Supplementary table S3. Character state matrix of extant Priapulida. Questionmark (?) represents an unknown character. Dash (-) represents an inapplicable character. For characters and their attributes see below.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Acanthopriapulus	1	?	?	1	1	1	1	1	0	0	0	1	0	0	0	1
Halicryptus	1	1	1	0	-	0	0	1	0	1	0	1	1	0	0	1
Priapulopsis	1	1	1	1	1	1	1	1	0	1	0	1	0	0	0	1
Priapulus	1	1	1	1	1	1	1	1	0	0	0	1	0	0	0	1
Maccabeus	0	1	1	0	-	0	0	1	0	1	1	0	1	0	1	0
Meiopriapulus	0	0	-	0	-	0	0	1	1	1	1	0	1	0	1	0
Tubiluchus	0	1	0	1	0	0	0	0	1	1	0	0	0	1	1	0
Kinorhyncha	0	0	-	0	-	0	0	2	1	1	0	0	0	1	0	0
Loricifera	0	1	-	0	-	0	0	2	1	1	0	0	0	1	0	0
Nematomorpha	1	0	-	0	-	0	-	2	0	0	1	0	0	1	0	0

1. Adult body size:

(0) Microscopic;

(1) Macroscopic

Priapulidans can be divided into two size classes, microscopic and macroscopic (meiobenthic) (Schmidt-Rhaesa, 2013a). Meiobenthic organisms are defined to surpass a 500 µm mesh and are held back by a 44 µm mesh (Giere, 2009), although body form and flexibility can be also of significance (Ptatscheck et al., 2020). The macroscopic species range from a few millimetres in postlarval stages to several centimetres in adults (up to ~40 cm). Larval and early postlarval stages of macroscopic species are temporarily meiofaunal (Worsaae et al., 2023). On the other side, microscopic species have total trunk lengths from a few millimetres in adults, excluding the posterior appendage if present (*Meiopriapulus* up to 3.4 mm [Sørensen et al., 2012], *Maccabeus* up to 3.5 mm [Malakhov, 1978], *Tubiluchus* between 0.87 mm in *T. remanei* [Van der Land, 1982] and up to 2.5 mm in *T. arcticus* [Adrianov et al., 1989]). The total body length can differ enormously between the living and fixed state of a priapulidan (own observations in *Priapulus caudatus*), but both size classes differ distinctly between adult specimens. Both related taxa Kinorhyncha and Loricifera are of microscopic

adult body size (Bang-Berthelsen et al., 2013; Neuhaus, 2013). In Nematomorpha, larval stages have microscopic sizes (<100 µm), whereas adult body sizes vary from a few centimetres to more than two meters (Schmidt-Rhaesa, 2013b).

2. Loricate larval stage:

(0) Absent;

(1) Present

Almost all priapulidan species have larval stages, which have a hardened cuticle, the lorica, in which the introvert can be inverted. A loricate larval stage is reported for all macroscopic species, except *Acanthopriapulus horridus* and *Priapulopsis papillatus* (Schmidt-Rhaesa, 2013a; Schmidt-Rhaesa and Raeker, 2024). For the microscopic species, a loricate larval stage for half of the currently described *Tubiluchus* species and *Maccabeus tentaculatus* is reported. *Meiopriapulus fijiensis* seems to have an internal direct development and lacks the loricate larval stage (Higgins and Storch, 1991). Loricifera have similar loricate larval stages (e.g., Bang-Berthelsen et al., 2013). In Nematomorpha, larval stages do not have lorica structures (Schmidt-Rhaesa, 2013b). Kinorhyncha have direct postembryonic development (Neuhaus, 2013).

3. Shape of lorica:

(0) Round (20 plates);

(1) Dorso-ventrally flattened (8 plates)

The lorica of the larval stages of priapulids occurs in two different shapes. In macroscopic species, the lorica is dorsoventrally flattened with two large dorsoventral plates and three smaller lateral plates built in a zig-zag pattern on each side, connecting the two dorsoventral plates (Schmidt-Rhaesa, 2013a). In microscopic species, the lorica has a more roundish form, consisting of 20 plates (Schmidt-Rhaesa, 2013a). The only exception for microscopic species is the larva of *M. tentaculatus*, whose shape is dorsoventrally flattened like in macroscopic species (Por and Bromley, 1974).

