μm longer and lower than the posterior end. The slope of the dorsal margin from the anterior end to the hinge line was also longer and more rounded than the posterior. Dimensional changes in shoulder length E and C with increases in length of larvae and the relationships between the shoulder are shown in Table 3.

UMBO LARVAE. The umbo stage, when the developing umbones obscure the hinge line, began at 175–207 μm long. The umbo was always long and did not project far dorsally. Initially it was round or broadly rounded, but in some individuals (especially older larvae) the umbo became very slightly knobby, and about 110–140 μm long. Umbo larvae were generally oval. Larvae increased to a maximum length of 270 μm, with height increasing from 135 to 240 μm and depth from 94 to 150 μm.

The anterior end usually continued to be slightly longer and more rounded than the posterior end. The dorsal margin above the anterior shoulder tended to be longer and more rounded than the posterior, though both were rounded. The anterior shoulder increased from about 116 μm to about 200 μm during the umbo stage while the posterior shoulder increased from about 100 μm to a maximum of about 160 μm. Shoulder height increased from 61 μm to about 122 μm during the umbo stage. The larval hinge structure consisted of numerous minute serrations in both valves along the entire length of the hinge, but there was no evidence of larval hinge teeth (Fig. 7).

Larvae possessed an apical flagellum (or flagella) 81–115 μm long; it was not always obvious and may be inconspicuous when not extended.

Setting changes began when larvae became 210–220 μm long and developed a foot and eyespot. The foot was large and blunt with a stubby byssal spur at the 'heel'; the clear byssus gland and a conspicuous statocyst were visible in the base of the foot. The small eyespot, about 5 μm in diameter, was not readily visible in some larvae, and could not be seen in one specimen 267 μm long. The velum was lost when larvae were between 235 and 267 μm in length. Gills first appeared at about 235 μm; larvae may possess both velum and gills simultaneously.

Table 2. Lengths, time in isolation, and numbers of larvae released by isolated adult *Arthritica bifurca* (–, no data; *, many eggs released along with larvae—this clam was 3.5 mm long when it released 1527 larvae in its third brood on days 25–28).

Length (mm)		Days in isolation before		Nos of larvae			Days
Initial	after 2nd larval release	1st release of larvae	2nd release of larvae	1st release	2nd release	Total	between release
2.2	–	10	30	892	5	897	20
2.2	–	14	–	136	–	136	–
2.3	2.5	4–5	14–17	1157	1011	2168	9–13
2.3	–	6	15–16	640*	1544	2194	9–10
2.5	2.6	3–4	17	1260	166	1426	13–14
2.5	2.5	4–5	26	1998	1832	3830	21–22
2.6	2.8	8	18	2531	3205	5736	10
2.7	2.8	11	31–32	1311	508	1819	20–21
2.8	–	14	–	1825	–	1825	–
3.0	3.0	4	17–19	1766	2513	4279	13–15
3.0	–	13–14	–	2232	–	2232	–
3.2	3.3	1	9–10	3517	5016	8533	8–9

Arthritica bifurca (Figs 6 & 8)

STRAIGHT-HINGE LARVAE. Larvae were D-shaped when released from the parent, and were 109–143 μm (average 124 μm) long. Larvae retained the straight-hinge shape until a length of 150–169 μm. Height increased from 76 to 136 μm and was usually 29–40 μm less than length; depth increased from 46 to 96 μm and was usually 60–74 μm less than length. The anterior end was rounder, and usually longer than the posterior end by 10–15 μm. The slope of the dorsal margin from the anterior end to the hinge line was longer, lower, and more rounded than the posterior margin. Dimensional changes in shoulder length E and C with increases in length of larvae and the relationships between the shoulder are shown in Table 3.

