The phylogeny, classification and zoogeography of the class Priapulida. II. Revision of the family Priapulidae and zoogeography of priapulids

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Modified diagnoses of species of the macrobenthic family Priapulidae, ecological notes on all species, and a key to adult representatives of the family are given. Geographical distribution of the extant priapulids and the problem of bipolarity within priapulids are discussed in detail. Maps of the distribution are given for all extant species.

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1. Introduction

The family Priapulidae consists of one fossil genus (*Priapulites* Schram, 1973) and three extant genera (*Priapulus* Lamarck, 1816, *Priapulopsis* Koren & Danielssen, 1875 and *Acanthopriapulus* Land, 1970). Diagnoses of the family and the genera are given in our previous publication in this series. In the monotypic *Priapulites* and *Acanthopriapulus*, the species diagnoses are identical to the diagnoses of genera and are also given in the previous paper (see *P. konecniorum* Schram, 1973 and *A. horridus* (Theel, 1911)). Here, we would like to propose new diagnoses of the species of the genera *Priapulus* and *Priapulopsis* and a new key to species of the family. The paper is also intended to discuss the zoogeographical distribution of priapulids and to propose a new perspective on the problem of bipolarity.

2. Taxonomic account and diagnoses of species

Priapulus caudatus Lamarck, 1816

Synonyms: *Priapus humanus* Linnaeus, 1758; *Holothuria priapus* Linnaeus, 1767; *Hirudo annulis* Olafsen, 1772; *Priapula priapus*: Blainville, 1826; *Priapula caudatus*: Blainville, 1826; *Priapula caudata*: Guérin-Méneville, 1829; *Priapulus vulgaris* Cuvier, 1836; *P. hibernicus* McCoy, 1845; *P. brevicaudatus* Ehlers, 1861; *P. glandifer* Ehlers, 1861; *Lacazia hibernica*: Quatrefages, 1865; *Priapulus multidentatus* Möbius, 1873; *P. intermedius* Lanz, 1878; *P. pygmaeus* Verrill, 1879; *P. humanus*: Guerne, 1888; *P. pygmaeus*: Collin, 1901; *P. caudatus* var. *antarcticus* (non Michaelsen): Skorikov, 1902; *P. c. kristinebergensis* Hérubel, 1904; *P. c. mofjordinensis* Herubel, 1904; *P. priapus*: Derjugin, 1906; *P. caudatus* var. *multidentatus*: Fischer, 1913; *P. tuberculatospinosus japonicus* Murina & Starobogatov, 1961; *P. profundus* Sanders & Hessler, 1962.

Up to 100-200 mm in length; at least 7 anterior circlets of teeth arranged in distinct pentagons; teeth of anteriormost circlet not much smaller than those of second pentagon; teeth of fourth pentagon subequal in size; usually 5-6 scalids per series, second scalid of each series not much smaller than first one; posteriormost trunk with 1-3 circlets of ringpapillae and numerous warts, with 1-3 enlarged annuli; tail slightly segmented in juveniles, unsegmented, with densely arranged vesicles in adults; larval tubuli telescopic, located at about 1/5-1/4 of total length from posterior border of lorica.

Ecological notes: northern circumpolar species; deep sea (cold-water) populations with wide distribution in northern hemisphere from high Arctic to low boreal waters; found from intertidal zone with low salinity to 2600 m depth; lives in sand, mud or silt; survives in sulphide biotopes.

Priapulus tuberculatospinosus Baird, 1868

Synonyms: *Priapulus fuegensis* Lahille, 1899; *P. caudatus* var. *antarcticus* Michaelsen, 1889; *P. humanus* var. *antarcticus*: Collin, 1901; *P. caudatus* (non Lamarck): Benham, 1916; *P. caudatus* f. *tuberculatospinosus*: Theel, 1911; *P. tuberculatospinosus* var. *fuegensis*: Marelli, 1912; *P. caudatus tuberculatospinosus*: Derjugin, 1915; *P. tuberculatospinosus tuberculatospinosus*: Murina & Starobogatov, 1961; *P. t. bahiensis* Olivier, Rappoport & Garsia, 1961.

