

1 A natural history of the deep-sea aplacophoran *Prochaetoderma yongei* and
2 its relationship to confamilials (Mollusca, Prochaetodermatidae)

3
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12

13 **Abstract**

14 Previously published studies are woven together into a natural history of a deep-sea
15 aplacophoran mollusc species, *Prochaetoderma yongei* Scheltema, 1985, and its confamilial species
16 in the Prochaetodermatidae. This amphi-Atlantic species occurs in sometimes great numbers at upper
17 bathyal depths, rivaling polychaetes in numerical dominance. It appears to be an opportunist, with
18 wide geographic and depth distribution, rapid development from lecithotrophic larva to settlement
19 and maturity, and omnivory. A short illustrated morphological description using characters useful for
20 identifying all prochaetodermatid species should prove useful to nontaxonomists whose business is
21 the deep-sea benthic fauna.

22

23 **Keywords:** Distribution, *Spathoderma*, collecting equipment, taxonomy, reproduction, feeding

24

25 **1. Introduction**

26

27 The aplacophoran mollusc family Prochaetodermatidae was known from only a single eastern
28 Mediterranean species, *Prochaetoderma raduliferum* (Kowalevsky, 1901), until the late 1960s, when
29 renewed interest in deep-sea dredging using more sophisticated techniques and gear than heretofore
30 available changed the perception of the deep-sea benthic fauna (Hessler and Sanders, 1967).

31 Collections made since then by United States and European deep-sea biologists have brought to light
32 riches of diverse macrofaunal benthic organisms with thousands of new species and inspired
33 ecological investigations of life beyond the continental shelves. Among the new organisms are
34 numerous Prochaetodermatidae from the World Ocean, excluding polar regions where they have not
35 been collected. Presently they comprise 39 published species in six genera, with an additional 17
36 Pacific species in manuscript (Scheltema, 1985, 1989, 1998; Salvini-Plawen, 1992, 1999; Ivanov,
37 1995, 1996; Scheltema and Ivanov, 2000; Ivanov and Scheltema, 2001a,b, 2002, 2004, 2008).

38 Prochaetodermatids range in depth from the Continental Shelf <200 m to hadal depths >6,000m.
39 Bathyal depths we define as those from the Continental Slope and Rise, 200–4,000 m; some authors,
40 e.g., Gage and Tyler (1991), place the lower boundary of the bathyal zone at 2,000 m.

41 *Prochaetoderma yongei* is a widespread Atlantic upper bathyal species, and in the
42 northwestern Atlantic is often found to be a numerical dominant in its mid-range. It has been one of
43 the important macrofaunal species that has formed the basis for deep-sea ecological and reproductive
44 studies, as well as for defining the taxonomic characters by which to distinguish species and genera.
45 Contributions about *P. yongei* have been published in various journals over a number of years. By
46 bringing them together here, one obtains a sense of the natural history of this deep-sea organism.

47 We emphasize that differences among species of prochaetodermatids in terms of their body
48 form, locomotion, internal anatomy, radula morphology, and food selection are so similar that we can
49 infer that natural history traits run through the family. Therefore, we include here some data from
50 eastern Pacific and eastern Atlantic confamilials. Actual patterns of life history, however, are known
51 most completely for *P. yongei*.

52

53 **2. Methods**

54

55 *2.1 Collections*

56

57 Global distributions of deep-sea benthic species have since the late 1960s been based mostly
58 on large collections from epibenthic sleds or other types of sledges, dragged along the bottom for
59 unmeasured distances. The samples collected and the use of fine screens (Sanders et al., 1967) have
60 provided great numbers of organisms, a boon for taxonomic treatment and geographic understanding
61 (Fig. 1), but giving no indication of community structure. Finer-grained structure has been revealed
62 through the use of quantitative box cores (Fig. 2, Table 2) and, more recently than the collections
63 reported here, by multicorers.

64 Appendix 1 lists the sources of collections we have used in describing the natural history of
65 *Prochaetoderma yongei*, including collections for which we were taxonomic consultants only or were
66 described in the literature. Usually the Aplacophora were given to us directly with accompanying
67 station data for description and identification. Details of stations where *P. yongei* were identified by
68 us may be found in Scheltema (1985) and Ivanov and Scheltema (2001b).

69

70 2.2 Taxonomy

71
72 The methods presently used for describing Prochaetodermatidae species are best spelled out
73 in Scheltema and Ivanov (2000) and Ivanov and Scheltema (2008), methods that have evolved over
74 time since first given in Scheltema (1985). They include light microscope examination and
75 measurements, drawings, and photographs of entire organisms; light microscope measurements and
76 drawings of sclerites including birefringent patterns showing thickness (Scheltema and Ivanov 2004);
77 scanning electron microscope (SEM) images of sclerites; and dissection of radula teeth and jaws.

