

Taxonomic Notes on Four Species of *Panagrellus* Thorne (Nematoda: Cephalobidae)

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Abstract: Four populations of *Panagrellus redivivus* (Linnaeus, 1767) Goodey, 1945, and syntypes of *P. dubius* Sanwal, 1960, *P. redivivoides* (Goodey, 1943) Goodey, 1945, *P. pycnus* Thorne, 1938, *P. zymosiphilus* (Brunold, 1950) Brunold, 1954, and *P. leucocephalus* Steiner, 1936 were examined. Additional information on the morphology of spicules and stoma is presented. *P. zymosiphilus* is synonymized with *P. redivivoides* and Rühm's synonymization of *P. silusiae* and *P. leucocephalus* with *P. redivivus* is supported. Lectotypes for *P. pycnus* and *P. redivivoides* are designated. **Key Words:** Taxonomy, *Panagrellus pycnus*, *P. redivivus*, *P. silusiae*, *P. dubius*, *P. redivivoides*, *P. zymosiphilus*, *P. leucocephalus*.

The sour paste nematode, included in Linnaeus' 1767 genus *Chaos* (7), was known to the earliest microscopists; nevertheless controversy over its name and detailed structure still remains. The forensics related to the validity of its generic name have been amply detailed by Stiles and Hassall (15), Goodey (3), Peters (10), and Rühm (11). The reasoning of Peters, and thus the name *Panagrellus* Thorne, 1938, is accepted here.

In addition to being found in sour paste, species of *Panagrellus* have been collected from such varied habitats as slime flux of trees, insect frass, pitchers of pitcher plants, beer mats, and spoiled cider. They are easily reared in culture and have been used in many biological studies. Supplementary to the original species descriptions, information on *Panagrellus* morphology is available in publications on the excretory system by Smith (13), on chromosome number and the development of the reproductive system by Hechler (6), and on an electron microscope study of the anterior region by Yuen (17). Four species of *Panagrellus* are redescribed below.

MATERIALS AND METHODS

Sources of living cultures of *P. redivivus* (Linnaeus, 1767) Goodey, 1945 populations were as follows: A. Florida soil; B. Established in axenic culture by E. C. Dougherty, source unknown; C. Belgium, habitat unknown; D. New Jersey soil. All were maintained in oatmeal culture and stained for chromosome study as described previously for Population A (6). Measurements were based on adults fixed in formalin and dehydrated to glycerine by the slow method. Syntypes of *P. pycnus* Thorne, 1938 were from the Gerald Thorne Collection of the U.S. Department of Agriculture Nematode Collection. Syntypes of *P. leucocephalus* (Steiner, 1936) Goodey, 1945, *P. redivivoides* (Goodey, 1943) Goodey, 1945, *P. zymosiphilus* (Brunold, 1950) Brunold, 1954, and *P. dubius* Sanwal, 1960 were made available by various workers. Females of *P. zymosiphilus* and *P. dubius* were not seen. Spicules were measured in a straight line between the ends, and the stomata from extreme anterior end of body to base of stoma funnel.

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GENERAL DESCRIPTION

Only the spicule shape and, occasionally, the form of the vulva, are useful to separate the species of *Panagrellus* described here. Therefore morphology common to all these

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species will be described first, then the features peculiar to individual species.

Cuticle with extremely shallow transverse striae less than 1μ apart, lateral fields with four deeper longitudinal striations at mid-body, fewer anterior to deirid. Head continuous with or only slightly offset from body and with six slightly separated lips (Fig. 1-5, 6, 13, 19). Cheilostom equilaterally hexagonal in cross sections (Fig. 6, 14, 19), lining not sclerotized. Prostom partially surrounded with esophageal collar (Fig. 1, 2), cross section nearly round, with one ventral and two subdorsal notches (Fig. 7, 15, 19), lining conspicuously sclerotized, thicker posteriorly. Stoma triangular behind prostom, dorsal wall slightly protruding with a small central wart (Fig. 1-5, 8, 16, 20). Three narrow dorsal teeth present just behind wart (Fig. 1, 2, 3, 5, 9, 10, 17, 21), two pairs subventral teeth borne posterior to dorsal teeth (Fig. 1, 2, 3, 5, 11, 18, 22). Shape of stoma increasingly triradiate posteriorly. A circular tube at the end of each arm of esophageal lumen extends between base of stoma and isthmus (Fig. 12). No cross sections of the stoma were available for *P. dubius*; lateral views appeared similar to those of the other species studied, but stomatal armature could not be verified.

Rühm (11) described the dorsal wall of the funnel-shaped part of the stoma of *P. redivivus* with an anterior wart and three posterior teeth and each subventral wall with two posterior teeth. Yuen (17), reporting on an electron microscope study, described and illustrated the two pairs of subventral teeth, but found no teeth on the dorsal wall. Fig. 9 of this report, showing the anterior ends of the three dorsal teeth, corresponds to Fig. 13 of Yuen's paper (labeled with a question mark). Possibly the ultra-section which would correspond to the present Fig. 10, showing the attachment of the dorsal teeth to the stoma wall, was lost during sectioning.

This would explain the discrepancy between the reports of Yuen and Rühm.