Up to 100-200 mm in length; usually only 6 anterior circlets of teeth arranged in distinct pentagons; anteriormost teeth much smaller than those of second pentagon; two dorsolateral teeth of fourth pentagon distinctly larger than other teeth of the same circlet; usually 4 scalids per series; second scalid of each series not much smaller than first one; posteriormost trunk without or with 1-2 circlet of ringpapillae and with numerous warts, usually without enlarged annuli; tail indistinctly segmented or smooth, with vesicles or tubercules; larval tubuli telescopic, located at about 2/5-3/5 of total length from posterior border of lorica.

Ecological notes: widely distributed, circumpolar, cold water species of southern hemisphere; distributed from antarctic to low notal waters; depth 0-625 m; lives in muddy sediments.

Priapulus abyssorum Menzies, 1959

Synonym: *Priapulus tuberculatospinosus abyssorum*: Murina & Starobogatov, 1961.

Up to 30 mm in length; usually only 6 anterior circlets of teeth arranged in distinct pentagons; anteriormost teeth about 3 times smaller than those of second pentagon; teeth of fourth pentagon nearly subequal in size; 9-10 scalids per series; second scalid of each series much smaller than first one; posteriormost trunk with 4-7 circlets of ringpapillae, usually without enlarged annuli; tail unsegmented, with vesicles; larval tubuli seta-like, located at about 1/5 of total length from posterior border of lorica.

Ecological notes: worldwide in distribution; deep sea species, from 3000 to 8000 m depth; lives in silt or muddy sediments.

Priapulopsis bicaudata (Danielssen, 1868)

Synonyms: *Priapulus bicaudatus* Danielssen, 1868; *Priapulopsis typica* Koren & Danielssen, 1875; *Priapuloides typicus*: Koren & Danielssen, 1877; *Priapuloides bicaudatus*: Guerne, 1888; *Priapulus atlantisi* Sanders & Hessler, 1962.

Up to 100 mm in length; first circlet consisting of 10 teeth arranged in pairs; anteriormost teeth rudimentary, with minute denticles; gap between distinct pentagons and following teeth remarkably wide; anterior series of scalids consisting of 4-7 papillae; series of scalids not separated by gaps; posteriormost trunk with up to 5 circlets of ringpapillae; tail with smooth unsegmented shafts; larval lorica with cuticular setae; larval closing apparatus consisting of dorsal, ventral and lateral placids.

Ecological notes: northern circumpolar cold-water species with wide distribution in northern hemisphere; depth from 7 to 2000 m; silt, mud, sandy mud.

Priapulopsis australis (Guerne, 1886)

Synonyms: *Priapuloides australis*: Guerne, 1886; *Priapulus australis*: Wesenberg-Lund, 1955; *Priapulus bicaudatus* var. *australis*: Fischer, 1921; *Priapulus bicaudatus australis*: Dell, 1955.

Up to 50 mm; first circlet consisting of 10 reduced denticles or papillae; gap between distinct pentagons and following teeth short; scalids of one series located close together, their basal parts often fused; anterior series consisting of 4-5 scalids; series separated by wide gaps; posterior series indistinct; posteriormost trunk with 3-5 circlets of ringpapillae; posteriormost annuli with circular and transverse cuticular ridges; tail shafts segmented, with longitudinal cuticular ridges and net-like microrelief; tail vesicles arranged in circlets; larval closing apparatus consisting of dorsal and ventral placids.

Ecological notes: species widely distributed in southern hemisphere in notal waters; depth 90-400 m; muddy sedimets, sand, coarse sand.

