NOTES ON RECENT BRACHIOPODS

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ABSTRACT. This note presents data relating to the relative vitality of articulate and inarticulate brachiopods and submits that representatives of each are probably fitted to and limited by particular, though in some instances very different, ranges of ecologic conditions. Information available suggests the life-span of the inarticulate *Lingula unguis* to be five years or more and that of the articulate *Terebratella inconspicua* about four years, although it appears that less than 10 percent of the latter live to the third year. The proportion of males to females among adult *Terebratulina septentrionalis* and *Terebratella inconspicua* appears to be about equal in both instances. Brief description of the sex products of *Terebratulina* is given, and the reader is referred to published sources of embrylogical data.

Attention is called to certain implications of E. Percival's recent significant paper on the embryology of *Terebratella inconspicua.* He shows that *ventral* and *dorsal* as applied to brachiopod valves should be supplanted by the formerly popular and more accurate terms *pedicle* and *brachial.* Percival also presents additional evidence relating to the growing idea that the articulates (Pygocaulia) and inarticulates (Gastrocaulia) belong to distinct phyla. However, detailed embryological studies of a rhynchonelloid and a neotremoid *at least* are necessary to critical evaluation of the problem. These, as well as physiological studies of representatives of major living groups, are needed before differentiation of the brachiopods on the phylum-level might be soundly established. Reference is made to possible subjects for such studies on the coasts of North America.

DISCUSSION

THE amazing vitality under conditions of extreme pollution, exposure at low tide, and lack of aeration of certain species of the inarticulate brachiopods *Lingula*, *Glottidia*, and *Crania* is well known, and it might be inferred from this that brachiopods as a group were insensitive animals. An attempt in the summer of 1947 to ship living specimens of the articulate brachiopod *Terebratulina septentrionalis* (Couthouy) from the Mount Desert Island Biological Laboratory in Maine to the Woods Hole Marine Biological Laboratory in Massachusetts shows that this is not the case. It is, moreover, likely that some of the living inarticulates are rather closely suited to situations that one might be prejudiced to think of as "unfavorable" for marine invertebrates. The information at hand suggests that *Lingula unguis* (Lin-

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naeus), as well as *Terebratulina septentrionalis*, may be fitted to and limited by particular ranges of ecologic conditions. Although the former displays remarkable vitality over a great range of certain striking variables, there is evidence that its resistance may be low toward changes in other directions.

Approximately 60 specimens of the terebratuloid brachiopod *Terebratulina septentrionalis*, dragged off Egg Rock, near Salsbury Cove, Maine, on the afternoon of July 30, 1947, were put in a one-gallon thermos jug of fresh, cold sea water and placed on the train in Ellsworth, Maine, at 9:00 P. M. of the same day by Dr. R. P. Forster, Director of the Mount Desert Island Biological Laboratory. For some reason they were held up in Boston and did not reach Woods Hole until August 2. They were placed immediately in a cold storage box, in the same container, but I did not receive the specimens until 6:30 P. M. August 3. At this time, although their shells were in good condition, the animals were quite dead, and, to judge from their odor, had been so for some time. It is scarcely surprising that a marine organism should fail to survive four days in unaerated sea water, even though kept cold, and an observation so crude would be unimportant were it not in such marked contrast to data, to be noted presently, on the vitality of certain inarticulate brachiopods under similar circumstances.

A further observation relating to the vitality and living habits of *Terebratulina* is to be credited to Messrs. William Schevill and Henry Stetson, who, in 1933, found *T. septentrionalis* on the dock pilings at Cape Porpoise, Maine, where it was within arm's reach at low tide. In July 1947 a collecting party of five visited Cape Porpoise expressly to obtain *Terebratulina*, but none was to be had. As there is only one small set of dock pilings at Cape Porpoise there is no question that we were at the spot where Schevill and Stetson saw the animal. These pilings were thoroughly searched and explored with scrape-nets at low tide and I think it safe to say that there were no *Terebratulina* on them in July 1947. In addition, two of the party crossed the tide flats to the tide pools on one of the outer ring of islands at Cape Porpoise Harbor and searched in the pools and along the shore with similar negative results so far as *Terebratulina* was concerned. However, the animal has been taken in waters from low tide mark (Morse, 1871, p. 30; Schevill and Stetson, oral communication) to depths as great as 1976 fathoms (Dall, 1920, p. 299) from Fishers Island, New York, east and north along the Atlantic coast to Nova Scotia and as far northeast as Iceland (all round the coast to 67° 09′ N., depths of 109 to 584 meters), Svalbard, north of Eurasia, the coast of Norway, and south to Scotland (Wesenberg-Lund, 1938, p. 6, 10; Dall, 1920, p. 297-299). The occurrences of *T. septentrionalis* recorded by Dall (1920, p. 297-299) are largely from depths below 190 fathoms south of Cape Cod and shallower than 50 fathoms north of the Cape.