Procorpus 55 to 65% of esophageal length, nerve ring just anterior to basal bulb, hemizonid opposite anterior margin of bulb, deirid at same level on lateral field. Excretory pore between nerve ring and anterior limits of isthmus, excretory duct straight anteriorly, but looped considerably within glands located ventral to posterior half of bulb.

Male and female gonads as described previously for *P. redivivus* (6). All species examined had post-vulvar sac as long as half the distance from vulva to anus or slightly longer, usually filled with sperm. Vulva and anus in females transverse slits, slightly curved anteriorly. Vagina shape varying between species.

Female tails elongate-conical in species considered here (Fig. 53-55), male tails tapering to slightly offset flagellum (Fig. 76-80). Posterior end of males with seven pairs of papillae: (i) subventral just anterior to spicule manubrium; (ii) subventral adanal; (iii) lateral adanal; (iv, v) two closely approximated subventral pairs midway between anus and beginning of tail flagellum; (vi) subdorsal, position variable within species, behind anus; (vii) subdorsal just anterior to tail flagellum. A single ventromedian papilla just anterior to anus, illustrated for *P. pycnus* by Thorne (16) and for *P. leucocephalus* by Steiner (14), also present in the other species. As pointed out by Rühm (11) and Brunold (2), the position of each pair of papillae may vary considerably within a species, and the right and left members of each pair may not be at exactly the same level. Phasmids obscure, located at 45 to 50%, rarely as far forward as 35%, of tail length in females; opposite posterior subdorsal papillae in males. Right and left phasmids may be at slightly different levels.

Spicules paired, curved, separate. Shape of spicules differing between species, but all with the general features described below: spicule with variously shaped head (manubrium) proximally, usually widening behind manubrium to a shoulder, then tapering to a shaft which may have parallel sides for much of its length. Distal terminus bifurcate, membranous velum extending between it and manubrium. Manubrium variously shaped, but always a single tube in cross section (Fig. 56, 57, 66) with an opening laterodorsally (Fig. 58, 67, 68) probably for muscle insertion. Spicule a double tube at shoulder level, divided in two by an additional sclerotized element (main ventral element) at shoulder level, with smaller tube ventral (Fig. 59, 69, 70). Still further posteriad yet another sclerotized element divides spicule into three tubes for short distance (Fig. 71) and dorsal-most element becomes thinner. (In *P. redivivoides* ventral element extending from manubrium often ends proximal to shoulder, and only two tubes are present (Fig. 60).) Ventral-most element gradually disappearing, so that each spicule is a double tube for most of its shaft length (Fig. 61, 62, 72). Near distal terminus main ventral element becomes thinner and, in *P. redivivus* and *P. redivivoides*, an additional element arises just within it. The two inner, thicker elements diverge, and short, proximally directed extensions of them join a short distance from terminus forming a bifurcation. The very thin outer elements cover the bifurcation and a short, straight, thicker inclusion at the very terminus extends back toward the bifurcation. In *P. pycnus* and *P. dubius* the main ventral element is continuous with the bifurcation. The thin, membranous velum arises slightly behind the proximal end of the spicule (Fig. 68), and extends to its distal terminus. The ventral margins of the two spicules (velum) are closer together than spicule shafts, some-

times nearly touching (Fig. 72), evidently causing de Man (9) to conclude that the spicules of *P. silusiae* were fused.

Gubernaculum a shallow trough proximally, surrounding spicules on three sides distally (Fig. 25, 33, 42, 43, 73-75). Proximal part thickened, distal part thinner and membranous but with slightly thicker lateral margins, rather than with bifurcate terminus as reported by Sanwal (12), and Rühm (11).

SPECIES DESCRIPTIONS

Panagrellus redivivus (Linnaeus, 1767) Goodey, 1945

- Syn: *Chaos redivivum* Linnaeus, 1767
Vibrio anguillula Müller, 1773
Vibrio glutinus Müller, 1783
Anguillula rediviva (Linnaeus, 1767) Stiles & Hassall, 1905
Turbatrix rediviva (Linnaeus, 1767) Peters, 1927
Turbator redivivus (Linnaeus, 1767) Goodey, 1945
Gordius glutinus Oken, 1815
Rhabditis glutinus Dujardin, 1845
Leptodera oxophila Schneider, 1866 (in part)
Cephalobus parasiticus Sandground, 1939
Neocephalobus leucocephalus Steiner, 1936
Turbator leucocephalus (Steiner, 1936) Goodey, 1943
Panagrellus leucocephalus (Steiner, 1936) Goodey, 1945
Anguillula silusiae de Man, 1913
Turbatrix silusiae (de Man, 1913) Peters, 1927
Turbator silusiae (de Man, 1913) Goodey, 1943
Panagrellus silusiae (de Man, 1913) Goodey, 1945

