calcium ratio observed early in relaxation (3); (ii) shifts in the force-pCa relation with changes in sarcomere length (18, 19); (iii) the apparent positive "cooperativity" in calcium activation that steepens the force-pCa curve (19–21); and (iv) an effect on calcium sensitivity of factors that may affect actomyosin interaction and influence cross-bridge turnover (for instance, Mg-ATP, Mg, pH, and fiber type) (20, 21).

ELLIS B. RIDGWAY
Department of Physiology and Biophysics, Medical College of Virginia, Richmond 23298

ALBERT M. GORDON
DONALD A. MARTYN
Department of Physiology and Biophysics, University of Washington Medical School, Seattle 98195

References and Notes

1. S. Ebashi, A. Kodama, F. Ebashi, *J. Biochem.* **64**, 465 (1968); S. Ebashi and M. Endo, *Prog. Biophys. Mol. Biol.* **18**, 123 (1968); A. G. Szent-Györgyi, *Biophys. J.* **15**, 707 (1975); W. Lehman, *Int. Rev. Cytol.* **44**, 55 (1976).
2. A. Sobieszek and J. V. Small, *J. Mol. Biol.* **102**, 75 (1976); R. Dabrowska, D. Aromatorio, J. M. F. Sherry, D. Hartshorne, *J. Biochem.* **17**, 253 (1978).
3. E. B. Ridgway and C. C. Ashley, *Biochem. Biophys. Res. Commun.* **29**, 229 (1967); C. C. Ashley and E. B. Ridgway, *J. Physiol. (London)* **209**, 105 (1970).
4. The data in Fig. 1C imply that the increased calcium sensitivity is not simply a function of the previous force level but is also dependent on the time spent at that force.
5. R. Natori, *Jikeikai Med. J.* **1**, 119 (1954).
6. C. C. Ashley and D. G. Moisescu, *J. Physiol. (London)* **270**, 627 (1977).
7. The relaxing solution is identical to that described in (8) with no added calcium and with EGTA as the chelator for calcium.
8. D. C. Hellam and R. J. Podolsky, *J. Physiol. (London)* **200**, 807 (1969).
9. The solutions contained 170 mM K propionate, 30 mM Na propionate, 4.5 mM Mg-ATP, 1.5 mM Mg^{2+}, 30 mM EGTA, 60 mM Tes (pH 7.1), 20 mM creatine phosphate, and 10 U/ml creatine phosphokinase. Calcium EGTA was added to achieve the desired pCa ($-\log_{10}$[Ca]). The relaxing solution contained no added calcium. Solutions were mixed as described in (5). Before each contraction, the fiber was transferred from an EGTA relaxing solution to one with HDTA (hexamethylenediamine-N,N,N',N'-tetraacetic acid, a weak Ca^{2+} buffer) replacing the EGTA, in which the fiber remained relaxed but from which force developed more rapidly when the fiber was transferred into a Ca^{2+} activating solution. Fibers immersed in an EGTA-buffered subthreshold Ca^{2+} solution showed the same effect and also the force-pCa hysteresis. All solutions were stirred to increase the speed of the force response to a solution change.
10. In addition, the slope of the relaxation curve is slightly less steep. We also observed this hysteresis in skinned frog and rat skeletal muscle.
11. We examined the effects of changing force in both directions. Stretch causes free calcium to disappear; release causes free calcium to appear (Fig. 1D) (E. B. Ridgway and A. M. Gordon, in preparation).
12. This is supported by the facts that the magnitude of extra free calcium (i) is increased under conditions when more activating calcium is present (increased or paired stimulation), (ii) is correlated with the force redeveloped after the length change (like the classical "active state" experiments), and (iii) has a time course intermediate between the calcium transient and force, as would be required for calcium bound to an activating site. Alternative sources of extra calcium—the sarcoplasmic reticulum (SR) or the surface membrane—can be ruled out on the basis of control experiments. See A. M. Gordon and E. B. Ridgway [*Eur. J. Cardiol.* **7**, 27 (1978)] and E. B. Ridgway and A. M. Gordon [*Biophys. J.* **33**, 30a (1981)] for the SR; and A. M. Gordon and E. B. Ridgway [*J. Gen. Physiol.* **68**, 653 (1976)] for the surface membrane, where it is shown that a shortening step increases the outward current and not the inward current under voltage clamp.
13. R. Bremel and A. Weber, *Nature (London)* **238**, 97 (1972).
14. F. Fuchs, *Biophys. J.* **17**, 161 (1977).
15. R. S. Adelstein and E. Eisenberg, *Annu. Rev. Biochem.* **49**, 921 (1980).
16. E. W. Taylor, *CRC Crit. Rev. Biochem.* **6**, 103 (1979).
17. J. S. Shiner and R. J. Solaro, *Proc. Natl. Acad. Sci. U.S.A.*, in press.
18. M. Endo, *Nature (London)* **237**, 211 (1972); M. G. Hibberd and B. R. Jewell, *J. Physiol. (London)* **290**, 30P (1979).
19. A. Fabiato and F. Fabiato, *J. Gen. Physiol.* **72**, 667 (1978).
20. F. J. Julian, *J. Physiol. (London)* **218**, 117 (1972).
21. P. W. Brandt, R. N. Cox, M. Kawai, *Proc. Natl. Acad. Sci. U.S.A.* **77**, 4717 (1980).
22. We thank A. O. D. Willows and the staff at Friday Harbor Laboratories for their hospitality. We thank O. Shimomura for the native aequorin. We thank S. Price, A. Fabiato, A. Snow, B. Hille, and W. Almers for useful comments on earlier drafts. This work was supported by grants NS 10919 and NS 08384 from the National Institutes of Health and by the Muscular Dystrophy Association.