Why *T. septentrionalis* should have disappeared from Cape Porpoise is as much a mystery as its occurrence there in the first place, in the polluted shallow waters about the dock. The animal is probably short-lived and its persistent habitats most likely must be continuously repopulated with spat from free-swimming larvae, but once having got a foothold there is no evident reason why it should not have continued to repopulate the pilings at Cape Porpoise. Of course it would there be in competition with normally more successful shore-line animals, and it is said by the local people that other organisms of the same region have become scarce or have disappeared with the dying out of the eel-grass (*Zostera*). Now that *Zostera* is returning to the area it will be of interest to see if *Terebratulina* also comes back into the harbor, and if so what the relationship might be. From the data already given it is evident that any such relationship would necessarily be indirect, and probably in most instances limiting as to population rather than determinant of occurrence. Its study would certainly involve such factors as diatom florescence, the fine detritus from triturated *Zostera*, the production of nitrogenous compounds from *Zostera*, or other nutritive elements subject to transport and not determinant to the survival of *Terebratulina* where lesser competitive pressure or other factors favor its continuance, as is apparently the case at Egg Rock (*see* Jensen, 1914; Blegvad, 1914). An association also to be studied in connection with the maintenance of populations of *Terebratulina* has to do with a dirty brownish encrusting sponge [identified by Dr. M. W. DeLaubenfels as *Iophon nigricans* (Bowerbank)] which covers to some degree practically all specimens of *T. septentrionalis* that I have seen. Factors bearing on growth and distribution of the sponge might have an effect on the brachiopod as well.

Evidently *Terebratulina septentrionalis* requires relatively cold, well aerated marine water and perhaps particular nutrient substances for its normal existence, and it appears to be sensitive to deviations from these conditions. Within the limiting conditions it has attained a wide areal and bathymetric range.

The powers of *Lingula*, *Glottidia*, and *Crania* to survive conditions generally regarded as adverse is in such marked contrast to the noted sensitivity of *Terebratulina* that it seems advisable briefly to review some of the data on the vitality of these inarticulates.

Striking data are given for the Japanese *Lingula unguis* (Linnaeus)[2] by Yatsu (1902a, p. 66), as related to him by "Mr. Hatta, Professor of Biology in the Peer's School." It seems that a large inlet called Matsubasé, in the Bay of Ariake, near Kumamoto in southern Japan, is primarily a sandy tide flat in which *Lingula* and certain edible pelecypods are found in great abundance. After "a season of heavy rain, which lasted twenty days or more" Mr. Hatta visited this inlet to find that "The sandy flat was . . . entirely covered by a tolerably thick layer of muddy sediment which had been brought down by a brook . . . All the Lamellibranchs had been completely destroyed . . . and were found already putrefied . . . (but) to his great surprise Mr. Hatta found that *Lingula alone had continued to live in as excellent a condition as it had ever been.*"

Yatsu also notes (1902a, p. 65) that "Lingula lives for a considerable length of time in aquaria even after the water has become spoiled and foetid." However, as he also states that *Lingula* prefers flats "of mud, blackened and ill-smelling from the decomposition of organic matter" and that "The flats of clean sand do not seem fit for the animal," it appears that the creature is actually rather closely fitted to conditions

[2] Referred to *Lingula anatina* Lamarck by Yatsu. Dall (1920, p. 262-263), however, has pointed out that *L. anatina* is a junior synonym of *L. unguis*. Curiously Dall records no Japanese representatives of this species in the collections of the U. S. National Museum, although he does list other species of *Lingula* from Japan. I have not studied the matter, and have simply accepted Yatsu's identification for the purpose of this note.

of pollution.[3] Other limiting factors, such as inability to migrate because of its predilection for very shallow waters or because of temperature restrictions, may be responsible for the failure of living *Lingula* to occur more widely in similar ecologic niches. Yatsu concludes from data on rate of growth that "at Misaki *Lingula* lives for five years or more on an average."

Observations by Morse and Joubin are equally remarkable. Morse (1902, p. 316) relates that in midsummer, and presumably without refrigeration, he transported living specimens of *Glottidia pyramidata* (Stimpson) from Bird Shoals in Beaufort Harbor, North Carolina, to Boston, a distance of 700 miles at a time when travel was slow. "These were kept in a small food bowl. They were afterwards carried to Eastport, Maine, and then to Troy, New York, yet none of them died until . . . six months later."[4] He also carried from Japan to Boston "a number of specimens of a small species of Lingula," and he states that "not one of these died until late in the year." Morse (*loc. cit.*) also quotes Joubin to the effect that "Crania remained exposed, upon my table, to the sun, cold, heat, without being injured . . . I have left them entire months without changing their water, which ought to have acquired a strong saltness. I have still the greater part of my Crania living seven months after their arrival in Roscoff and fourteen months after their gathering."

