PRIAPULUS FROM THE DEEP SEA (VERMES, PRIAPULIDA)

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With nine text-figures and two plates

INTRODUCTION

The species of the genus *Priapulus* occur in rather cold water. Hence, their shallow-water distribution is restricted to northern and southern waters (fig. 1); there are only a few isolated records from sub-tropical localities. However, in deep water the genus apparently has a world-wide distribution (fig. 2). The northern species (*P. caudatus* De Lamarck) and the southern species (*P. tuberculatospinosus* Baird) from shallow water are well defined but the specimens from the deep sea present systematical problems. In my survey of the Priapulida (Van der Land, 1970) I could not answer the question of their identity, because I had seen only very few specimens from deep water and not a single one from the tropical deep sea.

Meanwhile I could study the material collected during cruises of the Russian R.V. "Vitjaz" (10 specimens), the Danish R.V. "Galathea" (2 specimens), and the American R.V. "Vema" (1 specimen) and R.V. "Eltanin" (2 specimens), i.e., 15 of the 20 specimens known from abyssal and hadal depths. The results are given in the present paper, which should be considered an addendum to my earlier paper.

MATERIAL

Priapulids have not been obtained from the deep sea very often. Probably this is not due to their rarity but to their digging habits and their usually low population densities (they are predacious animals). Below are listed all specimens, to my knowledge, that have been taken from depths greater than 2000 m. Each specimen is given a number for easy reference. The specimens not seen by the author are indicated with an asterisk.

The three type specimens of *Priapulus profundus* (no. 1-3) could not be sent to me, but they are hardly important because they are postlarvae and were described already quite well. It is to be regretted that the type specimen of *Priapulus abyssorum* (no. 15) could not be traced; it is not present anymore in the Lamont Geological Observatory and it could not be found in the New York museum where it could be now. The original description is