78

79 3. Geographic and depth distribution of *P. yongei* and *confamilials*

80

81 3.1 Global distribution

82

83 *Prochaetoderma yongei* is an amphi-Atlantic species widespread at bathyal depths from the
84 Continental Slope to the Upper Continental Rise in the North American Basin, north Atlantic south of
85 Iceland, European Basin and Bay of Biscay, Cape Verde Basin, Angola Basin, and Cape Basin off
86 southwest Africa. Figure 1 shows the known global distribution of *P. yongei* and indicates the depth
87 ranges in each geographic region, number of samples with *P. yongei*, and total number of individuals.
88 *P. yongei* does not occur south of 34° N in the northwestern Atlantic, a natural zoogeographic barrier
89 (Cutler, 1975; Blake and Grassle, 1994), but crosses the Atlantic to south of Iceland (Ivanov and
90 Scheltema 2001b) and the entire eastern Atlantic coasts of Europe and Africa. As the map shows,
91 there have been few bathyal collections off Africa containing *P. yongei*, where it was taken in a
92 single sample in a single transect at each of the three indicated locations.

93 *Prochaetoderma yongei* overlaps a second, lower bathyal amphi-Atlantic prochaetodermatid
94 species, *Spathoderma clenchi* Scheltema, 1985, both geographically and by depth in the three most
95 intensively sampled regions where they are found: North American Basin, south and southwest of
96 Iceland, and the West European Basin, including the Bay of Biscay (Tables 1–3) (Scheltema, 1985;
97 Scheltema and Ivanov, 2000; Ivanov and Scheltema, 2001b). *P. yongei* occurs at shallower depths in
98 the bathyal zone than *S. clenchi*, and *S. clenchi* reaches nearly to the base of the Continental Rise
99 (Tables 1, 3). The data are few from along the west African coast, but in those transects where both
100 species were collected, *S. clenchi* occurred deeper in the bathyal than *P. yongei*.

101 *P. yongei* and *S. clenchi* are the only bathyal Prochaetodermatidae species in the northwest
102 Atlantic, and neither occurs on the Continental Shelf at <200 m depth. A third bathyal species,
103 *Spathoderma alleni* Scheltema and Ivanov, 2000, has been collected off Iceland and in the West
104 European Basin. These three are joined in the West European Basin by two more bathyal species:
105 *Prochaetoderma boucheti* Scheltema and Ivanov, 2000, which extends from 101 m on the
106 Continental Shelf to 860 m on the Continental Slope, and *Claviderma gladiatum* Salvini-Plawen,
107 1992, entirely within the bathyal zone, 1,267–3,814 m. A sixth species, *Claviderma iberogallicum*
108 (Salvini-Plawen, 1999) (= *Cl. tricosum* Scheltema and Ivanov, 2000) has been taken on the
109 Continental Shelf off the northwest European coast and does not occur in collections from bathyal
110 depths. The diversity of prochaetodermatid bathyal species in the northeastern Atlantic is thus more
111 than double that in the northwest Atlantic—five versus two. The Mediterranean prochaetodermatid
112 fauna, besides the nominate species *Prochaetoderma raduliferan* confined to the eastern
113 Mediterranean, includes *P. boucheti* and *S. alleni* from the West European Basin, but not *P. yongei* or
114 *S. clenchi*.

115

116 3.2 *Fine-scale distribution*

117
118 A series of replicate box cores was taken at 10 stations along a 176-km transect at a depth of
119 ~2,100 m off the mid-Atlantic east coast of the United States; three additional stations were made at
120 ~1,500 m depth and one additional station at 2,500 m (Table 2). Three replicate samples were taken
121 at the 14 stations during late spring, late summer, and late fall over a 2-year period for a total of
122 usually 18 box cores per station, except when exigencies of ship time or weather precluded successful
123 sampling (Maciolek et al., 1987; Grassle and Maciolek, 1992). From this enormous effort we now
124 know *P. yongei* and its confamilial *S. clenchi* are among the 20 most numerous species among the
125 798 species collected, sometimes ranking 1st or 2nd (Fig. 2, Table 2). When outnumbered, it is usually
126 by polychaetes (Grassle and Maciolek, 1992, table 3; for a similar study in the eastern Pacific with
127 *Spathoderma* sp., see Blake et al., 1992, in Scheltema, 1997).

128 The situation in the northeastern Atlantic seems unlike that in the northwest Atlantic, although
129 only two cruises were devoted to using quantitative spade box corers in the bathyal zone at the time
130 of Scheltema's (1985) paper: BIOGAS VIII and BIOGAS IX (Fig. 1; Appendix 1). Thirteen box
131 cores (0.25 m²), out of an unknown total number, collected no *P. yongei* and only one or two *S.*
132 *clenchi* per sample at depths between 2,170 m and 2,828 m (most too deep for finding *P. yongei*).
133 Even though we do not have complete data for BIOGAS VIII and IX, there seem to be far too few *S.*
134 *clenchi* to be one of the numerically dominant species at 2,100 m or greater depths (cf. Table 2). We
135 conclude that the bathyal prochaetodermatids in the eastern Atlantic are more diverse than those in
136 the northwest Atlantic but may lack dominance.