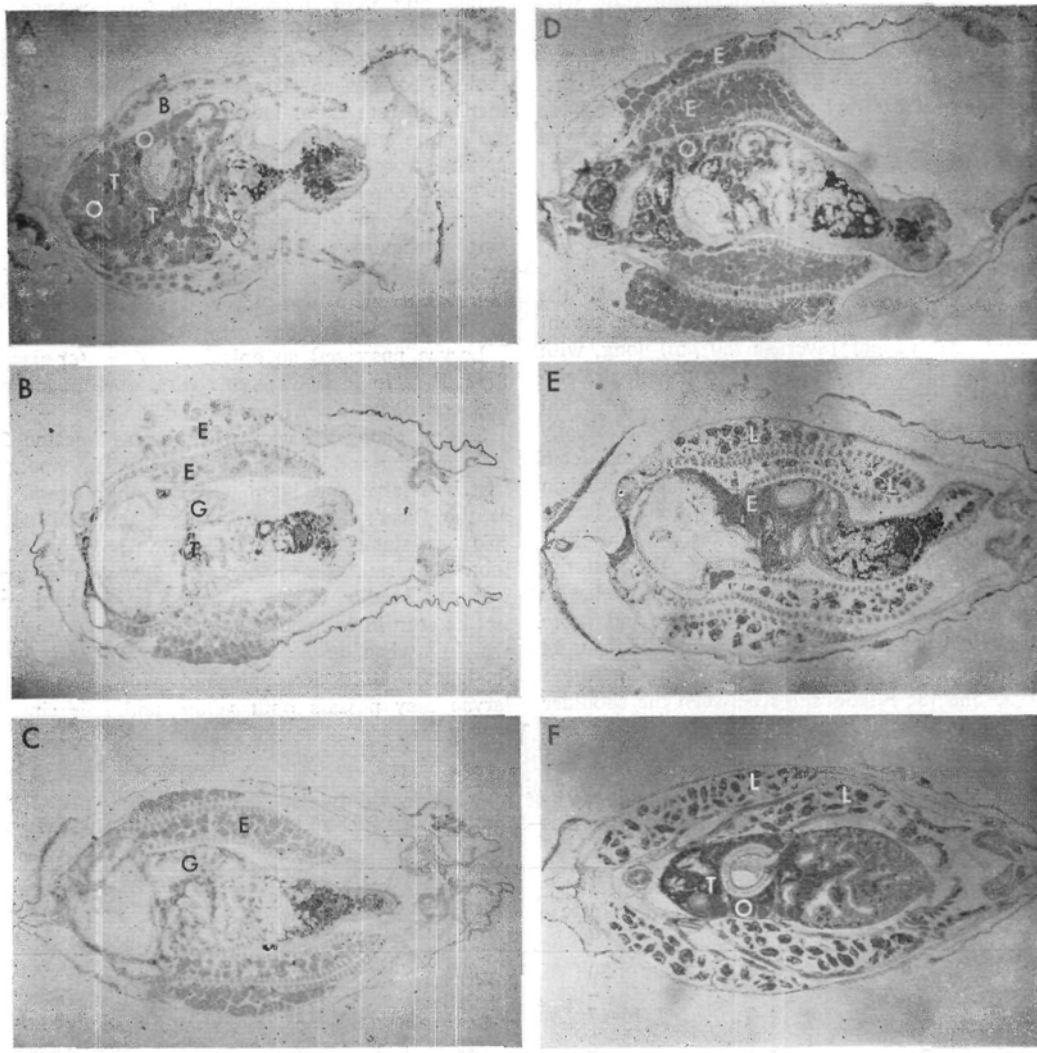


Fig. 4. Cross sections of *Arthritica crassiformis* showing various reproductive stages. **A:** Gonad full. Ovarian follicles containing eggs (O) surround smaller testicular regions (T) of sperm. Brood chambers (B) of gills empty. **B:** Gonad (G) empty except for small testicular region with sperm. Unfertilised eggs (E) in gill brood pouches. **C:** Fertilised eggs (E) in brood pouches. Gonads (G) empty but gametogenesis beginning. **D:** Gonads with sperm (T) and maturing eggs (O). Brood pouches packed with fertilised eggs (E). **E:** Eggs (E) in ovaries. Larvae (L) incubated in gill brood pouches. **F:** Gonads with mature eggs (O) and sperm (T). Straight-hinge larvae (L) almost ready for release in brood pouches.

UMBO LARVAE. The umbo stage began when larvae were 150–169 μm long. As with larval *A. crassiformis,* the umbo was always long and did not project far—initially it was round but long; in some larvae it remained round throughout development. However, in many larvae, especially those over 220 μm long, it became knobby and was more conspicuous than in larval *A. crassiformis.* Umbo length when measurable was 85–116 μm. Most umbo larvae were oval.

Larvae increased to a maximum length of 270 μm before becoming juveniles; during this period height increased from 118 to 239 μm and depth from 78 to 144 μm.

The anterior end of umbo larvae usually continued to be longer and more rounded than the posterior end. The dorsal margins from both ends to the umbo were rounded, but the anterior was longer than the posterior. The anterior shoulder increased from about 86 μm to about 200 μm during the umbo stage while the posterior shoulder increased from about 83 μm to about 143 μm. Though there was considerable variation, the anterior shoulder tended to be 6–25 μm longer than the posterior in early larvae and 20–50 μm longer in larger larvae. Shoulder height increased from 52 to 123 μm during the umbo stage. Initially it was about 100 μm less than length but the difference increased steadily with growth and length exceeded shoulder height by 145–160 μm at the end of the larval period.