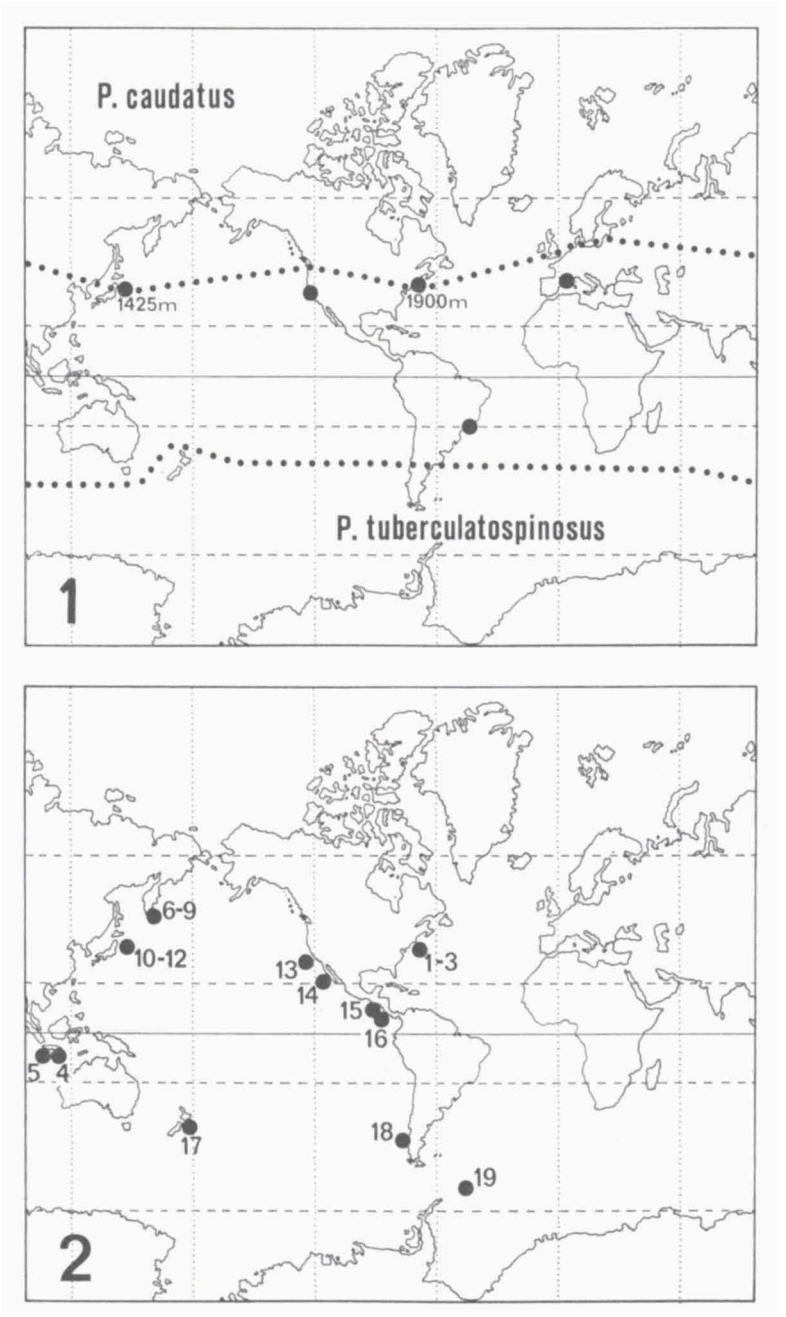

Fig. 1. General distribution of *Priapulus* in shallow water. The three isolated finds in subtropical waters and the two deepest records indicated. Fig. 2. Records of *Priapulus* from the deep sea (deeper than 2400 m).

insufficiently detailed but fortunately Menzies' figures are quite informative. Perhaps no. 12 was also lost.

*1-2. North Atlantic Ocean, off New England, 37°27'N 68°41'W, depth 4483 m, 2 Oct. 1961, "Scheltema" sta. JJ (postlarvae; type specimens of *Priapulus profundus* Sanders & Hessler, 1962).
*3. North Atlantic Ocean, off New England, 38°N 69°31'W, depth 3800 m, 9 August 1961, "Scheltema" sta. II (postlarva; type specimen of *Priapulus profundus*).
4. Indian Ocean, Java trench, 9°49'S 114°13'E, depth 3920-3940 m, 11 Sept. 1951, "Galathea" sta. 474 (Van der Land, 1970: 51).
5. Indian Ocean, Java trench, 8°42'S 105°31'E, depth 6433 m, 17 July 1962, "Vitjaz" sta. 5168 (Murina, 1964: map).
*6-7. Pacific Ocean, off Kamchatka, 50°0'8N 157°39'E, depth 2430-2670 m, 24 June 1953, "Vitjaz" sta. 2210 (Murina & Starobogatov, 1961: 185).
8. Pacific Ocean, Kuril-Kamchatka trench, 49°29'3N 158°41'E, depth 7210-7230 m, 22 June 1953, "Vitjaz" sta. 2208 (Murina & Starobogatov, 1961: 190).
9. Pacific Ocean, Kuril-Kamchatka trench, depth 7820-8040 m, 4 August 1966, "Vitjaz" sta. 5616 (posterior half only; new and deepest record).
10. Pacific Ocean, off Japan, 40°55'2N 144°48'2E, depth 3880-3998 m, 23 May 1957, "Vitjaz" sta. 3594 (Murina & Starobogatov, 1961: 190).
11. Pacific Ocean, Japan trench, 38°56'7N 143°57'4E, depth 7565-7587 m, "Vitjaz" sta. 3571 (Murina & Starobogatov, 1961: 190).
*12. Pacific Ocean, Japan trench, 38°2'N 143°57'E, depth 7190 m, "Vitjaz" sta. 3227 (Murina & Starobogatov, 1961: 190).
13. Pacific Ocean, off California, 34°56'2N 123°55'9W, depth 4231-4200 m, "Vitjaz" sta. 4231 (Murina & Starobogatov, 1961: 190).
14. Pacific Ocean, off Mexico, 24°57'6N 113°24'9W, depth 3315-3340 m, 13 Jan. 1959, "Vitjaz" sta. 4265 (postlarva; Murina & Starobogatov, 1961: 190).
*15. Pacific Ocean, off Nicaragua, Mid-America trench, 12°11'N 89°34'W, depth 5680-5690 m, "Vema" sta. 15-143 (type specimen of *Priapulus abyssorum* Menzies, 1959).
16. Pacific Ocean, off Costa Rica, 9°23'N 89°32'W, depth 3590 m, 6 May 1952, "Galathea" sta. 716 (Wolff, 1961: 142).
17. Pacific Ocean, off New Zealand, 41°29'7S 177°38'5E, depth 3013 m, 11 Jan. 1958, "Vitjaz" sta. 3838 (postlarva; Murina & Starobogatov, 1961: 190).
18. Pacific Ocean, off Chile, 46°59'5S 75°54'W, depth 2657 m, 24 March 1961, "Vema" sta. 17-13 (Van der Land, 1970: 51).
19-20. Antarctic Sea, near South-Orkneys, 60°7'S 45°19'W, depth 5289 m, 18 Febr. 1963, "Eltanin" 7 sta. 485 (new record).