137

138 3.3 *Vertical distribution in the sediment*

139
140 One study has been published that includes the vertical depth distribution in the sediment of
141 *P. yongei* and *S. clenchi* (Blake, 1994). Both species—like most of the benthic fauna—were found
142 mostly in the upper 2 cm of sediment: 94.7% of *P. yongei* (n = 113) and 87.6% of *S. clenchi* (n = 89),
143 although 1 or 2 individuals, respectively, occurred deeper, between 5 and 10 cm.

144

145 **4. Morphology**

146

147 *4.1 General morphology of the Prochaetodermatidae*

148

149 Species of Prochaetodermatidae are usually <5 mm in length. They are covered by aragonite
150 sclerites, the bases of which are embedded in mantle cuticle, and have a broad trunk and a narrow,
151 tail-like posterium (Figs 3, 4A). There is no foot. Uniquely there is a mouth opening between a
152 paired, specialized chitinous oral shield (Fig. 5) and a radula between a pair of large jaws often
153 visible in transmitted light (Fig. 4C, E). Details of taxonomic characters useful for identification
154 among all prochaetodermatid species were first given for *P. yongei* in Scheltema (1985) and are
155 briefly described here; a full description may be found in Scheltema and Ivanov (2000). All
156 identifications of Prochaetodermatidae have depended entirely on morphology, that is, they are
157 "morphospecies."

158

159 *4.1. Body*

160

161 Internal organs determine body shape (Fig. 4B). The wider trunk contains the feeding
162 apparatus, stomach, the single digestive gland, and single dioecious gonad; the narrower shank
163 contains primarily two tubes, the gonopericardial duct from the gonad to the pericardium, through
164 which the gametes pass, and the intestine. The longitudinal body-wall musculature of the trunk is
165 weak but stronger in the shank, where it acts as the chief source of propulsion, relaxed as the head
166 end digs its way through the sediment, then contracting, shortening and anchoring the posterium with
167 the long sclerites surrounding the cone. Prochaetodermatids do not move quickly except for the
168 probable ability to contract rapidly, judging from the usually contracted state of fixed animals.

169 The large numbers of *P.yongei* taken in the northwest Atlantic (Table 1) gave us great scope
170 in determining statistically significant body measurements (Scheltema, 1985). Measured lengths and
171 widths of numerous specimens were analyzed statistically for a sense of variation in *P. yongei*; these
172 measurements are now used for all prochaetodermatid species. One important ratio was shown to be
173 the length of the posterium (shank + cone) to trunk length (Scheltema, 1985), as well as body lengths
174 and widths of the body regions and size of the oral shield.

175

176 4.2. Sclerites

177

178 The sclerites are carried on the body in a specific manner (Fig. 3); in *P. yongei*, they are
179 adpressed to the body and lie parallel to the body axis. The morphology and measurements of
180 sclerites are unambiguous for species determination, but account must be made of all the types of
181 sclerites along the body and from dorsal to ventral (Fig. 3); a single type of sclerite can occur in more
182 than one species. The sclerites also determine genus. Beside the divided oral shield, within which lies
183 the mouth opening, are rows of oral shield sclerites different in shape from all other sclerites on the

184 body; they presumably have a sensory function (Figs 3 os, 5). Examination using polarized light
185 enables determination of thickness of a sclerite and whether this thickness is symmetrical or
186 asymmetrical about the sclerite axis (Scheltema and Ivanov, 2004).

187

188 *4.3 Radula and jaws*

189

190 There are two teeth per row on a radular membrane, with a small, flat plate between them
191 (Fig. 4C–E). There is great morphological similarity among species, differing mainly in size and
192 placement of the serrated medial membrane (Fig. 4D #25). The radula has a distinct bending plane
193 over which it can be moved (Fig. 4C). Prochaetodermatids are the only aplacophorans with the ability
194 to rasp like a gastropod (Fig. 6). The radula is small relative to the paired, large jaws, which also have
195 a conservative morphology among species but vary in size. The jaws are connected distally by a
196 tough membrane and lie within the pharynx; their bases lie within the haemocoel and are connected
197 by strong retractor muscles.