15 June 1982; revised 10 September 1982

Dwarf Males in the Teredinidae (Bivalvia, Pholadacea)

Abstract. *Extreme sexual dimorphism in the Bivalvia is rare. The occurrence of dwarf males in* Zachsia *appears to be the first case in the Teredinidae and the first outside the Leptonacea. Female* Zachsia *release straight-hinge larvae that develop in the plankton and settle on living rhizomes of* Phyllospadix. *Larvae entering mantle pouches of females become males. Evolution of this life history pattern is tied to problems of living in a fragile, patchy habitat—that is, the rhizomes of* Phyllospadix.

Studies of the life history of *Zachsia zenkewitschi* Bulatoff and Rjabtschikoff 1933 (1) conducted at the Vostok Field Station in the Soviet Union (2) revealed a case of marked sexual dimorphism—that is, dwarf males (3) in the Teredinidae. We investigated the "tailed larvae" of this little known species. These were described as occurring in lateral mantle pouches just anterior to the siphons (1). It was these so-called larvae that proved to be dwarf males.

The occurrence of dwarf males among the Bivalvia is rare and otherwise known only in the Veneroida, superfamily Leptonacea (4). Species with dwarf males are small, parasitic on or commensal with a marine invertebrate (except *Z. zenkewitschi*), and so far as known, brood their larvae.

Like other species with dwarf males,

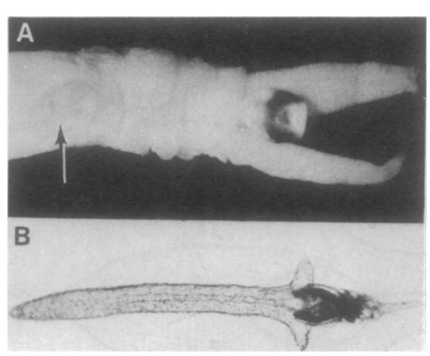

Fig. 1. (A) Lateral view of posterior end of a female *Zachsia zenkewitschi* showing siphons, left pallet, mantle collar, and left mantle pouch (arrow) containing dwarf males (preserved specimen, ×9). (B) Mature dwarf male *Zachsia zenkewitschi* removed from the pouch of the female (preserved specimen, ×30).

Z. zenkewitschi lives in a restricted, patchy habitat, but differs in that it inhabits living rhizomes of the sea grass *Phyllospadix iwatensis* Makino rather than associating with a marine invertebrate. Specimens studied were dissected from *Phyllospadix* collected at six localities in Vostok Bay. Additional specimens were collected by Y.Y. at Putjatin Island, about 25 km west of Vostok, and at Vladivostok, the type locality of *Z. zenkewitschi*. The following observations were based on the study of over 100 specimens collected from these various localities.

Superficially adult female *Z. zenkewitschi* look like other short-term larviparous shipworms. The larvae are brooded until the straight-hinge stage and released en masse when 80 μm long and 70 μm high. They reach the pediveliger stage after feeding in the plankton for 2 to 3 weeks. In laboratory cultures most larvae swim near the bottom of the culture dish, suggesting that in the field they probably swim in the sea grass beds rather than the turbulent surface waters and that wide-ranging dispersal is probably by adults in floating sea grass.