Differential characters

Priapulus caudatus and *P. tuberculatospinosus* from shallow water differ only in a few quantitative characters (1970: 47-48). In fact differences in growth rates of certain pharyngeal teeth present the only reliable differential characters (in adults only). I studied the specimens mentioned above and a considerable number of specimens from shallow water in order to find more characters that can be useful. The features that were found to be of importance are discussed below. Other features that were examined (shape and number of buccal papillae; number of annuli; distribution of spinulets on the tail vesicles) were found to be of no value and are disregarded.

Size

Size is not an important character in itself but it should be considered because several organs show allometric growth. Preferably one should compare specimens of approximately the same size. The problem is that it is not easy to measure the size of a highly contractile animal. The best way would be to determine the dry weight but this is not feasible. Determination of the wet weight is also impracticable in these coelomate animals. To obtain a rough, arbitrary measure of size I added the products of length and greatest width of the introvert and length and average width of the abdomen (see table 1). The tail is not taken into account because its size

TABLE 1

Measurements of the *Priapulus*-specimens from the deep sea

Specimen no.	Introvert			Abdomen			Tail	Introvert + Abdomen	
	Length mm	Width mm *)	L x W	Length mm	width mm •)	L x W	Length mm	Length mm	L x W
4	8.5	4	34	19	5	95	3	27.5	129
5	8.5	4	34	23	4.5	103.5	1.5	31.5	137
6	13	12	156	27	7	189	7	40	345
7	7.5	7	52.5	9.5	3.5	33	1	17	85
8	5	4	20	22	2.5	55	6	27	75
9	lacking			23	3	69	3	-	-
10	10	6.5	65	11	3.5	38.5	1.4	21	103
11	7.5	4.5	34	15	3.5	52.5	2	22.5	86
13	10	5.5	55	13.5	2.5	34	1.5	23.5	89
14	2	1	2	2.5	1	2.5	-	4.5	4
15	8	-	-	11.5	-	-	2.5	19.5	-
16	17	8	136	31	8	248	5	48	384
17	1.7	1	1.7	2.6	0.6	1.5	0.3	4.3	3
18	8.5	6.5	55	15.5	3	46.5	1.5	24	101
19	6	3	18	7.3	2	14.5	5	13.3	33
20	8	3.5	28	11	2.5	27.5	8	19	45

*) Greatest width. •) Average width.

is highly variable. To give an impression of the size range: a large larva, 1.6 mm long, has size 0.5; the largest available specimen of *P. caudatus*, 120 mm long, has size 2000. Compared with the specimens from shallow water the largest specimen from the deep sea (no. 16) must be called medium-sized, but is is possible that the animals never reach a large size in the deep sea.

Postlarvae of *P. caudatus* and *P. tuberculatospinosus* cannot yet be told apart (1970: 38, 45). Specimens nos. 1, 2, 3, 14, and 17 belong to this category. The specific characters are only sufficiently clear when the animals have reached size 10 to 15.

Scalids

The shape of the scalids is quite variable and depends on their size, on their age (they seem to wear off after each moult), on the size of the worm,

and on the way of fixation and state of conservation. Useful characters could only be found in the relative size of the scalids and their arrangement.

The scalids are arranged in 25 longitudinal rows and in each row they form series (a series consists of a large scalid followed by a number of smaller ones). Within the series four types of arrangement can be recognized (fig. 3):

Type A — The second scalid is much smaller than the first one (about half as high or even smaller) and the following scalids regularly decrease in height.

Type B — The second scalid is only slightly smaller than the first one. The scalids of the series regularly decrease in height posteriorly.

Type C — The second scalid is only slightly smaller than the first one. Within the series two or three subseries can be recognized.

Type D — The second scalid is much smaller than the first one and within the series two or three subseries can be recognized.