3. Key to adults of the Priapulidae

1. About 20 longitudinal rows of scalids; fossil forms . . . **Priapulites konecniorum** Schram, 1973
– 25 longitudinal rows of scalids; extant forms . . 7
2. Trunk bearing numerous tumuli; tail bicaudal (**Priapulopsis** Koren & Danielssen, 1875) 3
– Trunk without tumuli; tail monocaudal 4
3. First circlet of teeth consisting of 10 reduced denticles or papillae; series of scalids separated by wide gaps . . . . . **Priapulopsis australis** (Guerne, 1886)

- First circlet consisting of 10 pectinate teeth arranged in pairs; series of scalids not separated by gaps . . **Priapulopsis bicaudata** (Danielssen, 1868)

4. Tail with distinctly segmented shaft, club-shaped, with long spine-like tubuli or hooks; only anterior segments with vesicles . . . . . **Acanthopriapulus horridus** (Theel, 1911)
- Tail with unsegmented shaft or only slightly segmented in juveniles; without long spines or hooks; densely covered with vesicles bearing minute tubuli or papillae (**Priapulus** Lamarck, 1816) 5

5. Two dorsolateral teeth of fourth pentagon about twice large than other teeth of same circlet; usually 4 scalids per series . . . . . **Priapulus tuberculatospinosus** Baird, 1868
- Teeth of fourth pentagon nearly subequal in size; 5-10 scalids per series 6

6. Usually 5-6 scalids per series; posterior trunk with warts . . . **Priapulus caudatus** Lamarck, 1816
- Usually 9-10 scalids per series; posterior trunk without warts . . . . . **Priapulus abyssorum** Menzies, 1959

4. Zoogeography and the problem of bipolarity

The distributions of all the species of extant Priapulida are shown on maps (Figs 1-4). General remarks on the distribution of each species are given in the diagnoses above.

The distribution of the Priapulida, especially of the genera *Priapulus* and *Priapulopsis*, has always been considered one of the best examples of bipolarity (Land, 1970). General discussions on this topic can be found in the literature (Ekman, 1935; Murina & Starobogatov, 1961; Murina, 1964; Lattin, 1967; Land, 1970).

For example, Murina (1964) composed three vicarious pairs within the genus *Priapulus*, which are close to each other and restricted to northern and southern hemispheres respectively: *Priapulus caudatus* – *P. horridus*; *P. bicaudata* – *P. australis*; *P. tuberculatospinosus tuberculatospinosus* – *P. t. japonicus*. Such distribution was explained by probable migration through the abyssal. According to Murina (1964), this hypothesis is well evidenced by findings of the corresponding "intermediate" states: *P. profundus, P. atlantisi* and *P. tuberculatospinosus abyssorum*. She supposed that *P. tuberculatospinosus* originated in the southern hemisphere and could migrate in the south to north. For the pair *P. caudatus* – *P. horridus*, migration from north to south was supposed.

Since 1964, the classification of the Priapulida has been significantly modified (see above). *P. profundus* and *P. atlantisi*, based on postlarvae or young specimens, were synonymized with *Priapulus abyssorum* and *Priapulopsis bicaudata* respectively (Land, 1970, 1985). *P. horridus* is placed in a separate genus *Acanthopriapulus* (Land, 1970). *P. abyssorum* is now considered a separate species (Menzies, 1959; Land, 1985; present publication), not subspecies of *P. tuberculatospinosus* (Murina & Starobogatov, 1961; Murina, 1975) or its junior synonym (Land, 1970). Another subspecies of *P. tuberculatospinosus* discussed by Murina & Starobogatov (1961) was synonymized with *P. caudatus* (Land, 1970; present publication).

Nevertheless, we adopt the basic conclusion of Murina (1975) that bipolar distribution of priapulids may be best explained by migration through the deep sea in southern or northern direction. It is also correlated well with the migration theory I of Stiasny (see Land, 1970, p. 102). According to Land (1970), two other explanations of the bipolarity in priapulids (relict theory and migration from warm water to cold regions because of competition) seem to be more controversial.