Experimentally we have not succeeded in getting pediveliger larvae to metamorphose, but field and laboratory observations indicate that larvae which settle on *Phyllospadix* that is not inhabited by *Zachsia* will penetrate and metamorphose into females. Pediveligers settling on rhizomes already inhabited by a female will crawl into one of the mantle pouches, which open into the cavity of the mantle collar at the base of the siphons of the female, and metamorphose into males (5). The pouch containing dwarf males can be seen through the mantle of the female (Fig. 1A); there were 3 to 69 males per female in the specimens that we examined. Newly arrived pediveligers could not be distinguished from those taken in plankton tows made in the *Phyllospadix* bed or those newly settled on the sea grass rhizomes (Fig. 2A). However, as metamorphosis begins, the long foot of the pediveliger atrophies, a large highly contractile incurrent siphon and minute excurrent siphon develop, a granular appearing triangular lobe develops anteriorly, and the shell elongates and is internalized by the mantle (Figs. 1B and 2D). Midway in this process the male appears to have three appendages, all of which are apparently ciliated, because on removal from the pouch they can crawl on the foot, siphon, or anterior lobe (Fig. 2, B and C). Males in all stages of development may be found in a single pouch. The largest male was about 1 mm long, the valves 208.5 μm long.

Gonads of the female develop throughout the winter, and spawning of the eggs into the gills begins in mid-June, when the temperature of the water reaches 20°C, and continues through July. The gametogenic cycle in males appears to be short, perhaps a month or less. In ripe males the anterior lobe is greatly enlarged to accommodate the conspicuous sperm balls (Fig. 2E). We have not yet identified the path by which the sperm reach the eggs and were unable to locate a direct connection between the pouch and the mantle cavity using histological techniques. Limited observations suggest that the male releases sperm balls into the mantle pouch through its excurrent siphon, that contraction of the pouch forces the sperm out into the space between the mantle collar and the base of the siphons where they are picked up by the incurrent siphon of the female. Fertilization probably occurs as the eggs leave the gonopore or after they have been deposited in the gills. We do not know what triggers release of the sperm balls or coordinates this with spawning of the eggs into the gills.

Teredinids have a wide variety of reproductive patterns but *Z. zenkewitschi* has the most complicated and unique. It probably evolved along with the habit of (i) brooding the larvae until the straight-hinge stage, which necessitates mantle cavity fertilization but allows for a dispersal stage, and (ii) boring into *Phyllospadix*—that is, living in a dense forest of closely packed rhizomes where sperm released into the water column might be lost. We propose that (i) the presence of males in the pouches of the female ensures a high percentage of fertilization of the eggs, (ii) there is ample gene exchange because the males that reach the females as pediveligers are probably the progeny of some other female, (iii) a dioecious species that has dwarf males ensures the presence of both sexes should (as often happens) the sea grass be pulled from the rocks and float away, and (iv) the presence of only one borer (female) per rhizome reduces the possibility of overcrowding and breakage of the plant.

Zachsia zenkewitschi is now known from several localities in Japan, and its range is probably coextensive with that of *P. iwatensis*. However, it appears to be a rather rare species, apparently never sufficiently abundant to become a pest of *Phyllospadix*, since as we have been unable to locate any reference to the borer in the botanical literature. A few specimens of a second, probably new, species of *Zachsia* have recently been found living in the sea grass *Cymodocea rotundata* near Tulear, Madagascar (*6*). A search of living sea grass rhizomes may well produce additional interesting relationships. Fragments of dead plant material have long been known to harbor teredine borers (*7*), but this is the first case of living sea grass with the borers.

RUTH D. TURNER
Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138
YURI YAKOVLEV
Laboratory of Physiological Ecology, Institute of Marine Biology, Academy of Sciences of the U.S.S.R., Vladivostok 690022