4. Caudal appendage(s) in postlarval stages/adults:

(0) Absent;

(1) Present

The number of caudal appendages differs between genera of priapulids (Van der Land, 1970). While macroscopic *Halicryptus* and both microscopic *Meiopriapulus* and *Maccabeus* lack a caudal appendage, the macroscopic *Priapulus* and *Acanthopriapulus*, as well as the microscopic *Tubiluchus* have one caudal appendage. In the macroscopic priapulids, the caudal appendage is composed of a stem with lateral thin-walled vesicles. In *Tubiluchus*, it is a long muscular tail without vesicles. The only genus with two caudal appendages is the macroscopic *Priapulopsis*, that grow asymmetric during postlarval development (Schmidt-Rhaesa and Raeker, 2023), which can lead to difficulties in identification of young postlarval stages with *Priapulus* species. The function of the caudal appendage is still unknown. For *Priapulus* and *Priapulopsis* it was thought to be linked with respiration (Fänge and Mattison, 1961), although there is evidence against this (Lang, 1948; Nyholm and Bornö, 1969). *Acanthopriapulus* has, in addition to the lateral vesicles, cuticular spines, which may have an anchor-like function (Van der Land, 1970) or functions as defensive organ (Schmidt-Rhaesa et al., 2022), due to the spines on the posterior part of the stem. The caudal appendage of *Tubiluchus* presumably functions as anchor, due to its length, or as retractor, due to its musculature and contractility (Van der Land, 1970). Related taxa Kinorhyncha, Loricifera and Nematomorpha lack caudal appendages (Bang-Berthelsen et al., 2013; Neuhaus, 2013; Schmidt-Rhaesa, 2013b).

5. Vesicles on caudal appendage(s) of adults:

(0) Absent;

(1) Present

Either the stem of the caudal appendage of adult priapulids can be free of structures (*Tubiluchus*) or it can hold elongate balloon-like structures, the vesicles (*Priapulus*, *Priapulopsis*, and *Acanthopriapulus*). In young postlarval stages of *Priapulus* (own observations) and *Priapulopsis* (Schmidt-Rhaesa and Raeker, 2023) vesicles are often absent, showing only the stem of the caudal appendage. In *A*. *horridus* the anterior part of the stem (near the trunk) has vesicles, while the posterior part is scattered with hook-like structures (Schmidt-Rhaesa et al., 2022).

6. Posterior warts on posterior trunk:

(0) absent;

(1) present

On the posterior trunk of *Priapulus* occur wart-like structures with apical tubes functioning as excretory organs (Van der Land, 1970). However, in *P. abyssorum* posterior warts might be absent (Menzies, 1959; Van der Land, 1972). *Acanthopriapulus* was first thought to lack posterior warts, but recent studies show a possible presence (Raeker et al., 2024b).

7. Scalids arranged in series with decreasing sizes:

(0) Absent;

(1) Present

In all macroscopic priapulids (except *Halicryptus*), the scalid rows are composed of several scalid series, in which the size of the associated scalids decrease (Van der Land, 1970). One series is composed of about two to nine scalids, depending on age and species of the adult specimen. All microscopic species, *Halicryptus* and all larval stages do not have several scalid series (Van der Land, 1970).

8. Anterior teeth appearance of adults:

(0) Pectinate;

(1) Cuspidate;

(2) stylet-like

Two types of pharyngeal teeth exist in Priapulida. The anterior teeth of adults of all macroscopic species (Schmidt-Rhaesa, 2013a) and *Maccabeus* (Por and Bromley, 1974) have cuspidate teeth. Cuspidate teeth have a large median cusp and several smaller lateral cusps on each side of the median cusp. Sometimes, only the large median cusp can be present (Shirley and Storch, 1999; own observations in *P. caudatus*). Adult *Tubiluchus* and *Meiopriapulus* have a pectinate (comb-like) appearance of teeth (e.g. Kirsteuer and Van der Land, 1970; Morse, 1981). Related taxa Kinorhyncha, Loricifera and Nematomorpha have stylet-like structures (Bang-Berthelsen et al., 2013; Neuhaus, 2013; Schmidt-Rhaesa, 2013b).

9. Neck region between introvert and trunk in adults:

(0) Absent;

(1) Present

The neck region is present in larval stages of priapulids. In postlarval stages and adults of macroscopic species, the neck region is lost during development. In postlarval stages and adults of *Tubiluchus* species, the neck region is still present (cf. Fig. 3.17 and 3.28 in Adrianov and Malakhov (1996) for T. *corallicola* and *T. vanuatensis*). In *Meiopriapulus fijiensis,* the anterior region of the trunk with trunk scalids (Adrianov and Malakhov, 1996 termed them "neck scalids") could also represent a neck region. For adult *Maccabeus*, no neck region is reported. Adult Kinorhyncha and Loricifera have neck regions (Bang-Berthelsen et al., 2013; Neuhaus, 2013).