Measurements (Population A, 41 ♂♂): L = 1.399 (range 0.705-1.806) mm; a = 29.3 (22.0-35.4); b = 6.5 (4.1-7.8); c = 9.2 (6.9-11.5); spicules = 0.0580 (0.051-0.061) mm; gubernaculum = 0.0296 (0.024-0.032) mm; stoma = 0.0149 (0.009-0.017) mm; (44 ♀♀) L = 1.655 (1.455-2.090) mm; a = 24.8 (20.0-31.0); b = 7.6 (6.4-9.5); c = 8.9 (6.7-11.0); V = 65.6 (58-70)%; stoma = 0.0164 (0.014-0.018) mm.
(Population B, 10 ♂♂): L = 1.310 (1.160-1.530) mm; a = 25.4 (23.0-28.9);

b = 7.0 (6.3–8.3); c = 10.0 (9.1–11.2); spicules = 0.056 (0.050–0.059) mm; gubernaculum = 0.030 (0.028–0.031) mm; stoma = 0.014 (0.011–0.015) mm: (10 ♀♀) L = 1.500 (1.312–1.635) mm; a = 24.9 (21.0–31.2); b = 8.0 (7.4–9.2); c = 10.3 (9.5–11.6); V = 67.5 (65–69)%; stoma = 0.0138 (0.013–0.015) mm.

(Population C, 10 ♂♂): L = 1.252 (0.968–1.600) mm; a = 25.7 (21–32); b = 6.5 (5.6–7.9); c = 9.7 (8.0–11.2); spicules = 0.0573 (0.052–0.064) mm; gubernaculum = 0.0303 (0.029–0.031) mm; stoma = 0.0145 (0.011–0.016) mm: (10 ♀♀) L = 1.460 (1.110–1.660) mm; a = 22.1 (19–25); b = 7.0 (6.0–7.9); c = 9.1 (7.8–10.9); V = 67.0 (56–71)%; stoma = 0.0145 (0.011–0.015) mm.

(Population D, 14 ♂♂): L = 1.415 (1.245–1.720) mm; a = 27.9 (22.3–31.0); b = 6.5 (5.9–7.5); c = 9.6 (8.5–10.9); spicules = 0.0570 (0.051–0.061) mm; gubernaculum = 0.0304 (0.027–0.032) mm; stoma = 0.0153 (0.011–0.017) mm: 12 ♀♀: L = 1.722 (1.600–1.900) mm; a = 22.8 (22–30); b = 7.6 (6.9–8.4); c = 9.5 (8.4–10.5); V = 64.5 (62–66)%; stoma = 0.0166 (0.014–0.018) mm.

(Steiner's specimens, *P. leucocephalus* syntypes, 2 ♂♂): L = 0.870, 0.867 mm; a = (specimens flattened); b = 5.5, 5.0; c = 7.2, 7.9; spicules = 0.036, 0.039 mm; gubernaculum = 0.018, 0.020 mm; stoma = 0.010, 0.009 mm. 6 ♀♀: L = 0.970 (0.840–1.185) mm; a = (specimens flattened); b = 5.5 (5.0–6.8); c = 8.1 (7.4–8.6); V = 68.5 (65–71)%; stoma = 0.0105 (0.009–0.012) mm.

Distribution of specimens.—Population A slides G-2806, G-2807, G-2816, G-2817, G-2818, vial G-1273g; population B slides G-2808, G-2809, vial G-1274g; population C slides G-2810, G-2811, vial G-1275g; population D slides G-2812, G-2813, vial G-1276g; *P. leucocephalus* syntypes slides

T-863p-T-865p, U.S.D.A. Nematode Collection, Beltsville, Maryland.

Description.—Lateral fields with four parallel lines, the center two closer to each other than to the outer ones; or center lines broken, arranged diagonally as in Fig. 81.

Vaginal lumen flattened dorsoventrally, anteriorly directed (Fig. 24), lumen straight except for protrusion of anterior wall fitting into corresponding notch in posterior wall just within vulva. Cuticularization lining vaginal lumen thicker on anterior wall. Dorsal wall with lobe-like thickening present between outlets into ovary and post-vulvar sac, function unknown, comprised of four cells, two on each side, apparently connected to vagina by a duct.

Spicules moderately long. Manubrium usually hooked, occasionally trianguloid (Fig. 29, 30, 38). Shoulder region widened, with dorsal wall curved (Fig. 28, 30, 34, 35, 37, 39), angular (Fig. 27, 36, 40), or with intermediate shapes (Fig. 25, 31, 32, 33). Shoulder tapering gradually to shaft which has parallel sides for much of spicule length. Main ventral element more or less curved at proximal end, may extend to dorsal wall. Bifurcation 10 to 12% of spicule length, both branches, or only the dorsal branch, slightly thickened anteriorly. Many specimens found with dissimilar spicules within same specimen (Fig. 28, 29). Shape of gubernaculum somewhat variable, general structure as in Figs. 42, 43, six or more minute teeth on proximal margin. Thin distal portion 24 to 30% of length of gubernaculum.

Diagnosis.—*P. redivivus*, most similar to *P. pycnus*, can be separated by the shorter spicule with wider, less angular manubrium, wider shoulder and thicker shaft, main ventral element not continuous with ventral branch of bifurcation, and longer thin distal portion of gubernaculum.

Biology.—Females from all populations failed to reproduce when isolated from other

nematodes before their final molt, but after males were placed with virgin females progeny were produced. Nematodes from the various populations were able to interbreed. The chromosome behavior and number of all the populations was as reported previously (6) for population A.