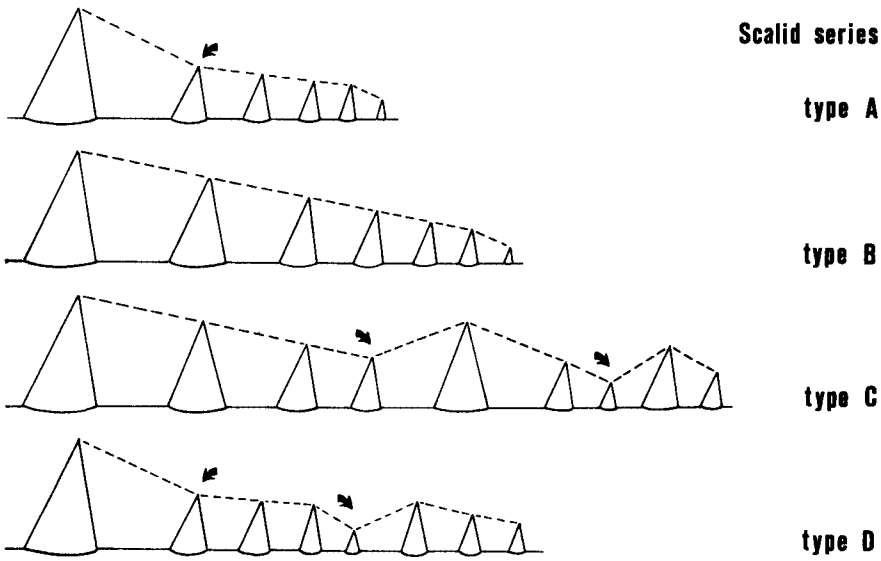

Fig. 3. Diagrammatic representation of the types of arrangement of the scalids in a series in the genus *Priapulus*.

When the state of conservation is not too poor these types can be recognized easily, although intermediates are common (A/B, B/C, and A/D). Usually the last series cannot be recognized easily because all scalids are small there and the arrangement tends to become irregular.

In postlarvae (fig. 4; 1970: fig. 12) the rows of scalids are not yet fully developed. On the anterior part of the introvert there are a few series