The larval hinge (Fig. 9) consisted of numerous minute serrations along the entire length of the hinge line and was indistinguishable from the hinge of larval *A. crassiformis.* The apical flagellum was

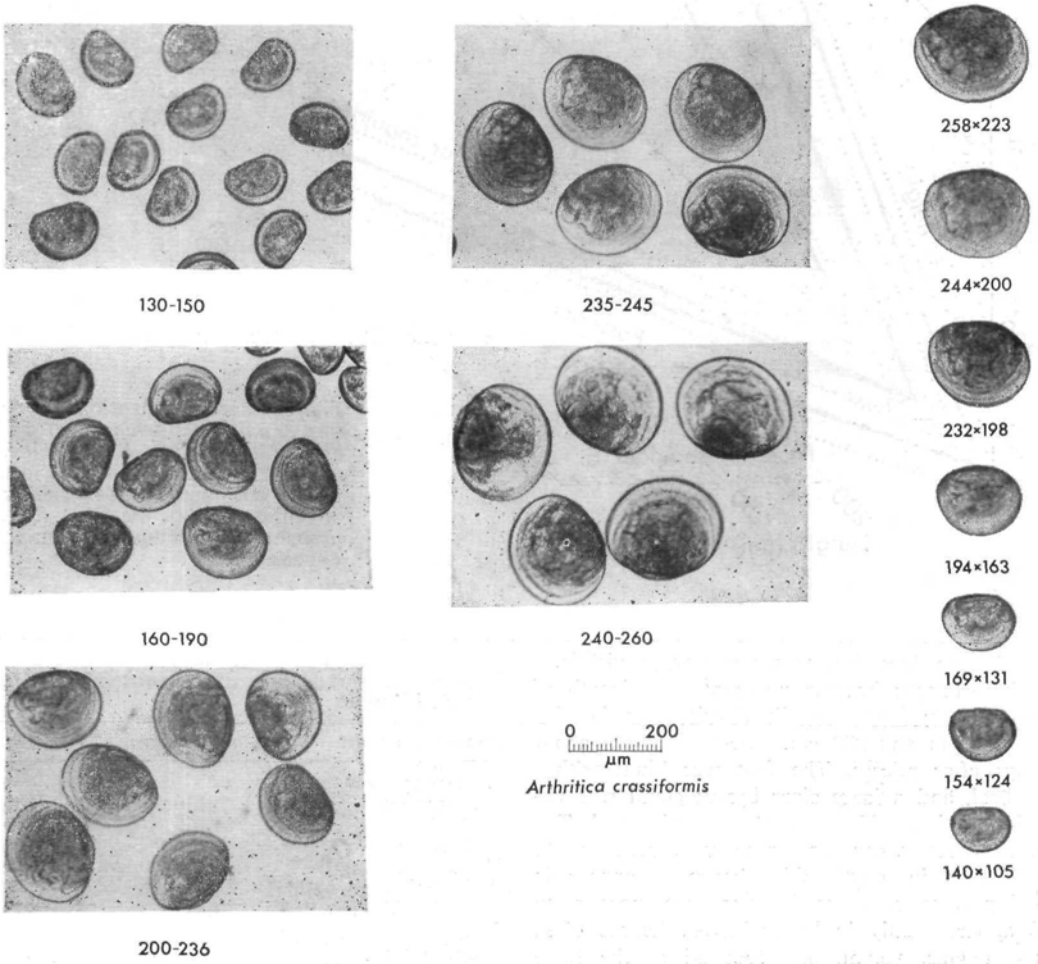


Fig. 5. Larval stages of *Arthritica crassiformis.* Larvae at right have anterior end to right.