Discussion.—De Man (8, 9) gave the first description of the sour paste nematode recognizable by modern standards, but, since it was collected from beer mats, presumably he did not connect it with the sour paste nematode of Linnaeus and the early microscopists. He gave it the specific epithet *silusiae*. The next recognizable description of the species, in which Goodey (3) settled the question of the separate identities of the sour paste and vinegar nematodes, was based on specimens actually taken from sour paste. Goodey, considering them to be the same animal often discussed by the early workers, used the specific epithet *redivivus*. The chief differences found between the descriptions of de Man and Goodey are in the body size and spicule shape. De Man reported longer nematodes than Goodey. As pointed out by Brunold (2) and Rühm (11) however, body size varies considerably with the nutritive state of nematodes in this genus. In the present study, moreover, considerable size differences were found in specimens from the same population all reared under the same conditions. The spicule shown in de Man's Fig. 1, g (9) is angular at the shoulder, straight between shoulder and hook, and with a narrow manubrium and small hook. In Goodey's Fig. 4A (3) the spicule is curved dorsally between shoulder and hook, and manubrium and hook are thicker than in de Man's specimen. The bifurcations are quite similar in both drawings. Considerable variability was found in spicule shapes in each of the populations studied here; spicules from each population could be found close to the shapes illustrated by both de Man

(Fig. 28, 31, 36, 40), and Goodey (Fig. 26, 32, 37, 39). Slight differences were even found between the two spicules from the same specimen (Fig. 28, 29). Neither differences in body size alone, nor the differences in spicule shape between those described by de Man and Goodey are considered great enough to separate the species, and Rühm's synonymization of *P. silusiae* with *P. redivivus* is accepted herein.

Rühm (11) synonymized *P. leucocephalus* with *P. redivivus*; Sanwal (12) disagreed. Syntypes of *P. leucocephalus* were found to be poorly preserved and quite shrunken, with many flattened, broken specimens. (Steiner (14) reported measurements of L = 0.90–0.94 mm for males, 1.00–1.11 mm for females.) On one female the vagina was well enough preserved to show it was quite similar to that of *P. redivivus*. The spicule illustrated in Fig. 41, a composite of two spicules, one well preserved distally, the other proximally, is similar in shape to some of the *P. redivivus* spicules. The bifurcations, as well as general body shape and the stoma, are very typical of *P. redivivus*. The specimens were considerably shorter than the average *P. redivivus* studied here; only a few *P. redivivus* specimens were as short. The spicules were much smaller than the smallest spicule found in all the other isolates. No differences but size could be found between Steiner's material and the other isolates and, since shrinkage of the *P. leucocephalus* specimens could account for some of the difference, and also since size differences alone are not considered of diagnostic value in this genus, *P. leucocephalus* is synonymized with *P. redivivus* in agreement with Rühm.

Panagrellus pycnus Thorne, 1938

Syn: *Turbator pycnus* (Thorne, 1938) Goodey, 1943

Measurements (δ Lectotype): L = 1.222 mm; a = 26.2; b = 6.8; c = 9.5; spicules

= 0.067 mm; gubernaculum = 0.026 mm; stoma = 0.012 mm.

(♀ Allolectotype): L = 1.388 mm; a = 18.5; b = 7.6; c = 9.2; V = 71%; stoma = 0.011 mm.

(14 ♂♂ Paralectotypes): L = 1.032 (0.900–1.163) mm; a = 24.5 (20.6–26.9); b = 6.4 (5.7–7.4); c = 9.0 (7.9–10.4); spicules = 0.0648 (0.060–0.070) mm; (an unusual specimen 0.939 mm long with 0.054 mm spicules); gubernaculum = 0.026 (0.025–0.027) mm; stoma = 0.0112 (0.010–0.013) mm.

(11 ♀♀ Paralectotypes): L = 1.313 (1.170–1.410) mm; a = 19.6 (16.0–21.5); b = 7.2 (6.1–8.0); c = 8.9 (7.6–10.4); V = 72.8 (71–77)%; stoma = 0.0132 (0.013–0.014) mm.

Distribution of specimens.—Lectotype ♂ on slide T-185t, allolectotype ♀ on slide T-186t, paralectotypes 14 ♂♂, 13 ♀♀, 6 y on slides T-840p–T-846p, head and tail mounts on slides T-852p–T-855p, U.S.D.A. Nematode Collection, Beltsville, Maryland.

Description.—Vagina anteriorly directed, notch present in lumen as in *P. redivivus*. Post vulvar sac present. A pair of minute caudal papillae present on anal lips of male tail in addition to papillae described above for all species. Spicules long, comparatively narrow throughout, manubrium angular, slender, hooked (Fig. 52). Shoulder angular, only slightly widened, shaft very narrow, sides parallel for much of spicule length, but diverging somewhat proximal to beginning of bifurcation. Main ventral element continuous with ventral branch of bifurcation. Bifurcation about 5% of spicule length. Shape of velum not determined because all spicules were either damaged or protruded from anal opening (Fig. 52). Thin distal portion of gubernaculum about 15% of length.