198

199 **5. Feeding—grasp and rasp**

200

201 *5.1 Radula and jaw, function and food source*

202 Feeding in the prochaetodermatids is unique among aplacophorans. Prochaetodermatids are
203 omnivores, feeding selectively on detritus (Fig. 4C) or on forameniferans (Fig.6) and other small
204 organisms such as polychaetes. The proboscis with the jaws and radula is protruded through the
205 mouth, as indicated by some fixed specimens. Presumably the jaws, with the muscles between their
206 bases relaxed, are then closed by the strong muscles between their bases, surrounding either a bolus

207 of detritus (Fig. 4C) or an organism. The food is then withdrawn into the pharynx where it is rasped
208 by the radula. As in gastropods, worn anterior teeth of the radula fall off, sometimes to be swallowed,
209 and are replaced by new teeth.

210

211 5.2 Feeding in prochaetodermatids vis-a-vis polychaetes

212 A Bray-Curtis analysis showed similarity among seven most numerous species over seven
213 samples taken by boxcores in the eastern Pacific off the Farallon Islands at 2,700 m (Blake et al.,
214 1992; summarized in Scheltema, 1997). One of the species was an undescribed *Spathoderma* sp., a
215 confamilial of *P. yongei*; the other six were polychaetes. One, a species of tubicolous Spionidae, was
216 least likely to maintain a presence in high numbers in the samples; it can feed either as a selective
217 deposit feeder or as a suspension feeder, depending on the flux of particles (Taghon et al., 1980). The
218 other five polychaetes belong to the Paraonidae, Cossuridae, and Cirratulidae; like the
219 prochaetodermatid *Spathoderma*, they are motile burrowers, the Paraonidae motile but tubicolous.
220 Paraonidae feed nonselectively on forameniferans (Fauchald and Jumars, 1979) and on organic
221 particles (J. Blake, personal communication); Cossuridae are nonselective deposit feeders (Tzetlin,
222 1994); and Cirratulidae are selective surface deposit-feeders (Fauchald and Jumars, 1979).

223 Prochaetodermatid species select both forams and flocks of organic detritus (seen in
224 dissections), and with their wide range of foods are apparently able to maintain themselves in often
225 high numbers among the most successful group of macrofauna in the deep sea, the Polychaeta. No
226 other aplacophorans, insofar as known, are omnivorous.

227

228 6. Reproduction and recruitment

229

230 *6.1 Size distribution in males, females, and juveniles*

231
232 Large epibenthic collections and quantitative samples from the North American Basin have
233 enabled analyses of size distributions and gonad development in *P. yongei* (Scheltema, 1987).
234 Lengths were measured in males, females, and juveniles, determined by light microscopy, from seven
235 samples collected over a ten-year period from 1966 to 1976 at depths between 1,470 and 2,024 m in
236 summer, fall, and winter (Table 4). The number of males was 1.3 to 2.0 times greater than females in
237 the four epibenthic trawls, but only 0.5–1.0 the number of females in quantitative corers. There was
238 little difference in mean size between males and females, indicating early sexual determination and
239 similar rates of growth, although a few females but no males reached lengths >3 mm. All seven
240 collections over three seasons contained juveniles, in which the gonad was but a thin, linear structure.
241 Although there were no pulses of juveniles, the data are too sparse to unequivocally indicate seasonal
242 recruitment. A more complete data set from replicate boxcore samples over a two-year period taken
243 south of George's Bank are far less equivocal, and one can infer from these data that reproduction in
244 *P. yongei* is not seasonal (Blake and Watling, 1994).

245

246 *6.2 Egg development and relationship to size of organism*

247 Egg sizes and stages of development were determined by dissecting out gonads of *P. yongei*
248 females from two epibenthic sled samples (Table 4, underscored samples) from August 1966 and
249 February 1969. There were three distinct and nonoverlapping stages of egg development. Mature
250 eggs in which the nuclear membrane had disappeared were free in the gonad lumen and varied in
251 diameter from 90–226 μm , but were usually >140 μm . There was not a linear relationship between

252 presence of mature eggs and length of specimens, with some juveniles as long as some females with
253 mature eggs:

254

255 Smallest female specimen, all eggs immature, 1.3 mm

256 Smallest female with mature eggs, 1.7 mm

257 Largest juvenile 1.8 mm

258 Smallest juvenile 0.3 mm

259 Smallest male with gonad developed, 1.0 mm

260

261 *6.3 Numbers of mature eggs and numbers of juveniles*

262

263 The percentage of females with mature eggs in the August 1966 trawl was 81.8%, with up to
264 13 and a mean of 2.7 mature eggs per female; in the February 1969 trawl, there were 47.6% with
265 mature eggs with up to 2 and a mean of 0.6 mature eggs per female. These numbers agree with the
266 relative percentage of juveniles in the same trawls, 21.0 % in August 1966 and 6.9 % in February
267 1969. More collections would be needed to determine whether these differences were seasonal and
268 hold up in all years and seasons. One can say that spawning is asynchronous, with all stages of egg
269 development present in summer and winter, and that potentially there may be a pulse of greater
270 reproduction in late summer. Unfortunately, the specimens of *P. yongei* from Grassle and Maciolek
271 (1992, see *Section 3.2*) were not available to the first author when Scheltema (1987) was being
272 prepared.