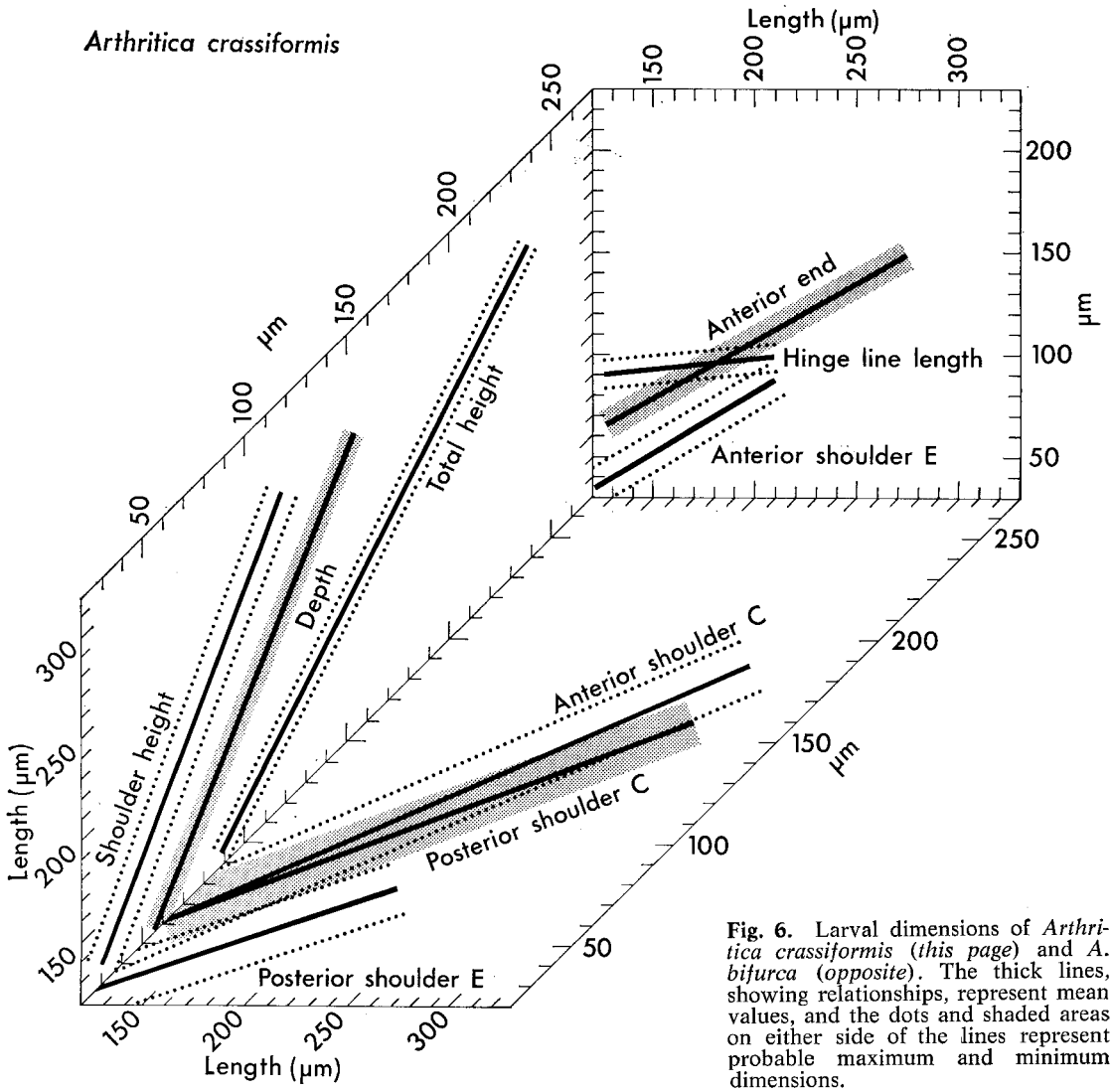


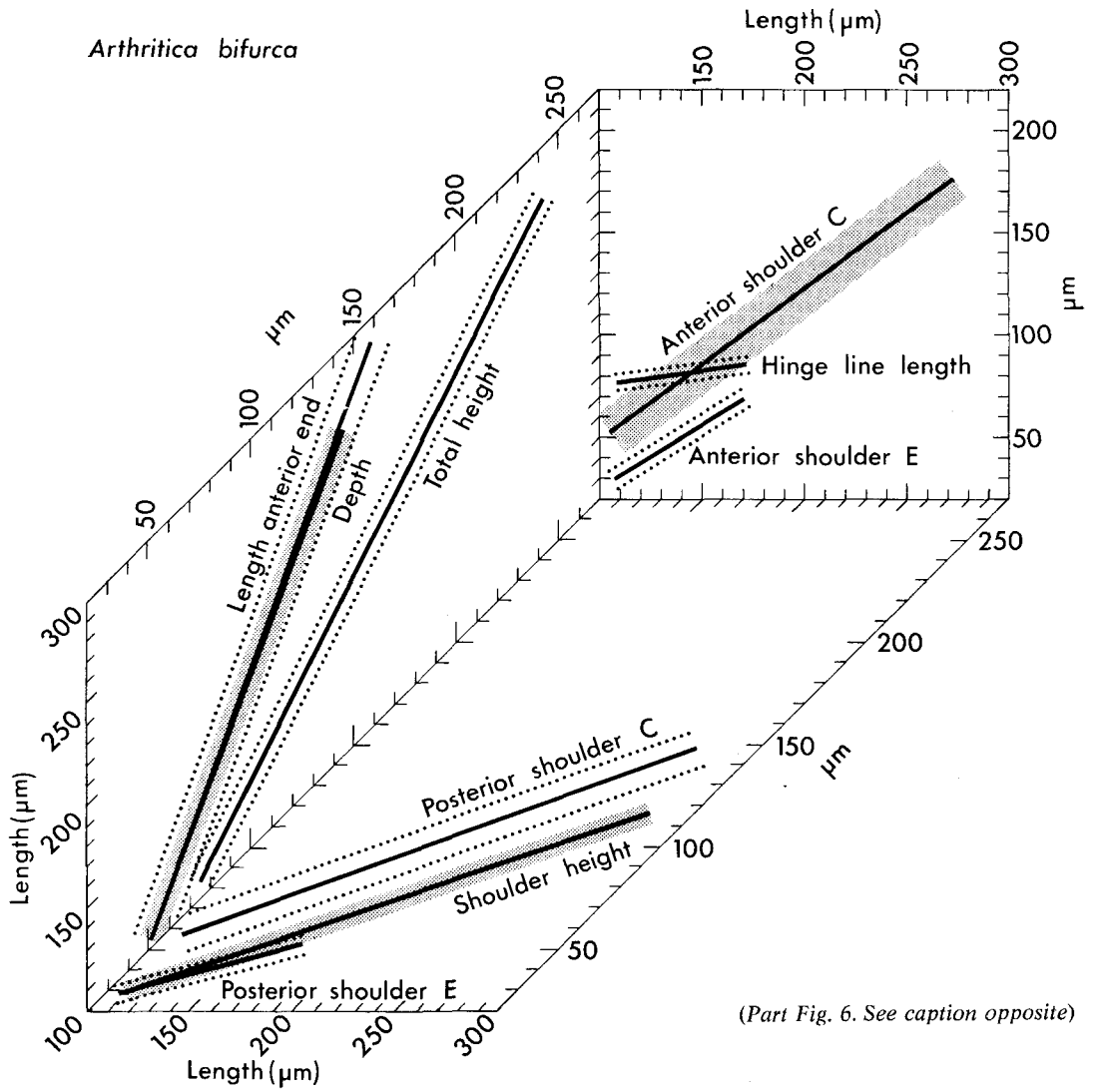
Fig. 6. Larval dimensions of *Arthritica crassiformis* (*this page*) and *A. bifurca* (*opposite*). The thick lines, showing relationships, represent mean values, and the dots and shaded areas on either side of the lines represent probable maximum and minimum dimensions.

about 65 μm long but was not always visible.

Setting changes became apparent at a length of about 210 μm; larvae usually developed a foot between 210 μm and 230 μm. Setting began about 16 days after release. The foot was blunt with a blunt heel, and a large clear byssus gland was visible in its base. No eyespot was observed. The velum was lost when the larvae were between 243 and 275 μm in length. Gills began to appear in some larvae as small as 215 μm, but more often were apparent only in larger larvae. Larvae often possessed gills, velum, and foot all at the same time.

Table 3. Comparison of larval dimensions useful in distinguishing larvae of *Arthritica crassiformis* and *A. bifurca*.

Dimension (μm)	*A. crassiformis*	*A. bifurca*
Length at release		
Minimum	126	109
Maximum	165	143
Average	150	124
Hinge line length	80–105	76–89
Ant. shoulder length E	40–90	30–67
Post. shoulder length E	30–75	28–54
Length at beginning of umbo stage	175–207	150–169
Umbo length	110–140	85–116



(Part Fig. 6. See caption opposite)

DISCUSSION