Diagnosis.—*P. pycnus*, most similar to *P. redivivus*, can be separated by the longer,

more slender spicule with angular slender manubrium and proportionately shorter bifurcation, main ventral element continuous with ventral branch of bifurcation, and shorter distal portion of gubernaculum.

Panagrellus dubius Sanwal, 1960

Measurements (Holotype ♂): L = 0.802 mm; a = 24.3; b = 5.3; c = 9.4; spicules = 0.044 mm; gubernaculum = 0.027 mm; stoma = 0.0085 mm. (Paratypes, 7 ♂♂): L = 0.856 (0.802–0.968) mm; a = 28.2 (24.3–32.2); b = 5.0 (4.7–5.4); c = 9.3 (8.1–10.0); spicules = 0.0435 (0.039–0.045) mm; gubernaculum = 0.024 (0.026–0.030) mm; stoma = 0.0113 (0.009–0.014) mm.

Description.—Stomatal armature not determined. Vaginal lumen straight and anteriorly directed in original description (12). Spicules medium sized, manubrium usually hooked (Fig. 44), occasionally shaped as in Fig. 45. Shoulder curved, barely widened. Shaft moderately narrow, sides nearly parallel. Main ventral element continuous with ventral branch of bifurcation. Bifurcation quite wide and long, occupying 18 to 25% of spicule length, both branches straight, without thickenings. Inclusion at terminus of velum possibly present, but not seen because no specimen had spicule protruded. Thin distal portion of gubernaculum about 20% of its length.

Diagnosis.—*P. dubius* is similar to *P. redivivus* and *P. pycnus*. It differs from both species in smaller body size, smaller spicules, and extremely large bifurcation on spicule, and from *P. redivivus* by the narrower spicule shoulder and main ventral element continuous with bifurcation.

Panagrellus redivivoides (Goodey, 1943)
Goodey, 1945

Syn: *Turbator redivivoides* Goodey, 1943

Anguillula redivivoides (Goodey, 1943) Rühm, 1956

A. zymosiphilus Brunold, 1950 n. syn.

P. zymosiphilus (Brunold, 1950) Brunold, 1954 n. syn.

Measurements: (δ Lectotype): L = 0.735 mm; a = 24.5; b = 4.6; c = 8.7; spicules = 0.026 mm; gubernaculum = 0.014 mm; stoma = 0.012 mm.

(19 $\delta\delta$ Paralectotypes): L = 0.804 (0.653–1.098) mm; a = 25.7 (20.3–32.7); b = 5.0 (4.5–6.1); c = 9.6 (7.9–11.8); spicules = 0.0268 (0.021–0.034) mm; gubernaculum = 0.0139 (0.010–0.018) mm; stoma 0.0112 (0.010–0.013) mm. 24 ♀♀ ; L = 1.117 (0.942–1.373) mm; a = 21.8 (18.7–25.7); b = 6.4 (4.9–8.2); c = 9.7 (8.3–12.2); V = 68.9 (62–73)%; stoma = 0.0122 (0.010–0.014) mm.

Brunold's specimens *P. zymosiphilus* syntypes, 8 $\delta\delta$: L = 0.979 (0.900–1.050) mm; a = 21.5 (17.3–25.2); b = 5.8 (5.5–6.0); c = 10.1 (9.6–10.9); spicules = 0.0280 (0.024–0.031) mm; gubernaculum = 0.0178 (0.016–0.019) mm; stoma = 0.0107 (0.009–0.012) mm.

Distribution of specimens.—Lectotype δ on slide 35/3/16; paralectotypes 25 $\delta\delta$, 44 ♀♀ on slides 35/3/1, 35/3/2, 35/3/3, 35/3/4, 35/3/6, 35/3/7, 35/3/11; syntypes of Brunold's specimens (*P. zymosiphilus*) on slide 35/4/1 in the nematode collection of the Nematology Department, Rothamsted Experimental Station, Harpenden, England. Paralectotypes 4 $\delta\delta$, 5 ♀♀ , 1 y on slides T-848p–T-851p of the U.S.D.A. Nematode Collection, Beltsville, Maryland.

Description.—Vagina perpendicular to body wall, otherwise similar to that of *P. redivivus* (Fig. 23). Vaginal cuticularization considerably thicker on anterior wall. Spicules comparatively short, wide (Fig. 46–51, 56–64). Shape of manubrium variable, trianguloid, not hooked; ventral end of manubria of the two spicules in a specimen much farther apart than dorsal portions. Shoulder quite wide, shaft tapering gradually, sides of

shaft parallel for only a short distance. Main ventral element usually irregularly curved at proximal end and extending nearly to dorsal element. Bifurcation about 10 to 15% of spicule length. In one specimen the manubrium of the right spicule was wide, that of the left spicule was quite narrow (Fig. 56–64). Distal thin portion of gubernaculum less than 5% of its length, proximal portion smoothly rounded.

Diagnosis.—*P. redivivoides*, with its short, wide spicule, is easily separated from the other species discussed here. It is most similar to *P. ludwigii* (de Man, 1910), but in the latter species the vagina is directed anteriorly, and the spicules have a small beak on the manubrium and very short bifurcations.