273

274 *6.4 Recruitment experiments*

275
276 Two sets of recruitment boxes of azoic mud provide data that indicate rapid growth of
277 individuals and time to egg maturation: (1) three boxes at 1,760 m placed by DSRV *Alvin*, and (2)
278 two free-vehicle boxes at 2,020 m. There were four recoveries in all (Table 5): 1 box after 2 months,
279 1 box after 6 months, 4 boxes after 8 months, and 1 box after 12 months (Scheltema, 1987; specimens
280 and collection data provided by J. F. Grassle). From Table 5 it can be seen that *P. yongei* (average
281 mature egg size >140 μm , section 6.2) has lecithotrophic larvae because of recruited into the boxes. The
282 recruitment boxes show a nice time series of growth (lengths) and maturity of eggs: a 2-month
283 juvenile had grown to a size (1.4 mm) when the gonad was ready to develop; a 2.6-mm male had
284 grown to maturity in 6 months; at 8 months, 1 female had grown to 2.1 mm with immature eggs
285 (although some trawl-sample females had mature eggs at this length); and at 12 months, a female of
286 the same length as one of the immature females in the 8-month boxes (2.1 mm) had 4 mature eggs,
287 the largest 162 μm . There was no significant difference between mean values of body length, number
288 of mature eggs, and size of eggs in the August 1966 epibenthic sled sample (N = 100) and the values
289 for the single female recruited into the 12-month box (Scheltema, 1987). This rapid development was
290 a surprise for an organism at bathyal depths of constant cold temperatures (3°C or less), faster than
291 many shallow water and intertidal molluscs.

292

293 ***P. yongei*, an opportunistic species**

294

295 Aplacophorans are generally considered to be a minor molluscan taxon and rare, which they
296 certainly are by numbers of genera (~100, perhaps overly split) and described species (~400). A few
297 species of the small taxon Aplacophora have come to numerically dominate some patches of the deep

298 ocean and therefore cannot be considered a minor component of the level-bottom benthic community.
299 *Prochaetoderma yongei* is one such species. Many characteristics of an opportunistic species are
300 indicated by its pattern of dominance, broad geographic range, and a depth distribution of >1800 m
301 (457–2270 m). It is motile within the sediment with a unique feeding apparatus that allows omnivory.
302 Development includes a swimming larva and rapid development to a mature adult. Thus some
303 members of the taxon Aplacophora should not be thought of as "rare."

304

305 **8. The importance of taxonomy to ecologists**

306

307 The animal kingdom is in reality comprised only of species, and species are what concern
308 ecologists. It is our human compulsion to order the universe of life into higher taxonomic categories
309 (thus keeping systematists constantly producing revisions) that reflect our ideas of relationship. This
310 ordering leads to insights about evolution and fuels many of the fantastic discoveries coming from
311 molecular and genomic biology. For understanding animal interactions in their natural environment,
312 the business of ecologists, it is species that matter. It was, after all, *species* that Darwin considered
313 when laying the foundations for understanding what we now call "The Tree of Life."

314

315 **Acknowledgments**

316

317 The importance of *P. yongei* was only discovered from fine screening the earliest deep-sea
318 epibenthic sled samples by Howard Sanders and Robert Hessler, including an amazing group in the
319 Sanders laboratory. The techniques were soon shared with John Gage, Dunstaffnage Marine
320 Laboratory, Scottish Association for Marine Science, and with Lucien Laubier, French Research

321 Institute for Exploration of the Sea (IFREMER), Brest, from whom further collections of benthic
322 macrofauna including *P. yongei* became available. Fred Grassle was the first to collect and examine,
323 with a fine team of colleagues, the fine-scale distribution of benthic deep-sea species quantitatively
324 over distance, depth, and time with the box cores taken off the east coast of the United States
325 described in section 3.2, and he was the first to set out screened deep-sea experimental boxes for
326 recruitment (Grassle, 1977; Grassle and Morse-Porteus, 1987). Through the collections of these
327 ecologists, *P. yongei* gained notoriety for the usually rare Aplousobranchia (Gage and Tyler, 1991), and
328 we have been fortunate to be one of the many taxonomists who have benefited from their work.

329 We thank Richard Lutz for the invitation to AHS to contribute to this volume of Deep-Sea
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331

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417 **Figure captions**

418

419 **Fig. 1.** Global distribution of *Prochaetoderma yongei*. Each filled circle stands for one to a number of
 420 closely spaced samples containing *P.yongei*, taken by various types of equipment; the large filled
 421 square indicates samples taken off New Jersey and Delaware by quantitative box cores (Table 2); and
 422 the small filled square denotes the southernmost extent of *P. yongei* in the western Atlantic between
 423 Cape Hatteras and Cape Lookout (~34°N) taken in a series of box cores (Blake and Grassle, 1994).
 424 Depth ranges in meters are indicated for each region, with number of samples/total number of
 425 *P.yongei* specimens shown in parentheses; not known for box cores (squares). Some epibenthic sled
 426 samples were so large that only half the sample was sorted.