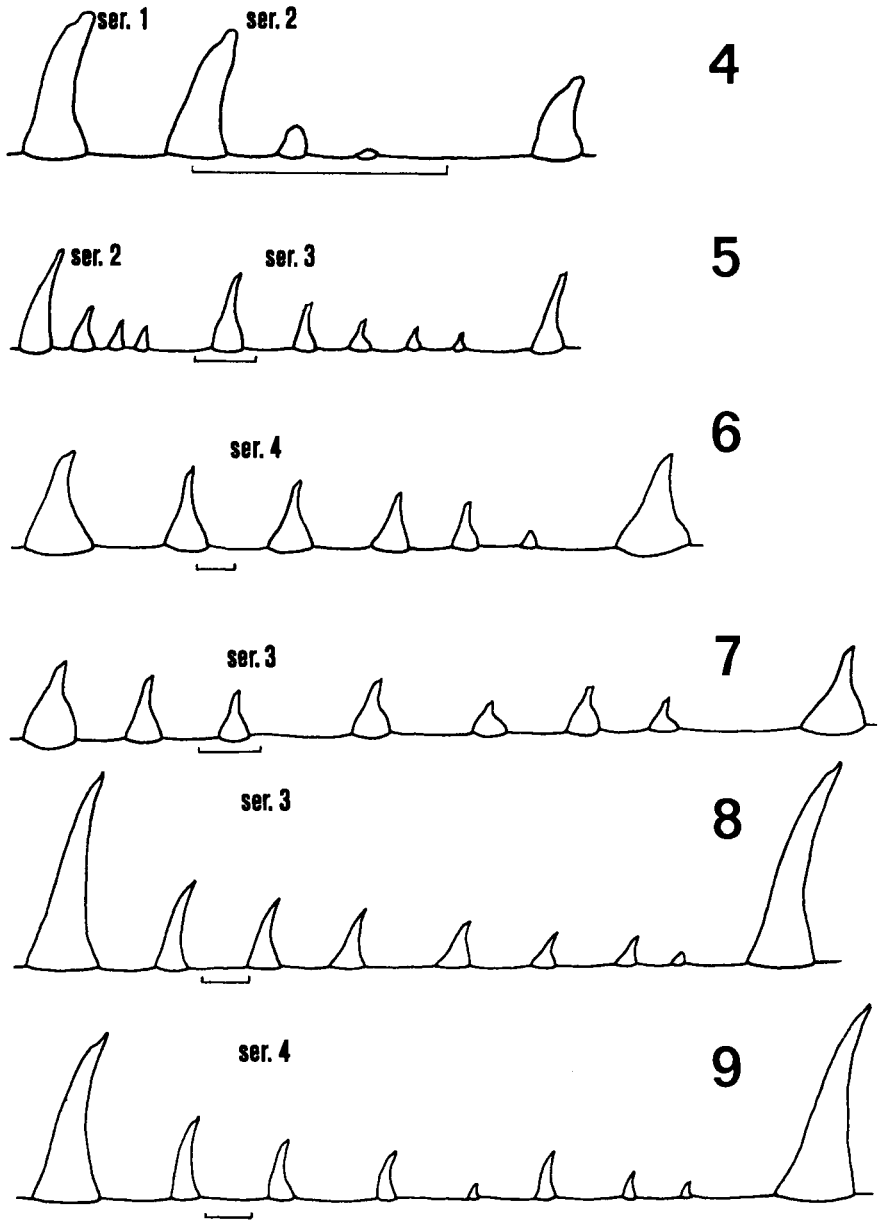

Fig. 4-9. *Priapulus*, scalid series. 4-6, *P. tuberculatospinosus* from shallow water; 4, post-larva (size 9); 5, small adult (size 41); 6, medium-sized adult (size about 400); 7, *P. caudatus* from shallow water, medium-sized adult (size about 300); 8-9, *Priapulus* specimen 16 from deep water, the largest specimen available (size 384). The numbers of the series are indicated. The scales represent 0.1 mm.

of 1 to 5 scalids in which the first scalid is very large, but on the rest of the introvert all scalids are very small and often hardly discernible. This is the starting point for all specimens, so all series probably start with an arrangement of type A, but there are differences during further development.

In small adults of *P. tuberculatospinosus* from shallow water (fig. 5) the anterior two series are still of type A and the other series of type B. In medium-sized and large adults (fig. 6) the anterior series may be of type A or of type B (even in one specimen), while intermediates are most common. The other series are of type B or C. In most specimens the majority of the series is of type B, but type C may also prevail (independent of the size of the specimen). The distribution of the two types on one specimen is irregular. As typical examples I give the distribution of the scalids in two adjacent rows on a medium-sized specimen (size 277) (the sub-series of type C between brackets):

10 series with 6, 5, 6, 5, 5, (3, 4), (3, 2), (3, 3), 4 and 3 scalids.

10 series with 3, 5, (4, 2), 6, (3, 3), (3, 2, 1), 4, (3, 2, 2), 4, and 4 scalids.

In the smallest adults of *P. caudatus* from shallow water the anterior series are of type A and the others of type B, as in the preceding species, but soon (before the animals have reached size 40) the situation is already as in large *P. tuberculatospinosus*. In all medium-sized and large specimens the two anterior series are of type B and all other series of type C (fig. 7). Type C is usually so pronounced in this species that it is often difficult to recognize the series, particularly on the posterior half of the introvert; the first scalids of the sub-series may be of nearly the same size as the first scalids of the series. Mostly there are three subseries in each series, the most common schemes being: (2, 2, 2), (3, 2, 2), and (4, 2, 2).

Of the specimens from deep water five (no. 1-3, 14, 17) show the typical post-larval arrangement, and two (no. 6 and 7) the arrangement as described above for adult *P. caudatus* (pl. 2 A), but most of the others (no. 4-5, 8, 10-13, 15-16, and 19-20) are peculiar in that type A is maintained on these small and medium-sized specimens (fig. 8; pl. 2 B, E). On the largest specimen (no. 16) part of the series show a subdivision into two subseries (type D; fig. 9). On the specimen from Chile (no. 18) the scalid series are of type A, type B, or intermediate.

The number of scalids per series is subject to considerable variation. In the anterior and posterior series it is always lower than in the series in between. Therefore the numbers in the third to the sixth series can best be used for comparison. In the material from shallow water the number varies from 5 to 7 on small and medium-sized adults and from 6 to 8(9) on large specimens. On most of the specimens from deep water there are 5 to 7

scalids per series, but four specimens (no. 10, 13, 15 16) have unusually high numbers: 7 to 9.

The number of series per row is remarkably constant and is independent of the size. The shallow-water specimens have 9 to 11(12) series per row. The same holds for most of the deep-water specimens, but three of them (no. 10, 15, 16) have an unusually high number of series per row: 12 or 13, 12 to 14, and 13 or 14, respectively. These specimens are notable for their extremely long scalid rows because they also have high numbers per series. The total number of scalids in a row on these specimens may be more than 80 while it is usually below 60.

Ringpapillae

In specimens from shallow water one to four abdominal annuli are provided with ringpapillae. The rings of papillae around the body may be complete, consisting of numerous papillae (hereafter indicated as *R*), but usually some of the rings are incomplete and consist of a small number of papillae, which are often quite small and inconspicuous (indicated as *r*). On adult specimens from shallow water there is always at least one complete ring, but never more than three. In addition there are one or two incomplete rings, sometimes three. The most common combinations are: *Rr*, *Rrr*, *rRr*, *RRr*, and *RRrr* (1970: fig. 13).