Discussion.—Brunold (2) separated *P. zymosiphilus* from *P. redivivoides* by differences in vaginal cuticularization and differences in spicule size and shape. Apparently she believed that the vaginal cuticularization of *P. redivivoides* was thicker on the posterior wall. The present study shows it to be thicker on the anterior wall, as in *P. zymosiphilus*. Differences in spicule size and shape could be found in type specimens of both *P. redivivoides* (Fig. 46–48, 63, 64) and *P. zymosiphilus* (Fig. 49–51). However, no spicule feature could be found consistently in one group and not in the other, whereas spicules from one group could be found which were similar to some in the other group. Therefore *P. zymosiphilus* is synonymized with *P. redivivoides*.

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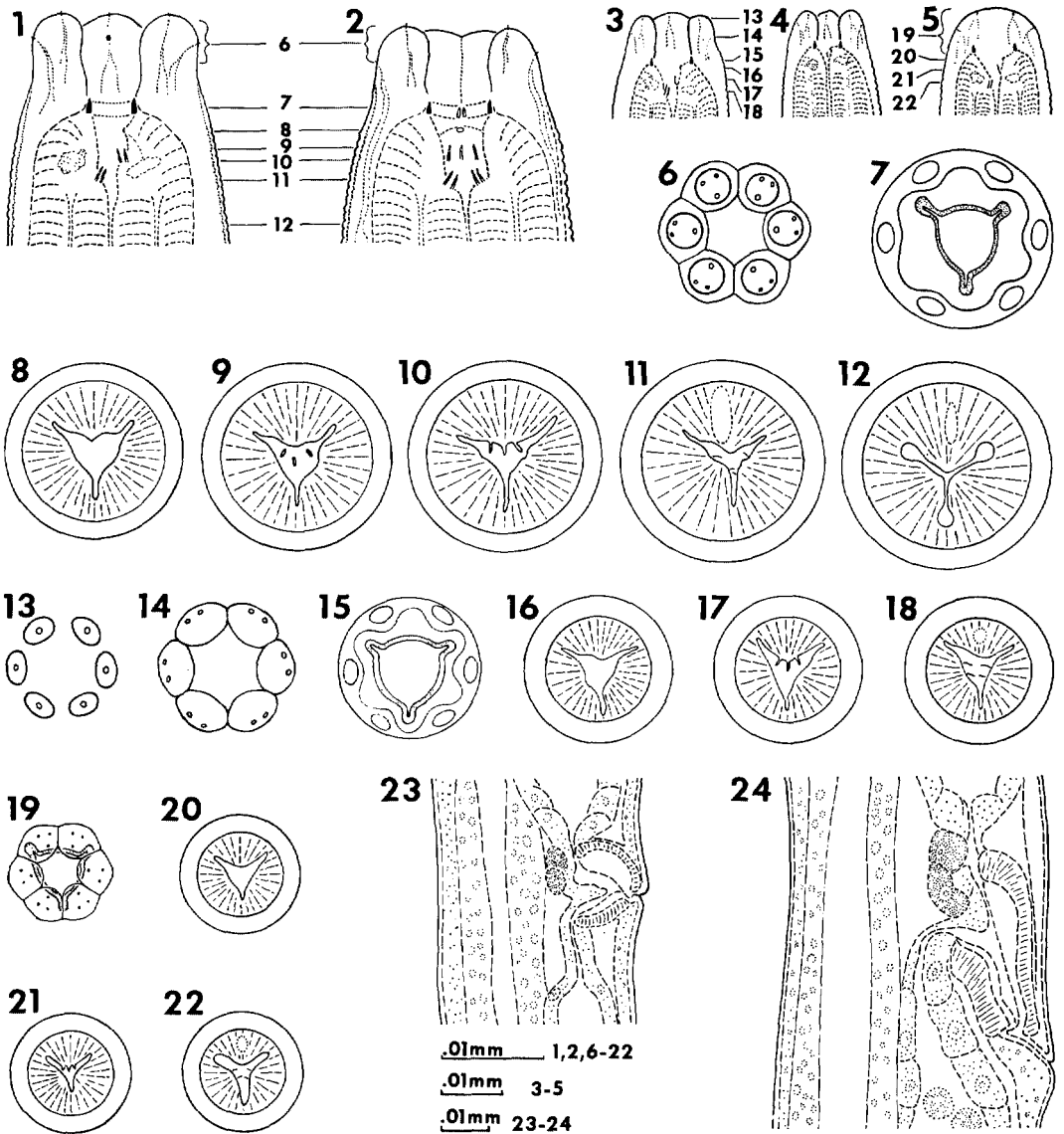


PLATE 1. Fig. 1. *P. redivivus* head, lateral view (small numbers indicate level of cross sections); Fig. 2. *P. redivivus* head, dorsoventral view; Fig. 3. *P. pycnus* head, lateral view (small numbers indicate level of cross sections); Fig. 4. *P. dubius* head, lateral view; Fig. 5. *P. redivivoides* head, lateral view (small numbers correspond to level of cross sections). Fig. 6-12. *P. redivivus* head, cross sections: 6. Lips; 7. Prostom; 8. Dorsal wart; 9. Anterior ends of three dorsal teeth; 10. Base of three dorsal teeth; 11. Subventral teeth; 12. Esophagus. Fig. 13-18. *P. pycnus* head, cross sections: 13. Anterior lips; 14. Posterior lips; 15. Prostom; 16. Dorsal wart; 17. Three dorsal teeth; 18. Subventral teeth. Fig. 19-22. *P. redivivoides* head, cross sections: 19. Lips and prostom; 20. Dorsal wart; 21. Dorsal teeth; 22. Subventral teeth; Fig. 23. *P. redivivoides*, vaginal area; Fig. 24. *P. redivivus*, vaginal area.