The breeding seasons for both *A. crassiformis* and *A. bifurca* are long, if not continuous. Booth (1979) suggested at least a 5-month spawning season for *A. crassiformis* (no samples were taken beyond this period) and a continuous reproductive period for *A. bifurca*. His tentative identification of late stage planktonic *A. bifurca* larvae appears to be correct; certainly his larvae closely resemble those reared from known parents and they disappear from the plankton at about the size at which cultured *A. bifurca* larvae completed their larval development.

There was considerable individual variation, but commonly *A. crassiformis* completed a gonadal cycle every 11–17 days. During spawning all mature eggs were expelled from ovaries. Within hours or days sperm was also released. Spawned eggs were fertilised and incubated in gill brood pouches where they developed into straight-hinged larvae. Almost immediately after spawning gametogenesis began in the gonad and gametes developed rapidly. Six to 10 days after spawning, incubated larvae were released into the plankton. About 4 days later a new batch of eggs was spawned and the cycle was repeated.

The gonadal cycle of *A. bifurca* was similar, but shorter and with greater individual variation. Often *A. bifurca* completed a gonadal cycle every 9–15 days. The major differences between the gonadal cycles of the two species seemed to be that *A. bifurca* spawned much nearer the time of larval release and sometimes even simultaneously with it. The incubation period was also about 1 week.