On most of the specimens from deep water the ringpapillae are quite conspicuous and on several they are exceptionally numerous. We can recognize three groups based on the number of ringpapillae:

(1) Number of ringpapillae within the normal range of shallow-water specimens: *Rr* (nos. 6-7), *rRr* (no. 19), *RRr* (no. 20), *rRR* (no. 9), *rRRr* (no. 8).

(2) Number of ringpapillae within the range of shallow-water specimens, but unusually high considering the size of the specimen: *RRR* (nos. 11 and 18), *RRRr* (no. 5).

(3) More ringpapillae than have ever been observed on specimens from shallow water: *RRRR* (no. 10), *RRRRr* (no. 13), *rRRRRr* (no. 4), *RRRRR* (no. 16). Specimen no. 15 also belongs to this groups as is evident from Menzies' figure 1I.

Posterior warts

In medium-sized and large adults from shallow water the last abdominal annuli are always covered with warts (1970: fig. 13). Sometimes there are only few of them and sometimes they are inconspicuous, either because they are covered with foreign matter or because they are small (during

periods of apparent inactivity of the glands) but, anyhow, they can always be recognized. In small adults they are sometimes conspicuous, but often they are absent or so small as to be practically invisible.

Specimen no. 6 is the only specimen from deep water on which conspicuous posterior warts are present. On all others they seem to be lacking. In part of the specimens this cannot be called abnormal, considering their size, but on the largest specimens (above size 100) they should be recognizable if they were normally developed. Small papillae are always present on the last annuli; I will not absolutely preclude the possibility of part of these being reduced posterior warts.

Pharyngeal armature

Three features of the pharyngeal armature are of systematic significance: (1) the relative size of the teeth of the first circlet; (2) the relative size of the latero-dorsal teeth of the fourth circlet; (3) the number of teeth in the seventh circlet.

In all postlarvae (1970: figs. 5-7) the teeth of the first circlet are comb-shaped (without an evident median cusp), but they are not much smaller than those of the second circlet. The latero-dorsal teeth of the fourth circlet are considerably larger than the other teeth of this circlet. Reliable counts of the number of teeth in the seventh circlet are practically impossible. The specific identity of postlarvae can only be determined on the basis of geographical evidence.

In adult *P. caudatus* the teeth of the first circlet have an evident median cusp and they are not much smaller than those of the second circlet (I have seen only one specimen in which they were much smaller). All teeth of the fourth circlet are equal in size. In those cases in which reliable counts could be made (this is very difficult in small specimens) there were five teeth in the seventh circlet.

In adult *P. tuberculatospinosus* the teeth of the first circlet remain comb-shaped or get the normal shape (with a large median cusp) but they always remain very small (much smaller than those of the second circlet). The latero-dorsal teeth of the fourth circlet remain larger than the other teeth of this circlet, although sometimes the difference becomes quite small. In those cases in which reliable counts could be made there were more than five teeth in the seventh circlet. I have seen only two southern specimens in which the pharyngeal armature had the same characters as in *P. caudatus* (if no mislabeling has occurred; 1970: 48).

In the adults from deep water the situation is as follows. In specimens no. 9 and 11 the pharynx is lacking. In specimens no. 6 and 7 the pharyngeal

armature is exactly as described above for *P. caudatus*. In all other specimens the armature is of the *P. tuberculatospinosus* type or close to it (pl. 2 C, D). The teeth of the first circlet are quite variable in shape, but they are always very small. In specimens no. 4, 13, and 15 the teeth of the fourth circlet are subequal in size but in the others two teeth stand out by their larger size. The number of teeth in the seventh circlet is unknown in specimens no. 5, 15, and 19, but in the others it is more than five. Specimen no. 20 is peculiar in having already more than five teeth in the sixth circlet.

Discussion

Seven specimens from the deep sea cannot be identified either because they are postlarvae (no. 1-3, 14, 17) or because the introvert is lacking (no. 9) or because neither the specimen nor a description is available (no. 12).

Two specimens (no. 6, 7) are identical in all details with *P. caudatus* from shallow water.