Finally, we propose three other pairs of bipolar vicarious taxa of the Priapulida with corresponding distribution in north and south hemispheres: (1) *Priapulus caudatus* – *P. tuberculatospinosus* (deep water *P. abyssorum* is the "intermediate link" with worldwide distribution) (Fig. 1); (2) *Priapulopsis bicaudata* – *P. australis* (Fig. 2); (3) *Halicryptus spinulosus* – *Acanthopriapulus horridus* (Fig. 3). The last two pairs have no distinct "intermediate links". Moreover, in contrast to species of *Priapulus* and *Priapulopsis, H. spinulosus* and *A. horridus* are thought to be phylogenetically far from each other (see above).

As noted above, *P. abyssorum* shows more primitive characters as compared with *P. caudatus* and *P. tuberculatospinosus*. We suppose that deep water ancestral priapulids could migrate in both directions in polar cold waters. This migration resulted in the rise of the isolated species *P. caudatus* and *P. tuberculatospinosus*, which are not found in the abyssal depth. The primitive deep water priapulids with worldwide distribution, in turn, could be remnants of ancestral forms which left coastal waters as a consequence of strong competition.

According to Land (1970, p. 103), *H. spinulosus* is thought to be a shallow water marine-glacial relict. It is a euryhaline spe-

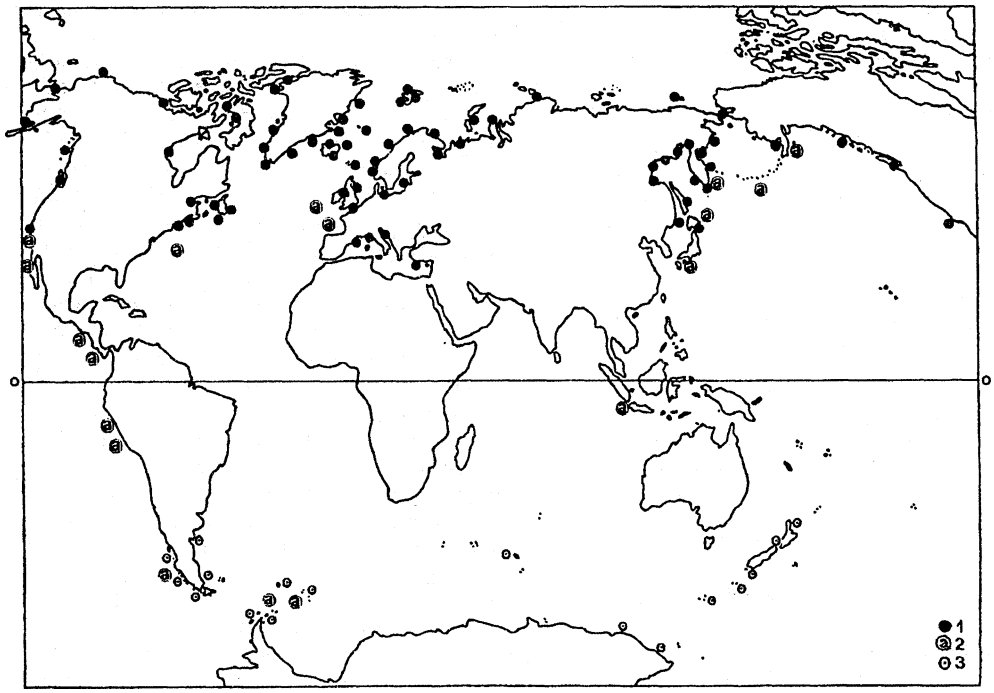

Fig. 1. Distribution. **1**, *Priapulus caudatus*; **2**, *P. abyssorum*; **3**, *P. tuberculatospinosus*.