Although these experiments clearly demonstrate the ability of both species to reproduce by self-fertilisation, it is possible that under natural conditions cross-fertilisation also occurs. At least some eggs are released into the brood chambers before sperm is released because unfertilised eggs were being incubated in some of the preserved specimens with empty ovaries and full testes. Presumably these eggs were fertilisable and could have been fertilised by sperm from other adults in the water. In the absence of sperm in the water, eggs are self-fertilised when sperm is released.

The larvae of these two species are very similar. There are a few points of difference, however, that

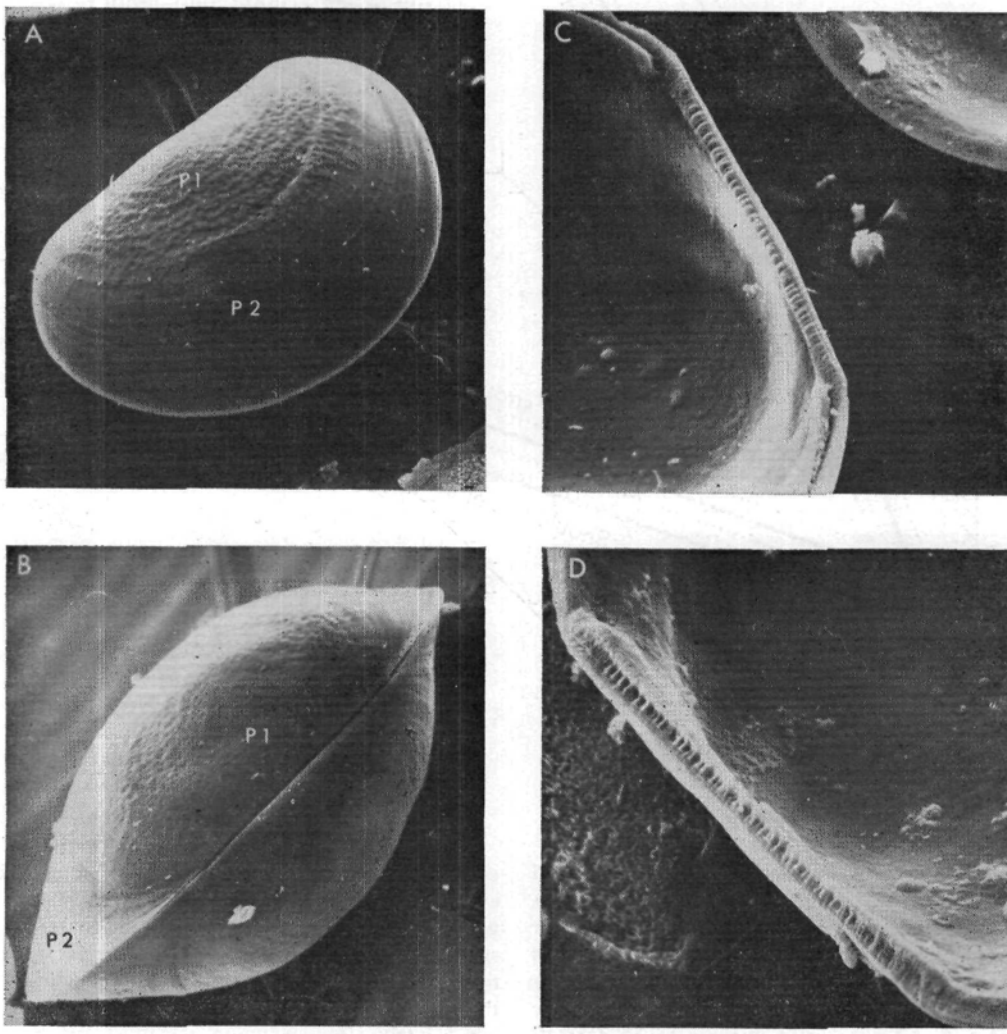


Fig. 7. Scanning electron micrographs of larval *Arthritica crassiformis*. **A:** Lateral view with right valve up. The Prodissoconch I (P 1) portion of the shell is punctate while the Prodissoconch II (P 2) portion of the shell has concentric growth lines (×650). **B:** Dorsal view also showing Prodissoconch I (P 1) and Prodissoconch II (P 2) (×700). C: Internal view of right valve showing minute serrations or irregularities of provinculum (×1100). **D:** Internal view of left valve of larger larva. Provinculum with fine serrations but no definite hinge teeth (×300).

may be of help in identifying planktonic specimens (Table 3). Most significant is the usually longer hinge line in *A. crassiformis* larvae and the resulting larger size before the beginning of the umbo stage. The umbo length of larval *A. bifurca* is also shorter than the umbo length of *A. crassiformis*, and there are pronounced differences in the lengths of the shoulders of the straight-hinge larvae.