427

428 **Fig. 2.** Location of deep-sea box-coring stations at bathyal depths on the Continental Slope along a
 429 176-km transect at 2,100-m between 37.9°–39.1°N and 72.1°–73.8°W with three additional stations at
 430 1,500 m and 1 additional station at 2,500 m (Table 2). Three replicate samples were taken at the 14
 431 stations during late spring, late summer, and late fall over a 2-year period for a total of usually 18
 432 boxcores, except when exigencies precluded successful sampling. (From Grassle and Maciolek, 1992,
 433 with permission of the University of Chicago Press.)

434

435 **Fig. 3.** Arrangement of sclerites along the body of an adult 2-mm *Prochaetoderma yongei*: oral shield
 436 sclerites (os), anterium (ant), dorsal trunk (dt), ventral trunk (vt), shank (sh), and knob (kn)(cf. Fig.
 437 4). Sclerites viewed under crossed polarized light which shows thickness by birefringence of
 438 aragonite: white, 1 μm; yellow, 3 μm; magenta, 3.5 μm; blue, 4 μm; and greenish, 5 μm (see
 439 Scheltema and Ivanov. 2004, for full explanation). Sclerite scale 0.1 mm (100 μm).

440
 441 **Fig. 4.** *Prochaetoderma yongei*, anatomy and measurements used in describing species of
 442 Prochaetodermatidae. A. Body regions; shank + knob = posterium. B. Internal anatomy of entire
 443 animal. C. Internal arrangement of radula in situ. D. Radula tooth. E. Jaw. 1, precerebral ganglion; 2,
 444 cerebral ganglion; 3, jaw; 4, buccal cavity; 5, radula; 6, esophagus; 7, beginning of intestine; 8,
 445 gonad; 9, gonopericardial duct; 10, pericardium; 11, mouth; 12, oral cavity; 13, radula bolster; 14,
 446 stomach; 15, digestive gland; 16, haemocoel; 17, fecal pellet within intestine; 18, vertical septum;
 447 19, gametoduct; 20, mantle cavity with ctenidia; 21, food bolus held within jaws; 22, food bolus
 448 extending into pharynx beyond jaws; 23, salivary glands; 24, jaw base (held within haemocoel); 25,
 449 serrated medial membrane; 26, crown; 27, wing; 28, grasper; 29, stem. (From Scheltema and Ivanov,
 450 2000.)

451
 452 **Fig. 5.** Divided (paired) oral shield (os) with mouth opening in between (mo), oral shield sclerite
 453 rows 1–3, and anterium (ant) of *Spathoderma alleni*, an eastern Atlantic confamilial of *P. yongei*,
 454 which has only 2 rows. (From Scheltema and Ivanov, 2000.)

455
 456 **Fig. 6.** Feeding in Prochaetodermatidae. A. Anterior tooth worn by rasping. B. Forameniferan with
 457 holes presumably made by rasping, taken from pharynx of a specimen of *Claviderma australe*
 458 (Scheltema). (From Scheltema, 1997.)

459

460 **Table 1**

461 Numbers of *P. yongei* and *S. clenchi* by depth taken by
 462 epibenthic sled in the North American Basin during 13
 463 cruises along transects between 65°N–70°N from the
 464 Upper Continental Slope and Rise. Number of stations
 465 varied with each cruise; success of sled hauls varied on
 466 any one cruise. (From Scheltema 1985 table 1).

Depth m	Station no. ^a	No. <i>yongei</i>	No. <i>clenchi</i>
457	Kn-35 stn 346	3	0
530	Ch-58 stn 105	1	0
805	Ch-88 stn 207	166	0
1102	Ch-50 stn 87	986	0
1254	AII-30 stn128	45	0
1470	AII-12 stn 73	911	19
1501	Ch-88 stn 209	435	6
2022	Ch-88 stn 103	7	18
2024	Ch-88 stn 210	78	274
2030	AII-24 stn 115	175	211
2178	AII-30 stn 131	21	71
2496	AII-12 stn 62	0	5
3264	Kn-35 stn 340	0	1

467 ^a AII = RV *Atlantis II*, Ch = RV *Chain*, Kn = RV

468 *Knorr*. (Source of material Appendix 1).

469

470

471

472 **Table 2**

473 *Spathoderma clenchi* and *Prochaetoderma yongei* from the northwest Atlantic off New Jersey: mean
 474 number of individuals m⁻², numerical rank, and percentage of total fauna by depth calculated from
 475 nine inner 0.01m² subcores per box core (BC). Data from 20 top-ranked species. (From Scheltema
 476 1997, based on data from Maciolek et al., 1987.)