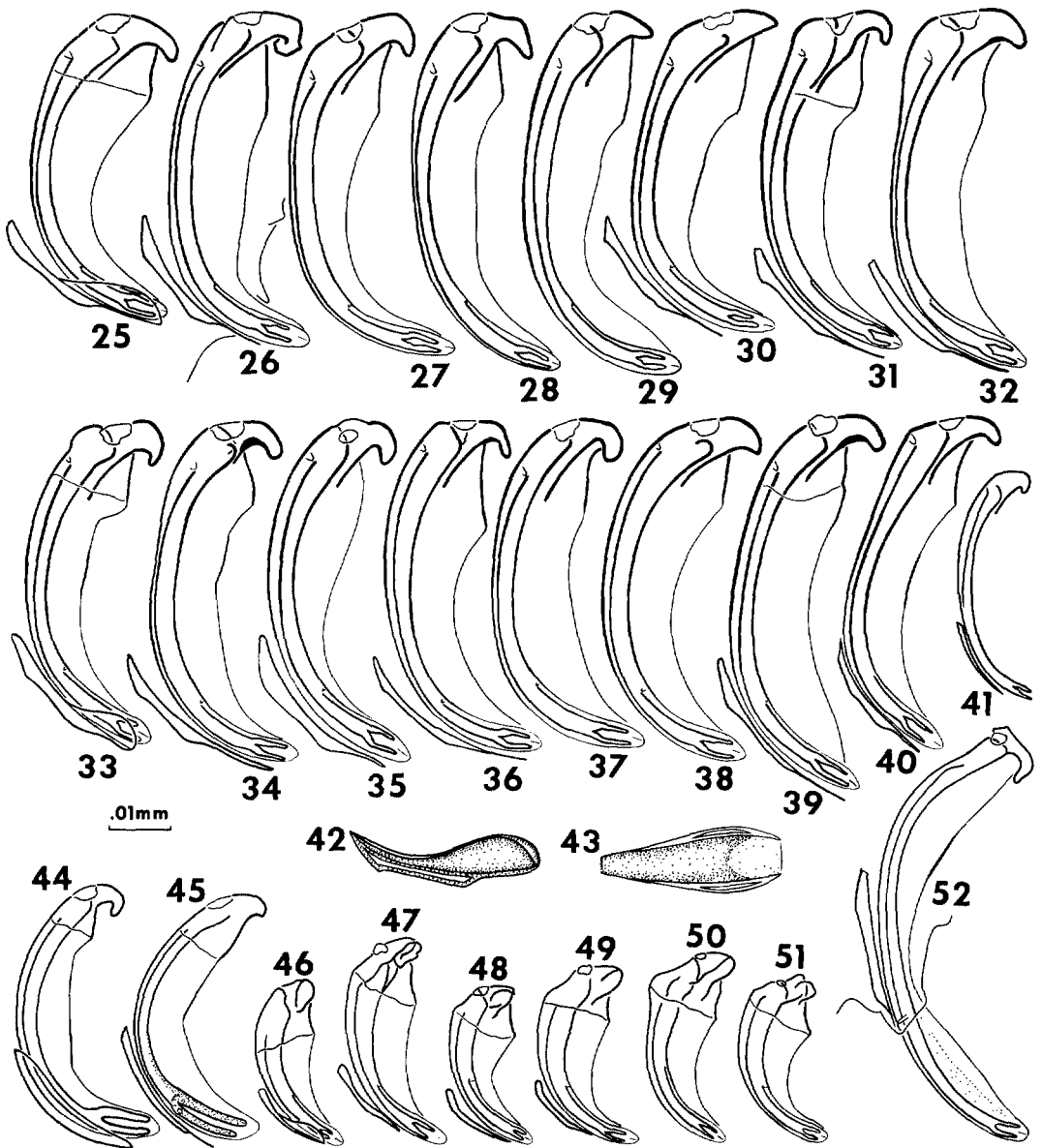
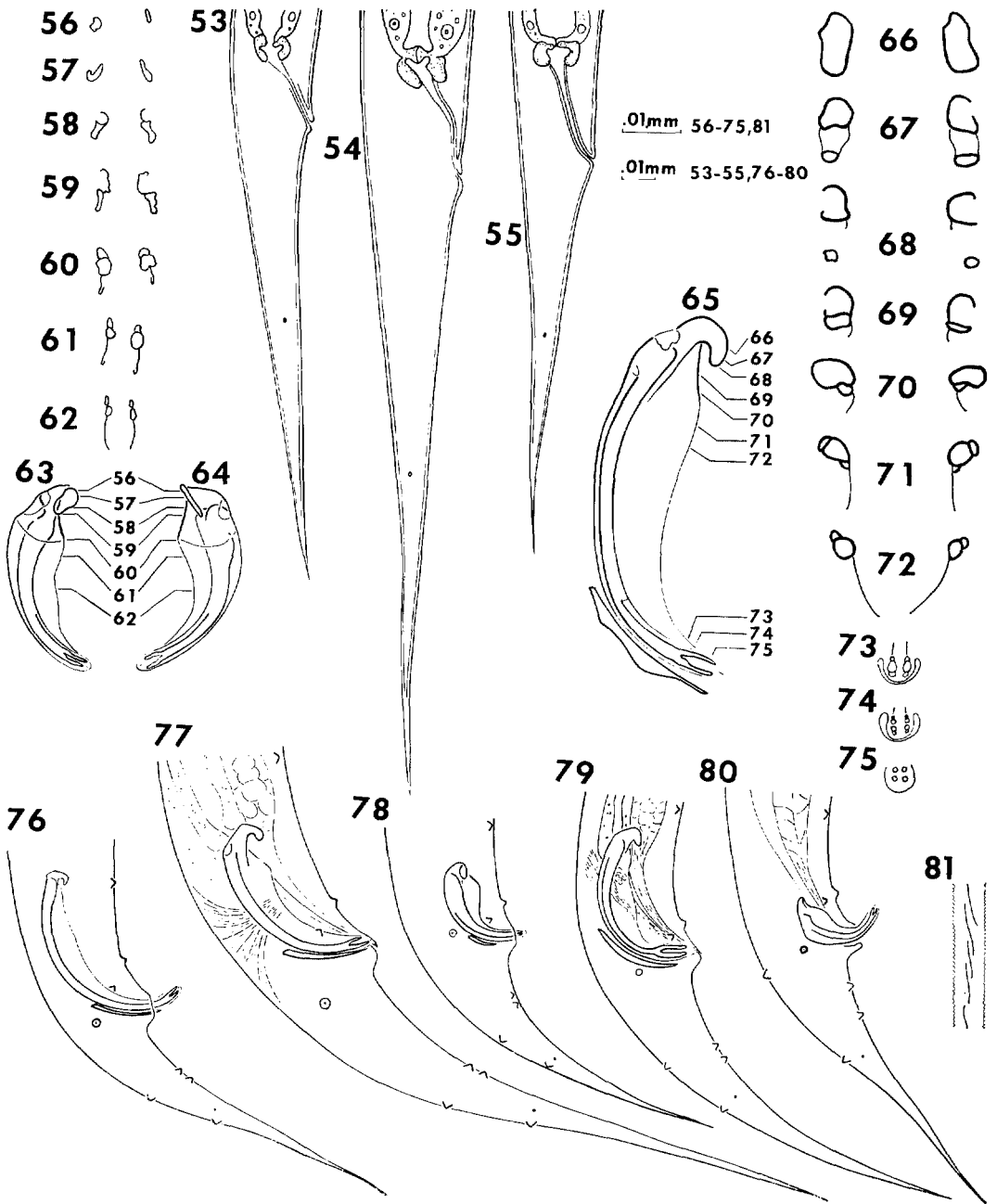