Although the *A. bifurca* used in these experiments were smaller than the *A. crassiformis*, they released more larvae per brood than the latter, and also produced more broods per unit time. *A. crassiformis* produced 7.75 larvae per adult per day, and *A. bifurca* 8.56 larvae per adult per day. Under natural conditions the differences probably would have been greater because on at least two occasions eggs were 'aborted' by *A. bifurca* and not counted. These abortions could have been induced by disturbances associated with changing the water in the laboratory, especially in those clams spawning and releasing larvae almost simultaneously. Eggs and larvae of *Montacuta percompressa* have been released prematurely under similar conditions (Chanley & Chanley 1970). There is some evidence that at least some *A. bifurca* also released larvae prematurely. Larvae released by adult *A. bifurca* in these experiments averaged 124 μm long, but Booth (1979) found that incubated larvae in 'wild' clams were

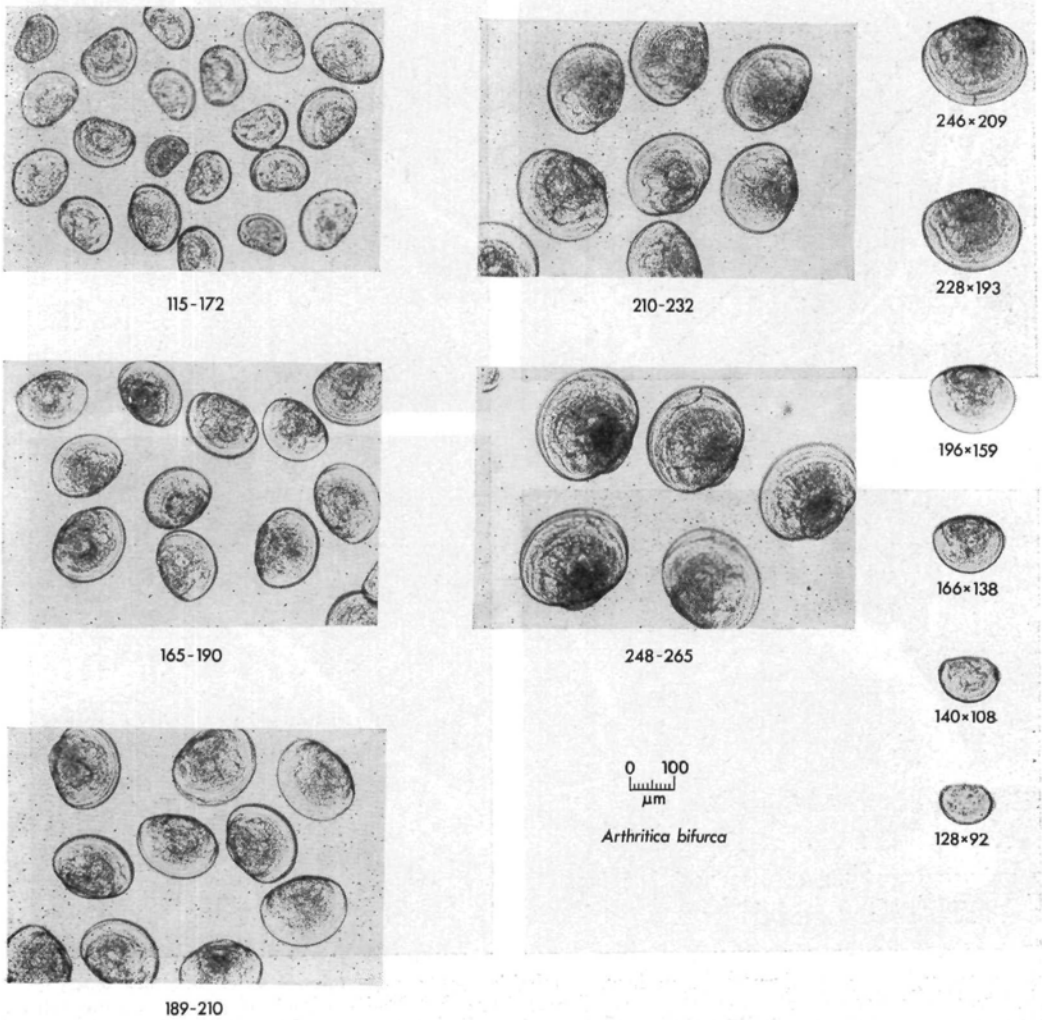


Fig. 8. Larval stages of *Arthritica bifurca*. Larvae at right have anterior end to right.

up to 130 μm long.

Spawning and larval release were not so clearly associated in *A. crassiformis*. Apparently this species has a 3–4-day period between larval release and spawning and there were no abortions of eggs. Also larvae were probably not released prematurely as the average size at release (150 μm) was precisely the maximum size of incubated larvae reported by Booth (1979).