To return to the articulates it may be noted that the *Terebratulina* obtained from the Mount Desert Island Biological Laboratory were got with a view to making embryological studies on the living egg. They would have been ideal for this, as about half contained both unfertilized eggs in the germinal-vesicle stage, as well as eggs apparently freshly fertilized and cleaved once. Morse (1873, 1902) records that animals with eggs apparently ripe and ready for discharge were col-

[3] Dr. Katsuma Dan informs me (letter of 9/28/47) that the mud flat near the Misaki Marine Biological Station from which Yatsu obtained his *Lingula* for embrylogical study (Yatsu, 1902b) has been filled in since then and that at present it is difficult to find at Misaki more than enough *Lingula* for class demonstration.

[4] Professor P. E. Raymond tells me (informal communication 11/10/47) that according to one of Morse's anecdotes these specimens were actually spilled on debarking from the train at Boston and were carried, in fresh water, from Boston to Cambridge before they were transferred to sea-water again. They showed no apparent ill effects from this treatment.

lected at Eastport, Maine, on various dates from April through August 20. He also described the general external morphology of the living embryo from the uncleaved egg to attachment of the free-swimming, trochophore-like but enterocoelic larva; revolution of the mantle lobes; and assumption of essentially adult characteristics (Morse, 1871, 1873, 1902). Conklin (1902) has described in much greater detail, from studies of prepared slides and sections, the early stages in the embryology of *Terebratulina*, previous to attachment of the larva and revolution of the mantle lobes.

Of 14 of the dead specimens of *T. septentrionalis* from Egg Rock that were opened by me about half were ripe females and the others apparently males. Although not externally different, and although the ripe products of both sexes were located in the same parts of the pallial sinuses in both valves, females could be predicted with a practical frequency by spreading the valves enough to see the pattern of the concentrated sex products. In about half of the females the eggs tended to gather in a relatively open meshwork pattern within the pallial sinuses, while the similarly located sperm of the males was concentrated in dense aggregations or a very close meshwork. The eggs, which are ellipsoidal and about 160 microns long by 145 wide, are said to be discharged through the nephridiopores into the mantle cavity and to develop into free-swimming ciliated larvae "in the course of a few hours" (Morse, 1873). In view of the large proportion of ripe females found in the material dredged on July 30 it seems very likely that the individual brachiopod produces several "broods" during the long breeding season (sometime in April, through August).

Under proper conditions *Terebratulina septentrionalis* should make an excellent subject for further embryological studies, but it is doubtful if the animal or its eggs could keep healthy for long at Woods Hole without special refrigeratory conditions. Of the 23 occurrences south of Cape Cod recorded by Dall (1920, p. 299) two were from 5 fathoms, one from 7 fathoms, and one from 21 fathoms, but the other 19 were from depths between 192 and 1976 fathoms. North of the Cape it occurs most commonly at depths less than 50 fathoms. It appears that as a rule the animal prefers relatively cold water, and Morse (1873) has recorded that developing eggs must be kept at low temperatures. Further studies on the living animal and its eggs could probably be made without serious difficulty at the Mount Desert Island Biological Laboratory at Salsbury Cove, or at the Canadian biological station at St. Andrews-by-the-Sea. It seems likely that material for study of the rhynchonelloid *Hemithiris psittacea* (Gmelin) could also be obtained and handled at either of these places (Dall, 1920, p. 285).

Percival (1944) in an excellent, thought-provoking paper on the embryology of *Terebratella inconspicua* (Sowerby), has described how that brachiopod lives between tide marks in Lyttleton Harbour, New Zealand. The population ranges from small to dense and extensive, and individuals have been found "up to about half tide mark, attached to stones and other solid objects, but hidden in such a way as not to be disturbed by currents." Statistical study of a population sample of 711 specimens taken in late March, just before the beginning of the breeding season suggests a life-span of about four years for the species. Of the four year-classes suggested by the data "nearly two-thirds of the population consists of the first year class, nearly one-quarter of the second year class, nearly one-seventh of the third year class, and nearly one thirty-fourth of the fourth year class." Mortality is high, growth is slow, and the maximum length attained in Lyttleton Harbour is 13.5 mm. (up to 22 mm. long in Foveaux Strait). Percival's observations on sex ratio in *Terebratella inconspicua* tally with mine for *Terebratulina septentrionalis*, being about 1 to 1 in both instances.