Eleven specimens are more closely related to *P. tuberculatospinosus* than to *P. caudatus* considering the characters of the pharyngeal armature (in specimen no. 11 the pharynx is lacking now, but Murina & Starobogatov, 1961, have seen it). Menzies (1959) described his specimen (no. 15) as a new species: *Priapulus abyssorum*. Murina & Starobogatov (1961) who had four of these specimens available, considered this material from the deep sea to belong to a separate subspecies: *P. tuberculatospinosus abyssorum*. In my opinion the available material is too scanty to permit a definite conclusion. On the basis of our present knowledge we cannot simply include the deep-sea specimens in the species *P. tuberculatospinosus* because the several typical characters must not be disregarded. We cannot speak of a separate species either because there are several intermediates between the most typical "*abyssorum*" specimens (no. 10, 15 and 16) and the shallow-water specimens. We cannot consider the deep-sea material a single subspecies because it lacks uniformity; however scanty, it already shows a much greater variation than the numerous specimens from shallow water that have been studied. I expect that ultimately we will be able to recognize several subspecies when many more specimens have become available.

The following characters only occur in specimens from the deep sea: (*a*) on adults the arrangement of the scalids in the third to the sixth series is of type A (or of type D in the larger specimens); (*b*) there are many (7-9) scalids in the third to the sixth series of small and medium-sized adults; (*c*) there are many (12 to 14) series of scalids in each row; (*d*) there are many ringpapillae (groups 2 and 3 of page 365); (*e*) posterior warts are lacking even on medium-sized specimens.

This combination of characters is present only in specimens no. 10, 15 (as can be deduced from Menzies' figures) and 16. Among the other specimens *a* to *d* are distributed as follows (characters *e* is of no use for comparison): *a*, *b*, and *d* in no. 13; *a* and *d* in no. 4, 5, and 11; *a* in 8, 19, and 20; *d* in 18.

These results cannot yet be explained from the geographical and bathymetrical distribution. The three southern specimens are very close to the shallow-water *P. tuberculatospinosus* but the northernmost specimen (no. 8) as well. A positive point is that in a few cases specimens from the same area have the same combination of characters, viz., the pairs 4-5, 15-16, and 18-19.