A. bifurca produce more larvae than *A. crassiformis* and their larvae are smaller and develop from smaller eggs. However, since both species set at approximately the same size, the greater numbers of larvae produced by *A. bifurca* may be an adaptation to the longer larval life. It is also possible that the commensalism of *A. crassiformis* in rock burrows provides more protection from predation and hence better juvenile survival than does the free-living worm association of *A. bifurca*. On the other hand the greater number of larvae of *A. bifurca* and the

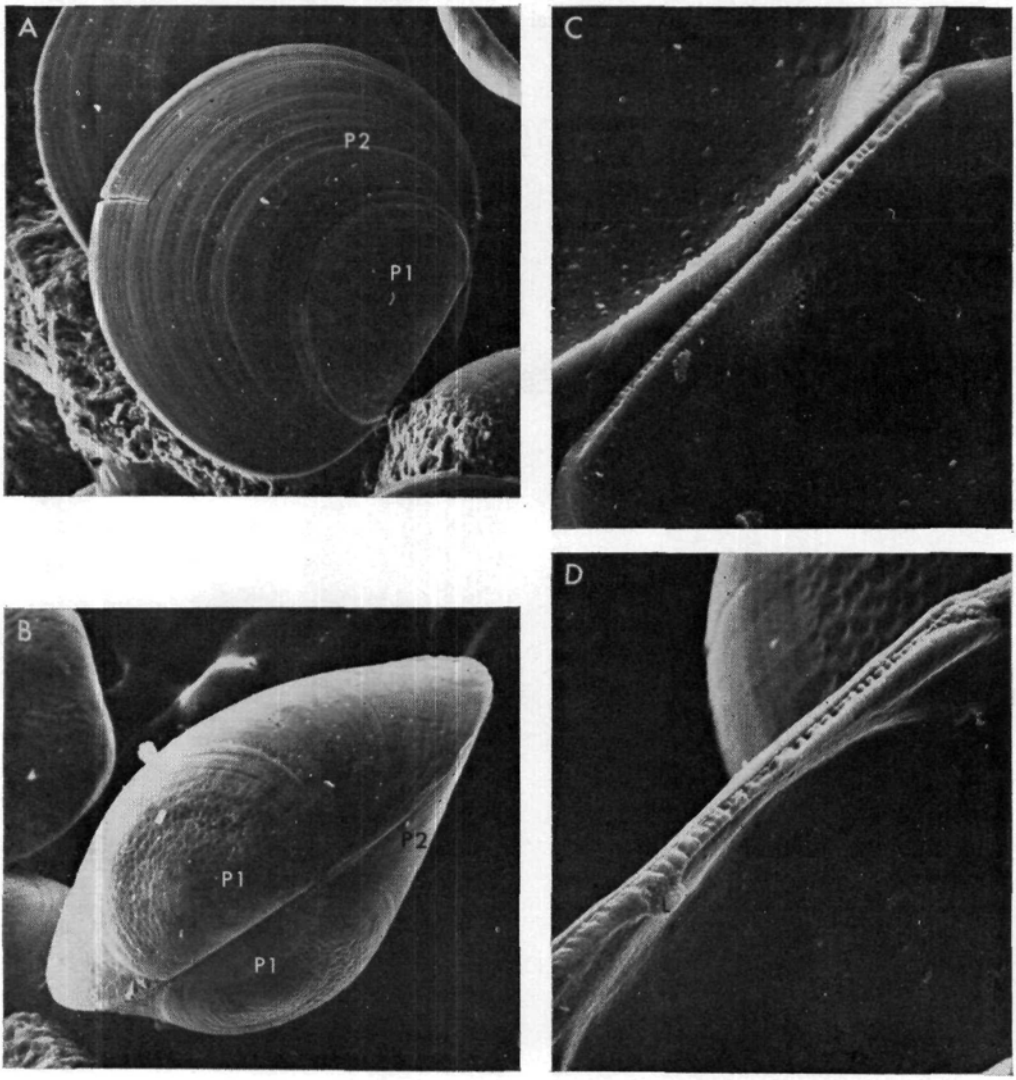


Fig. 9. Scanning electron micrographs of larval *Arthritica bifurca*. **A:** Lateral view with left valve up. The Prodissoconch I portion of the shell (P 1) is distinct from the Prodissoconch II (P 2) portion with concentric growth lines (×350). **B:** Dorsal view showing laterally compressed shape, punctate Prodissoconch I (P 1), and the concentric growth lines of the Prodissoconch II (P 2) (×500). **C:** Hinge structure of larval *A. bifurca* showing fine serrations.

slightly longer planktonic life should result in greater dispersal of the species, thus enhancing survival. Also the less selective substrate requirements of *A. bifurca* could result in a higher percentage of the larvae that survive the planktonic stage finding a satisfactory substrate.

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