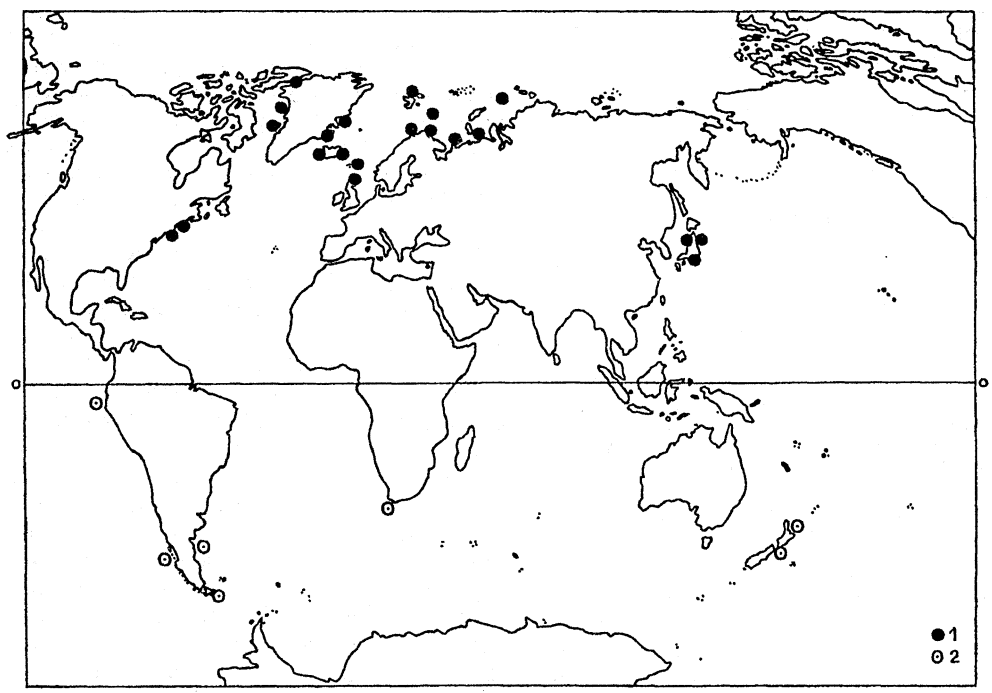

Fig. 2. Distribution. **1**, *Priapulopsis bicaudata*; **2**, *P. australis*.

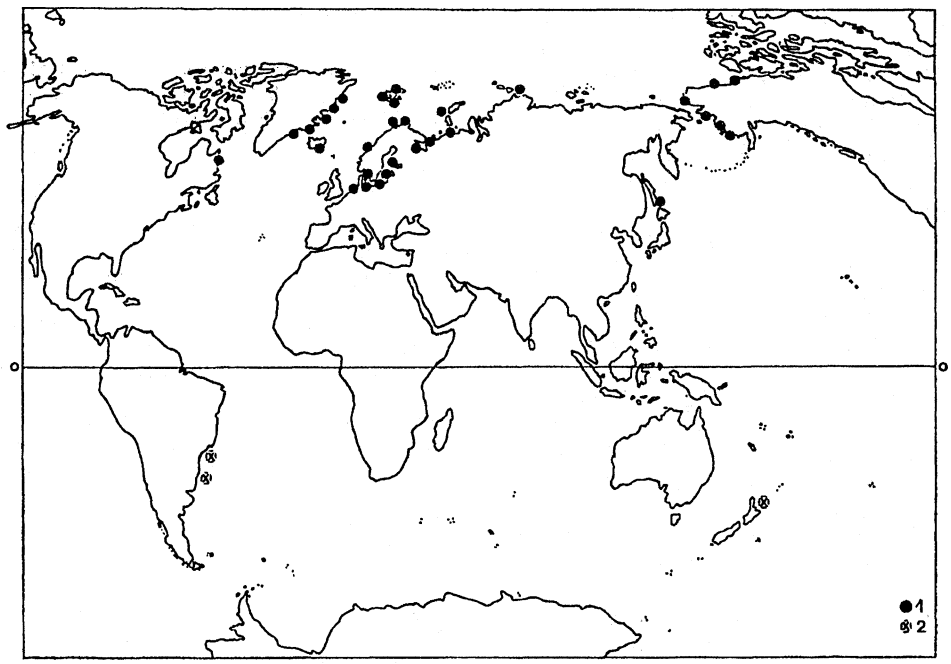

Fig. 3. Distribution. **1**, *Halicryptus spinulosus*; **2**, *Acanthopriapulus horridus*.