10. Adults with flosculi:

(0) Absent;

(1) Present

Flosculi are flower-shaped sensory structures with about 7-11 cuticular protrusions (petals) around a central opening with a bristle (e.g. Todaro and Shirley, 2003). Sometimes, an accessory seta (Todaro and Shirley, 2003) or tubulus (Schmidt-Rhaesa et al., 2013) is present lateral of the flosculus. Flosculi appear on the neck, trunk and sometimes on the tail of *Tubiluchus* or on the trunk of *Meiopriapulus*. In *Maccabeus*, flosculi appear as accessory structures lateral of the sensory spines (Por and Bromley, 1974). As accessory flosculi, they also appear on small trunk papillae and flosculus-tubulus-complexes on the posterior trunk of *Halicryptus* (Merriman, 1981; Raeker et al., 2024a) and on trunk papillae of *Priapulopsis papillatus* (Schmidt-Rhaesa and Raeker, 2024). Adults of remaining species have no reports of flosculi on the trunk. Flosculi are present in Kinorhyncha and Loricifera (Bang-Berthelsen et al., 2013; Neuhaus, 2013).

11. Adults with ring of hooks on posterior trunk:

(0) Absent;

(1) Present

A ring of recurved hooks is present in *Meiopriapulus* and *Maccabeus* (Por and Bromley, 1974; Morse, 1981). The hooks of both taxa differ in composition, as they are apically bifurcated in

M. fijiensis and may have a sensory function due to a median tubular structure (Sørensen et al., 2012). In *Maccabeus*, the hooks have a large flattened basal part and only a single hook-like structures, a sensory structure is not reported (Por and Bromley, 1974). For *Maccabeus*, these hooks may be considered as homologous to the ring papillae (Por and Bromley, 1974), which we declined here (also for *M. fijiensis*), as they structurally differ to strongly from the papillae of other species (see below).

12. Adults with ring papillae on posterior trunk:

(0) Absent;

(1) Present

On the posterior trunk of *Priapulus*, *Priapulopsis* and *Acanthopriapulus* are sensory ring papillae organized in one or more rings (Schmidt-Rhaesa, 2013a). As ring papillae of these genera only differ slightly, they are reported as homologous structures (Raeker et al., 2024b). *Halicryptus* has a ring of flosculus-tubulus-complexes on the posterior trunk, which are considered as homologous to the ring papillae of Priapulinae, due to the sensory function (see Raeker et al., 2024b). In *Tubiluchus* ring papillae have not been reported, which makes it the only genus without structures organized in rings on the poster trunk.

13. Adults with two structures lateral of anus:

(0) Absent;

(1) Present

Halicryptus and *Maccabeus* have two structures lateral to their anus. In *Halicryptus*, these structures were first described as anal setae (Van der Land, 1970; Merriman, 1981). Having apical tubular structures, the term “anal tubuli” was introduced (Raeker et al., 2024a). *Maccabeus* has two similar structures lateral to the anus (Por and Bromley, 1974). If the structures of *Maccabeus* have similar tubular structures apically is not reported. The anal tubuli of *Halicryptus* have additional accessory structures (one seta in Lemburg, 1999); various papillae in Raeker et al., 2024a) on the stem, whereas no information is given for *Maccabeus*.

14. Sexual dimorphism:

(0) Absent;

(1) Present

Only the males of the genus *Tubiluchus* have species-specific genital regions, separating them from the female specimens, which sometimes cannot be clearly separated from the ones of a different *Tubiluchus* species (Schmidt-Rhaesa et al., 2013). No other priapulidan species has a sexual dimorphism. Related taxa Kinrohyncha, Loricifera and Nematomorpha have sexual dimorphisms (Bang-Berthelsen et al., 2013; Neuhaus, 2013; Schmidt-Rhaesa, 2013b).

15. Adults with muscular polythyridium at entrance of the intestine:

(0) Absent;

(1) Present

Tubiluchus and *Meiopriapulus* have a thick muscular structure with valvulae (cuticular plates) posterior of the pharyngeal teeth, the polythyridium (e.g. Morse, 1981; Kirsteuer and Van der Land, 1970). The function of this organ is unclear, although it is thought to break up food (Kirsteuer and Van der Land, 1970) or it functions as a filter organ (Van der Land, 1970). For *Maccabeus*, Por and Bromley (1974) reported 15 scimitar-like spines at the posterior end of the pharynx that could resemble a homologous structure to the polythyridium.