PLATE 2. Fig. 25-41. *P. redivivus* spicules: 25-30. Population C; 28, 29. Right and left spicule from same specimen; 31-35. Population A; 36-38. Population D; 39, 40. Population B; 41. Steiner's specimens (*P. leucocephalus* syntypes). Fig. 42. *P. redivivus* gubernaculum, lateral view; Fig. 43. *P. redivivus* gubernaculum, dorsoventral view; Fig. 44, 45. *P. dubius* spicules; Fig. 46-48. *P. redivivoides* spicules; 46. Lectotype; Fig. 49-51. *P. zymosiphilus* spicules; Fig. 52. *P. pycnus* spicule.

PLATE 3. Fig. 53-55. Female tails: 53. *P. pycnus*; 54. *P. redivivus*; 55. *P. redivivoides*; Fig. 56-62. *P. redivivoides*, cross sections through spicules corresponding to right and left spicules in Fig. 63, 64: 56, 57. Manubrium; 58. Manubrium and muscle insertion opening; 59. Shoulder; 60, 61, 62. Anterior shaft; Fig. 63. *P. redivivoides*, right spicule (small numbers indicate level of cross sec-



tions); Fig. 64. Left spicule, from same specimen as Fig. 63; Fig. 65. *P. redivivus* spicule, population B (small numbers indicate level of cross sections). Fig. 66-75. *P. redivivus*, cross sections through spicules and gubernaculum: 66-68. Manubrium; 69. Shoulder and muscle insertion opening; 70. Shoulder; 71, 72. Anterior shaft; 73-75. Bifurcation and gubernaculum. Fig. 76-80. Male tails: 76. *P. pycnus*; 77. *P. redivivus*; 78. *P. redivivoides*; 79. *P. dubius*; 80. *P. zymosiphilus*. Fig. 81. *P. redivivus*, lateral field.