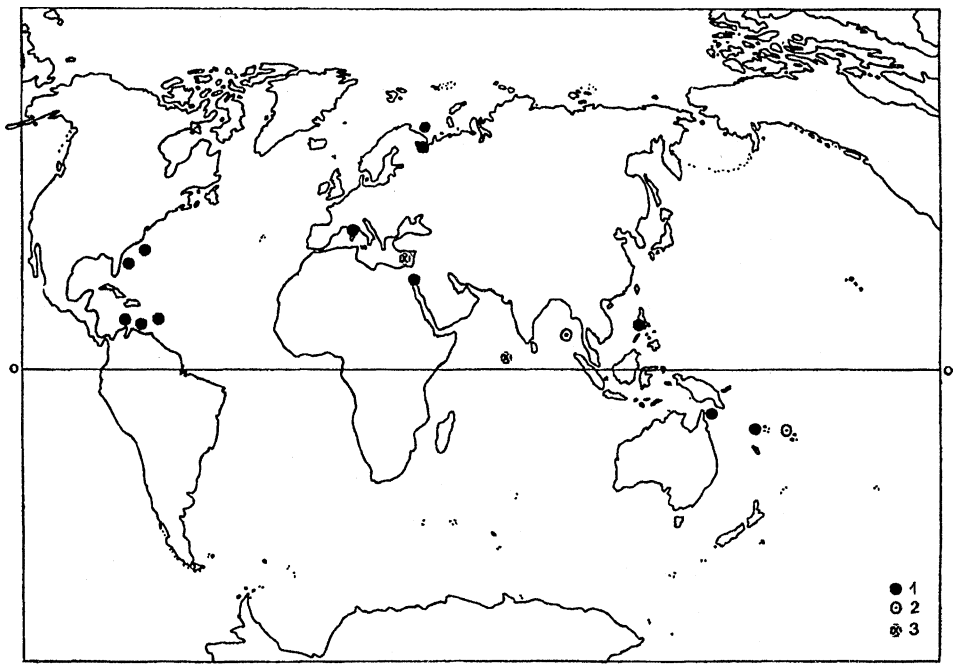

Fig. 4. Distribution. **1**, *Tubiluchus*; **2**, *Meiopriapulus fijiensis*; **3**, *Maccabeus*.

cies which becames adapted to brackish shallow waters. Now, *H. spinulosus* is mainly restricted to brackish waters, perhaps because of strong competition in marine environments. Evidently, *Halicryptus* originated in the northern hemisphere, and the tropical region is an effective barrier for this genus, which has no representative in the southern hemisphere (Land, 1970). In contrast, *Acanthopriapulus* is restricted only to the southern hemisphere.

Being meiobenthic interstitial forms, more advanced Tubiluchidae became worldwide in distribution and entered into both warm and cold shallow waters (Fig. 4). Moreover, they are more numerous in tropical waters. Warm water *Meiopriapulus* and *Maccabeus* are still less investigated, with only a few known localities (Fig. 4).

We adopt the opinion of Land (1970) that macrobenthic priapulids, being "primitive" relict worms with remarkably "slow evolution", cannot withstand strong competition with other benthic burrowers. They survived only because they can live in the marginal biotopes with: (1) low oxygen contents; (2) hydrogen sulphide poisoning; (3) low salinities; (4) cold waters and abyssal depth; (5) absence of food for a long time (Land, 1970).

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