Depth m	Station ^a	No. BCs	Lat N	Long W	<i>S.clenchi</i>			<i>P. yongei</i>		
					No.m ⁻²	Rank	%	No.m ⁻²	Rank	%
1500	M14	12	37°53.91'	73°44.62'	— ^b	— ^b	— ^b	346	2	6.1
1515	M11	17	38°40.17'	72°56.37'	— ^b	— ^b	— ^b	345	1	6.7
1613	M13	18	37°53.33'	73°45.09'	62	17	1.2	331	2	6.2
2020	M2	18	38°35.78'	72°53.65'	116	8	2.2	149	7	2.8
2055	M3	18	38°36.84'	72°51.35'	81	12	1.9	121	5	2.8
2065	M5	18	38°50.49'	72°33.01'	236	3	5.0	199	5	4.2
2090	M6	17	38°05.54'	72°02.97'	157	3	4.3	115	7	3.2
2095	M10	18	37°51.80'	73°19.84'	158	4	3.2	— ^b	— ^b	— ^b
2100	M7	17	38°27.36'	73°03.44'	171	2	4.1	96	6	2.3
2100	M4	18	38°44.47'	72°33.01'	165	4	3.3	154	6	3.1
2105	M9	18	38°17.28'	73°14.51'	166	2	4.3	103	6	2.6
2150	M8	8	38°27.31'	73°04.87'	172	2	4.6	62	15	1.7
2195	M1	18	38°35.98'	72°52.97'	240	3	5.1	113	8	2.4
2505	M12	18	38°29.30'	72°42.15'	59	11	1.7	— ^b	— ^b	— ^b

477 ^a Stations from Grassle and Maciolek (1992) located on Figure 2 herein.

478 ^b Not among the 20 most abundant species.

479

480 **Table 3**

481 Shallowest depths at which *P. yongei* was collected, the depths at which *P. yongei* and *S. clenchi*
 482 overlap, and the greatest depths at which *S. clenchi* was collected in three intensively sampled
 483 regions. There is great variation in equipment used, time intervals, and depths at which samples were
 484 taken among the three regions. ES, epibenthic sled; BC, box core.

Region ^a	<i>P. yongei</i>	<i>P. yongei</i> & <i>S. clenchi</i>	<i>S. clenchi</i>
	Shallowest depth m	Overlap m	Greatest depth m
North American, ES	457	1470–2178	3264
North American, BC	1500	1613–2195	2505
Off south Iceland	656	1295–2270	2270
West European Basin	1175	1913–2081	3356

485 ^a See Appendix 1 for sources of material.

486

487 **Table 4**

488 Samples from which lengths of males, females and juveniles of *Prochaetoderma yongei* were
 489 measured, listed in order of month; samples from which egg stages and sizes were determined in
 490 measured females are underscored. OC, RV Oceanus; AII, RV Atlantis II; AL, DSRV Alvin dive
 491 number; CH, RV Chain. (From Scheltema 1987.)

492

Station/dive ^a	Date	Lat. N	Long. W	Depth	Gear ^b	Sample N
OC-10 stn 367	Jul 76	39°45.5'	70°37.2'	1764	SBC #1	46
OC-10 stn 370	Jul 76	39°44.9'	70°35'	1815	SBC #2	20
AII-12 stn 73	Aug 64	39°46.5'	70°43.3	1470	ES	133
AII-24 stn 115	Aug 66	39°39.2'	70°24.5'	2030	ES	<u>100</u>
AL 459, 460	Sep 72	39°46'	70°40'	1760	SC	18
AII-30 stn 128	Dec 66	39°46.5'	70°45.2'	1254	ES	44
CH-88 smn 210	Feb 69	39°43'	70°46'	2024	ES	<u>72</u>

493

494 ^a OC = RV *Oceanus*, AII = RV *Atlantis II*, AL = DSRV *Alvin*, CH = RV *Chain* (Appendix 1 for
 495 sources of material.)

496 ^b SCB, spade box core 0.25 m² (#1, all 25 subcores sampled; #2, inner 9 subcores sampled); ES,
 497 epibenthic sled; SC, tube corer manipulated from submarine, ten 35 cm² combined

498

499

500 **Table 5**501 Colonization by *Prochaetoderma yongei* into recruitment boxes of azoic mud.