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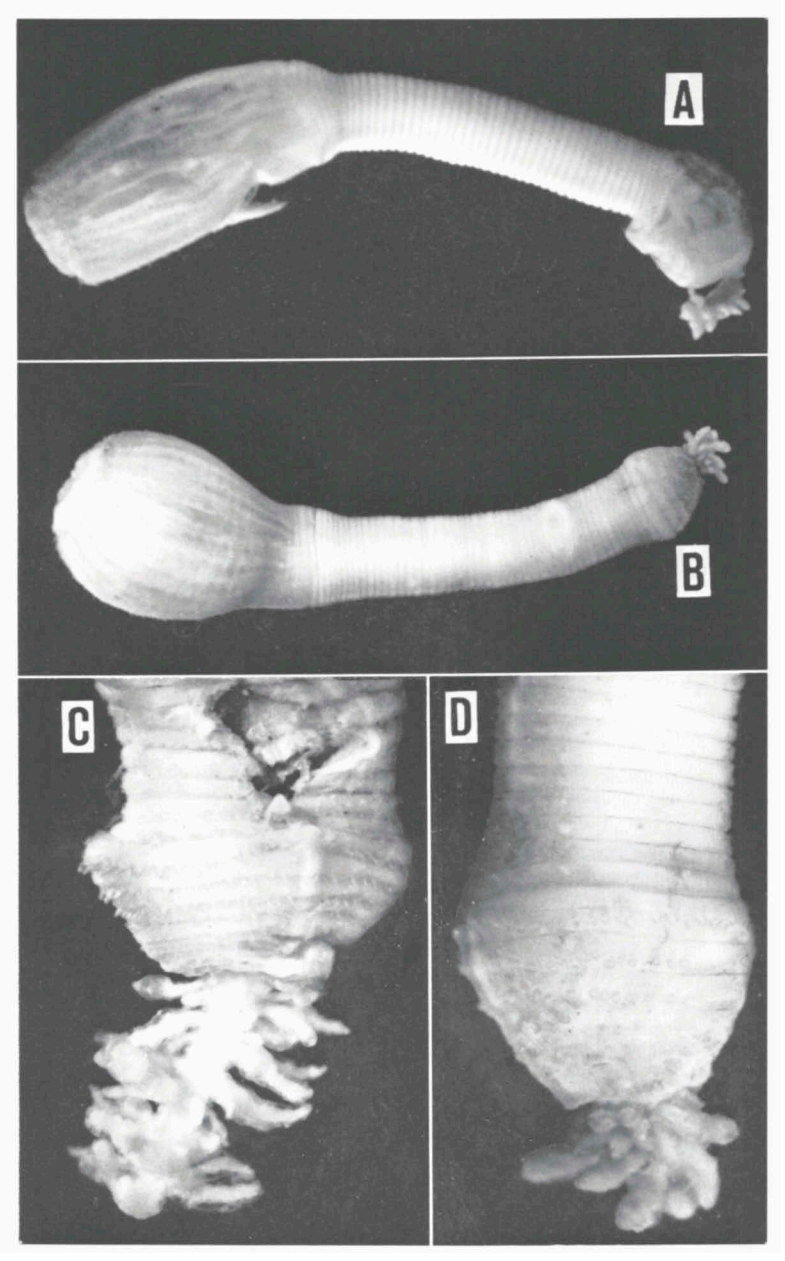
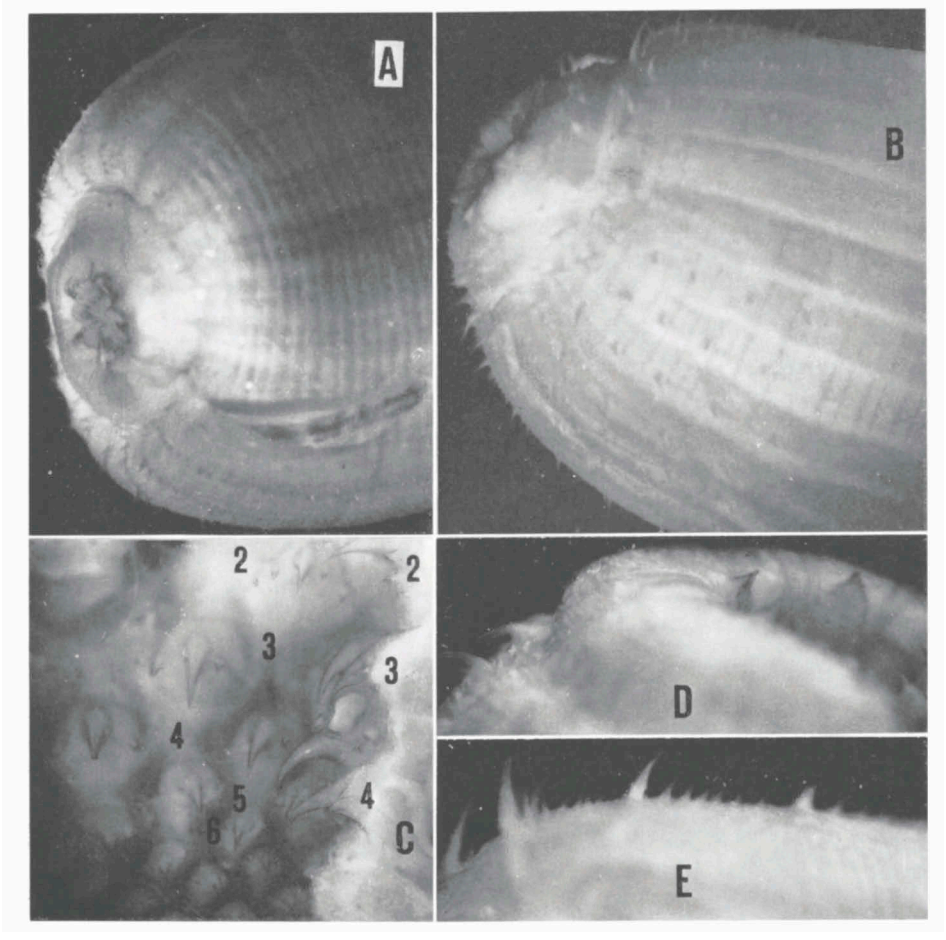
Note added in proof

Three specimens were recorded from the Kuril-Kamchatka trench ("Vitjaz" sta. 5616). I had seen only one of these specimens (no. 9). See Murina, V. V., 1971. Vstrečaemost glubokovodnyh sipunkulid i priapulid v Kurilo-Kamčatskom želobe. — Trudy Inst. Okean. 92: 41-45.



A, specimen no. 13 (total length 25 mm). B, specimen no. 18 (total length 25.5 mm). C, posterior part of specimen no. 4 (length of this part about 6 mm). D, posterior part of specimen no. 18 (length of part about 7 mm).



A, anterior part of specimen no. 7 (*Priapulus caudatus*). B, anterior part of specimen no. 10. C, part of the pharyngeal armature of specimen no. 16. D, buccal nerve ring and teeth of first circlet of specimen no. 13. E, anterior scalid series of specimen no. 13.