It will interest the paleontologist that Dr. Percival's embryological studies show that the current use of dorsal and ventral for the valves of articulate brachiopods is the reverse of their primary embryological orientation in relation to the blastopore. He proposes a return to the once popular use of the words *brachial* and *pedicle* for the valves of brachiopods, a proposal that should be acceptable to all. The so-called ventral and dorsal valves of *Lingula*, however, have been shown by Yatsu to be embryologically ventral and dorsal, and Percival has now given us another link in the chain of comparative embryological evidence that has been leading, along with significant anatomical and biochemical differences, to the growing view that the articulate and inarticulate brachiopods may belong to distinct phyla. Percival has expressed this view but wisely refrains from making the split at this time. To date we have a reasonable amount of information about the embryology of only one inarticulate (*Lingula*) and four articulates (*Terebratulina*, *Terebratella*, *Argyrotheca*, and *Lacazella*). We need to know the embryology of a rhynchonelloid and a neotremoid *at least* before subdivision of the "group" might rationally be made at the phylum-level, and it is to be hoped that the present highly suggestive evidence will not be made the basis for premature discrimination of phyla.[5]

If studies of a rhynchonellid, a neotremoid, and more representatives of other groups continue to show that the so-called articulate brachiopods (Pygocaulia) rotate their mantle lobes after fixation and produce the pedicle as a primary lobe of the body on the embryologically dorsal side, while inarticulates (Gastrocaulia) never rotate their mantle lobes and produce the pedicle from the embryologically ventral side at a

[5] The probable availability of the rhynchonellid *Hemithiris psittacea* (Gmelin) at marine biological stations on the Gulf of Maine has been mentioned. The lingulid *Glottidia pyramidata* (Stimpson) has been recorded from Norfolk, Virginia, to the coast of Florida (Hertlein and Grant, 1944, p. 19) and could probably be obtained without difficulty at Beaufort Harbor, North Carolina (Morse, 1902) and handled at any station on the East Coast. Additional data for brachiopods of the East Coast are given by Dall (1920).

Biological stations on the West Coast have available to them various species of the 13 genera of brachiopods recorded as living between Bering Sea and Cape San Lucas, Lower California (Hertlein and Grant, 1944). Of the articulates the terebratulid *Terebratulina unguicula* (Carpenter), the terebratellid *Laqueus californianus* (Koch), and the ubiquitous boreal rhynchonellid *Hemithiris psittacea* (Gmelin) would seem to be particularly favorable subjects for study. The lingulid *Glottidia albida* (Hinds) may be obtained at localities between Monterey Bay and San Diego, California, in waters from the beach to 60 fathoms. Embryological studies of the neotremoids would be of first importance, and representatives of two genera may be obtained on the West Coast. The cranid, *Crania californica* Berry has been taken from 100 fathoms off Santa Monica, California, and the discinids *Discinisca cumingii* (Broderip) and *D. laevis* (Sowerby) have been taken at depths presumably less than 60 feet at Point Arbeojos, Lower California. Comprehensive records of the occurrence of these and other species may be found by reference to a very useful paper by Hertlein and Grant (1944) from which the data above were taken. See also Dall (1920). Of special interest is Dr. G. A. Cooper's discovery (oral communication) of numerous specimens of the neotremoid *Discinisca* on the under sides of rocks in knee-depth water four miles south of Pozole, Sinaloa, Mexico, along the shore at the north side of the mouth of a small creek.

late stage in development the case for division on the phylum level will be greatly strengthened. Add to this the really quite variant musculature of the two groups, the fundamentally different intestinal tracts, and the differences in composition of the shell and one could then make a reasonably good case for division of recent brachiopods into two phyla. On the other hand studies of cell lineage are yet to be made on any brachiopod, and it would seem quite important to know more about the mechanics and sequence of mesoderm formation. The coelomic mesoderm of all brachiopods whose embryology is known apparently begins with similar proliferations of initially endodermal cells. However, from this stage the coelom develops by schizocoely in *Lingula* (Yatsu, 1902b; p. 24, 103-104) and probably in *Lacazella* (= "Thecidium." *See* Yatsu, 1902b; Balfour 1885, p. 312), and by enterocoely in *Terebratulina*, *Terebratella*, and *Argyrotheca* (Conklin, 1902; Percival, 1944; Balfour, 1885). *Lacazella* is of particular importance as a living protremate, and its known development is sufficiently distinct from the telotremate articulates to weigh heavily in questions of classification immediately below the phylum level. It is now evident, however, that *Terebratulina*, *Argyrotheca*, and *Lacazella* need to be restudied throughout development using living material and modern techniques before many important details of their embryology can be considered firmly established.

It is well known that the fossil brachiopods as now understood are susceptible to a twofold major division. The nature of this division is a problem on which the information obtainable from recent forms has decisive bearing. The fossils will contribute the basis for ordinal and lesser divisions.

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