502 (From Scheltema 1987 from specimens and data provided by F. Grassle)

No. months	Source of sample	Box/ Tray no.	Length mm			Largest egg diameter μm
			Juvenile	Male	Female	
2	<i>Alvin</i> dive 597 ^a	—	1.4	0	0	
6	M6 Stn 2 ^b	H	0	2.6	0	—
8	<i>Alvin</i> dive 834 ^a	A	0	1.7	1.4	<75
8	<i>Alvin</i> dive 834 ^a	A	0	1.7	1.4	75
8	<i>Alvin</i> dive 834 ^a	C	1.7	1.7	2.1	<75
8	<i>Alvin</i> dive 834 ^a	C	0	2.3	0	
8	<i>Alvin</i> dive 834 ^a	C	0	2.0	0	
8	<i>Alvin</i> dive 834 ^a	D	1.0	0	0	
12	M4 Stn 2 ^c	C	0	0	2.1	162

503 ^a Put in place and recovered by DSRV *Alvin*; 1760 m.504 ^b Free vehicle H, tray 6 (Maciolek et al., 1986); 2020 m.505 ^c Free vehicle C, tray 2 (Maciolek et al., 1986); 2020 m.

506

507 **Appendix 1**

508 Summary of sources of collections with *P. yongei* either described by the authors, or with AHS as
509 consultant; other sources taken from the literature .

510

511 A. North American Basin

512 (1) Gay Head–Bermuda Transect: Sanders et al. (1965), Hessler and Sanders (1967); Woods
513 Hole Oceanographic Institution cruises 1961–1976: RV *Atlantis*-264, 298; RV *Atlantis II*-12, 17, 24,
514 30, 40; RV *Chain*-50, 58, 88; RV *Knorr*-35; RV *Oceanus*-10. Most collections by epibenthic sled,
515 some by anchor dredge or 0.25 m² spade boxcores (recorded in Scheltema 1985 for *P. yongei* and *S.*
516 *clenchi*).

517 (2) South of George's bank: Blake and Watling (1994); U.S. Department of the Interior,
518 Minerals Management Service (MMS), U.S. Atlantic Continental Slope and Rise Program (ACSAR)
519 cruises 1984–1986. Three replicate seasonal collections by 0.25 m² spade boxcores.

520 (3) Deep Ocean Dumpsite off New Jersey: Grassle (1977), Grassle and Morse-Porteus (1987);
521 Woods Hole Oceanographic Institution, DSRV *Alvin* dives (recorded in Scheltema 1985 for *P. yongei*
522 and *S. clenchi*).

523 (4) Experimental boxes, continental slope off southern New England and New Jersey: boxes
524 placed and retrieved by Woods Hole Oceanographic Institution DSRV *Alvin*; Maciolek et al. (1986,
525 1987), U.S. Atlantic Continental Slope and Rise Program (ACSAR), MMS data, free-fall vehicles
526 (recorded in Scheltema 1987 for *P. yongei* with data provided by F. Grassle).

527 (5) Off New Jersey: Grassle and Maciolek (1992); seasonal replicate 0.25 m² box core
528 samples along a 176-km transect, three times per year for two years, 1985–1985 (AHS consultant).

529

530 B. Western Atlantic south of Pt. Lookout, 34°N531 Seasonal 0.25 m² box cores 1993–1994, Blake (1994), Blake and Grassle (1994), U.S.

532 Atlantic continental Slope and Rise Program (ACSAR), MMS data (AHS consultant).

533

534 C. North Atlantic south of Iceland

535 Exclusive Economic Zone around Iceland: program BIOICE, a collaboration of a number of

536 Icelandic and Scandinavian universities, museums, and research institutes, administered by the

537 Icelandic Ministry for the Environment. Data available at <ftp://ftp.hafro.is/pub/bioice>; recorded in538 Ivanov and Scheltema (2001b) for *P. yongei* and *S. clenchi* from material provided by G.

539 Gudmundarsen, Icelandic Museum of Natural History.

540

541 D. West European Basin

542 (1) Centre National de Tri d'Océanographique Biologic (CENTOB), cruises 1972–1981:

543 INCAL, THALASSA-73, BIOGAS-IV, VI; sled and perch trawls, cruise data supplied from L.

544 Laubier (recorded in Scheltema 1985 for *P. yongei* and *S. clenchi*).545 (2) National Institute of Oceanography (U.K.), 1967 cruise RV *Sarsia*. Epibenthic sled. Cruise546 data supplied by J. A. Allen (recorded in Scheltema 1985 for *P. yongei* and *S. clenchi*).

547

548 E. Cape Verde Basin549 Woods Hole Oceanographic Institution, 1967 cruise RV *Atlantis II*-31. Cruise data supplied550 by H. L. Sanders laboratory (recorded in Scheltema 1985 for *P. yongei* and *S. clenchi*).

551

552 F. Angola Basin

- 553 (1) Centre National de Tri d'Océanographique Biologic (CENTOB), 1971 cruise WALDA.
554 Data supplied by L. Laubier (recorded in Scheltema 1985 for *P. yongei* and *S. clenchi*).
- 555 (2) Woods Hole Oceanographic Institution, 1968 cruise RV *Atlantis-42*. Cruise data supplied
556 by H. L. Sanders laoratory (recorded in Scheltema 1985 for *P. yongei* and *S. clenchi*).