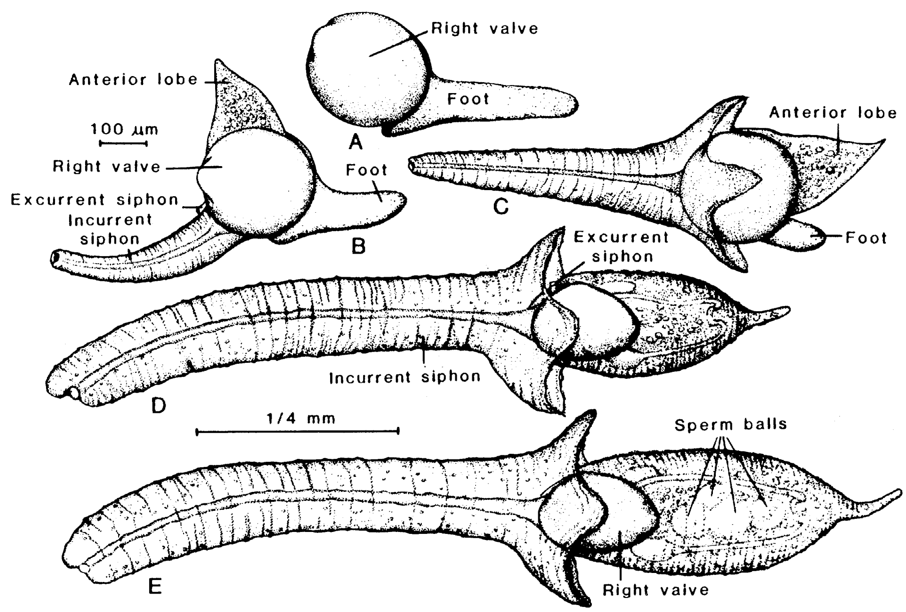

Fig. 2. Stages in the metamorphosis and development of the dwarf male *Zachsia zenkewitschi*. (A) Pediveliger larva at the time of entering the mantle pouch of the female. (B) "Trefoil stage," an early stage in metamorphosis when the foot, anterior lobe, and incurrent siphon are all nearly the same size. (C) Specimen about midway in the process of metamorphosis. (D) Nonreproductive male. (E) Reproductive male. (A) through (C) Scale bar, 100 μm; (D) and (E) scale bar, 1/4 mm.

References and Notes

1. G. A. Bulatoff and P. I. Rjabtschikoff, *Zool. Anz.* **104**, 165 (1933), figures 1 to 20.
2. Vostok Field Station, the summer laboratory of the Institute of Marine Biology, Vladivostok, is located on a small peninsula in the upper reaches of Vostok Bay, about midway between Nahodka and Vladivostok.
3. The term "dwarf male" here refers to cases in which minute males are closely associated with the female—that is, partially or completely enclosed in the female or attached externally.
4. Dwarf males are known in the Leptonacean families (i) Montacutidae: *Montacuta percompressa* Dall [P. Chanley and M. Chanley, *Annu. Rep. Am. Malacol. Union* **1968**, 28 (1968); *Proc. Malacol. Soc. London* **39**, 59 (1970)]; *M. percompressa* Dall, *M. floridana* Dall, and *Entovalva* n. sp. [C. E. Jenner and A. McCrary, *Annu. Rep. Am. Malacol. Union* **1968**, 43 (1968)]; and *M. phascolionis* Dautzenberg (G. Deroux, *C. R. Acad. Sci.* **250**, 2264 (1960)]. (ii) Galeommatidae: *Ephippodonta oedipus* Morton [B. S. Morton, *J. Conchol.* **29**, 31 (1976)]. (iii) Chlamydoconchidae: *Chlamydoconcha orcutti* Dall [B. S. Morton, *J. Zool.* **195**, 81 (1981)].
5. This recalls the situation in *Bonellia viridis* Rolando (an echiuran) as reviewed by M. Gould-Somero [in *Reproduction of Marine Invertebrates*, A. C. Giese and J. S. Pearse, Eds. (Academic Press, New York, 1975), vol. 3, p. 279].
6. Specimens received from B. A. Thomassin, Centre d'Oceanographie, Marseilles, France.
7. T. Wolff, *Aquatic Botany* **2**, 161 (1976).
8. We are grateful for the interest and financial support of the USSR-USA Joint Program for the Study of the Productivity and Biochemistry of the World Oceans which made this cooperative research possible. Thanks are extended to A. Zhirmunsky, director of the Institute of Marine Biology, Vladivostok; to V. Kasyanov, head of the Embryology Laboratory; to the staff at the Vostok Station, particularly the interpreters who, in the early stages of the work, eased communication problems; to F. Grassle, R. Mann, and J. A. Pechenik for critical reading of the manuscript; and to C. B. Calloway for photographic assistance and stimulating discussion. Supported by ONR grant N00014-76-C-0281, NR 104-687.

19 August 1982; revised 9 November 1982