16. Fertilization mode:

(0) Internal fertilization;

(1) External fertilization

Macroscopic priapulidans have external fertilization due to large quantities of produced gametes (Schmidt-Rhaesa, 2013a). Microscopic species (*Tubiluchus*, *Maccabeus*) have small gonads and only produce a few gametes, resulting in an internal fertilization (see Schmidt-Rhaesa, 2013a). Additionally, spermatozoa differ between macroscopic (round-headed spermatozoa, see Afzelius and Ferraguti, 1978) and microscopic (modified, filiform spermatozoa, see Alberti and Storch, 1983) priapulidans. *Meiopriapulus fijiensis* is assumed to have internal fertilization, although it has round-headed spermatozoa, similar to macroscopic species (Storch et al., 1989). Kinorhyncha, Loricifera and Nematomorpha have internal fertilization modes (Neuhaus, 2013; Bang-Berthelsen et al., 2013; Schmidt-Rhaesa, 2013b).

References

Adrianov, A.V., Malakhov, V.V., Chesunov, A.V., Tsetlin, A.B., 1989. A dwarf priapulid *Tubiluchus arcticus* sp. n. from the White Sea (Priapulomorpha, Tubiluchidae). Zool. Zhurn. 68, 126-131. [In Russian]

Adrianov, A.V., Malakhov, V.V., 1996. Priapulida: Structure, development, phylogeny, and classification. Moscow: KMK Scientific Press. [In Russian with English summary]

Afzelius, B.A., Ferraguti, M., 1978. The spermatozoon of *Priapulus caudatus* Lamarck. J. Submicrosc. Cytol. 10, 71-80.

Alberti, G., Storch, V., 1983. Fine structure of developing and mature spermatozoa in *Tubiluchus* (Priapulida, Tubiluchidae). Zoomorphology 103, 219-227. https://doi.org/10.1007/BF00310479.

Bang-Berthelsen, I., Schmidt-Rhaesa, A., Kristensen, R.M., 2013. Loricifera. In: Schmidt-Rhaesa, A., editor, Handbook of Zoology: Nematomorpha, Priapulida, Kinorhyncha and Loricifera. Volume 1. Berlin: De Gruyter, 349-378. https://doi.org/10.1515/9783110272536.349.

Fänge, R., Mattisson, A., 1961. Function of the caudal appendage of *Priapulus caudatus*. Nature 190, 1216-1217.

Giere, O., 2009. Meiobenthology: the microscopic motile fauna of aquatic sediments, 2nd ed. Springer Berlin, Heidelberg, 1-527. https://doi.org/10.1007/978-3-540-68661-3.

Higgins, R.P., Storch, V., 1991. Evidence for the direct development in *Meiopriapulus fijiensis*. Trans. Am. Microsc. Soc. 110, 37-46. https://doi.org/10.2307/3226738.

Kirsteuer, E., Van der Land, J., 1970. Some notes on *Tubiluchus corallicola* (Priapulida) from Barbados, West Indies. Mar. Biol. 7, 230-238. https://doi.org/10.1007/BF00367493.

Lang, K., 1948. Contribution to the ecology of *Priapulus caudatus* Lam. Ark. Zool., 41A, 1-12.

Lemburg, C., 1999. Ultrastrukturelle Untersuchungen an den Larven von *Halicryptus spinulosus* und *Priapulus caudatus*. Hypothesen zur Phylogenie der Priapulida und deren Bedeutung für die Evolution der Nemathelminthes. Cuvillier, Göttingen.

Malakhov, V.V., 1978. New representative of sedentary priapulid *Chaetostephanus cirratus* sp.n. Zool. Zhurn. 58, 1410-1412.

Merriman, J.A., 1981. Cuticular structures of the priapulid *Halicryptus spinulosus*: A scanning electron microscopical study. Zoomorphology 97, 285-295. https://doi.org/10.1007/BF00310281.

Morse, M.P., 1981. *Meiopriapulus fijiensis* n. gen., n. sp.: An interstitial priapulid from coarse sand in Fiji. Trans. Am. Microsc. Soc. 100, 239-252. https://doi.org/10.2307/3225549.

Neuhaus, B., 2013. Kinorhyncha (= Echinodera). In: Schmidt-Rhaesa, A., ed., Handbook of Zoology: Nematomorpha, Priapulida, Kinorhyncha and Loricifera. Volume 1. Berlin: De Gruyter, 181-348. https://doi.org/10.1515/9783110272536.181.

Neuhaus, B., 2013. Kinorhyncha (= Echinodera). In: Schmidt-Rhaesa, A., ed., Handbook of Zoology: Nematomorpha, Priapulida, Kinorhyncha and Loricifera. Volume 1. Berlin: De Gruyter, 181-348. https://doi.org/10.1515/9783110272536.181.

Nyholm, K.G., Bornö, C., 1969. Introductory studies of the oxygen intake of *Priapulus caudatus* Lam. Zoologiska Bidrag 38, 262-264.

Por, F.D., Bromley, H.J., 1974. Morphology and anatomy of *Maccabeus tentaculatus* (Priapulida: Seticoronaria). J. Zool. Lond. 173, 173-197. https://doi.org/10.1111/j.1469-7998.1974.tb03125.x.

Ptatscheck, C., Gehner, S., Traunspurger, W., 2020. Should we redefine meiofaunal organisms? The impact of mesh size on collection of meiofauna with special regard to nematodes. Aquat. Ecol. 54, 1135-1143. https://doi.org/10.1007/s10452-020-09798-2.

Raeker, J., Worsaae, K., Schmidt-Rhaesa, A., 2024a. David versus Goliath: an interspecific comparison between small-sized *Halicryptus spinulosus* and large-sized *Halicryptus higginsi* (Priapulida). Zool. Anz. 313, 1-20. https://doi.org/10.1016/j.jcz.2024.08.003.

Raeker, J., Worsaae, K., Schmidt-Rhaesa, A., 2024b. New morphological structures of *Priapulus caudatus*, Lamarck 1816 (Priapulida) and analysis of homologous characters across macroscopic priapulids. Zool. Anz. 312, 135-152. https://doi.org/10.1016/j.jcz.2024.08.005.

Schmidt-Rhaesa, A., 2013a. Priapulida. In: Schmidt-Rhaesa, A., editor, Handbook of Zoology: Nematomorpha, Priapulida, Kinorhyncha and Loricifera. Volume 1. Berlin: De Gruyter, 147-180. https://doi.org/10.1515/9783110272536.147.

Schmidt-Rhaesa, A., 2013b. Nematomorpha. In: Schmidt-Rhaesa, A., editor, Handbook of Zoology: Nematomorpha, Priapulida, Kinorhyncha and Loricifera. Volume 1. Berlin: De Gruyter, 29-146. https://doi.org/10.1515/9783110272536.29.

Schmidt-Rhaesa, A., Cañete, J.I., Mutschke, E., 2022. New record and first description including SEM and µCT of the rare priapulid *Acanthopriapulus horridus* (Priapulida, Scalidophora). Zool. Anz. 298, 1-9. https://doi.org/10.1016/j.jcz.2022.03.001.

Schmidt-Rhaesa, A., Raeker, J., 2023. Morphology of larval and postlarval stages of *Priapulopsis bicaudatus* (Danielssen, 1869) (Priapulida) from the North Atlantic Ocean. Zool. Anz. 302, 1-16. https://doi.org/10.1016/j.jcz.2022.11.006.

Schmidt-Rhaesa, A., Raeker, J., 2024. Review of the Priapulida of New Zealand with the description of a new species. New Zealand J. Zool. (online first) https://doi.org/10.1080/03014223.2023.2278738.

Schmidt-Rhaesa, A., Rothe, B.H., Martínez, A.G., 2013. *Tubiluchus lemburgi*, a new species of meiobenthic Priapulida. Zool. Anz. 253(2), 158-163. https://doi.org/10.1016/j.jcz.2013.08.004.

Shirley, T.C., Storch, V., 1999. *Halicryptus higginsi* n.sp. (Priapulida) – a giant new species from Barrow, Alaska. Invert. Biol. 118, 404-413. https://doi.org/10.2307/3227009.

Sørensen, M.V., Rho, H.S., Min, W.-G., Kim, D., 2012. A new recording of the rare priapulid *Meiopriapulus fijiensis*, with comparative notes on juvenile and adult morphology. Zool. Anz. 251, 364-371. https://doi.org/10.1016/j.jcz.2011.10.001.

Van der Land, J., 1970. Systematics, geography, and ecology of the Priapulida. Zool. Verhand. Leiden. 112, 1-118.

Van der Land, J., 1972. *Priapulus* from the deep sea (Vermes, Priapulida). Zoologische Mededelingen 47, 358-368.

Worsaae, K., Vinther, J., Sørensen M.V., 2023. Evolution of Bilateria from a Meiofauna perspective - Miniaturization in the focus. In: Giere, O., Schratzberger, M., editors. New Horizons in Meiobenthos Research: Springer, Cham, 1-31. https://doi.org/10.1007/978-3-031-21622-0_1.