The beer mat nematode, *Panagrellus redivivus*: A study of the connectedness of scientific discovery

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Summary.-The taxonomic lineage of the nematode currently known as *Panagrellus redivivus* can be traced, through numerous generic assignments and species synonymies, to the library paste nematode, *Chaos redivivum*, described by Linnaeus in 1767. In a synonymy that has survived several reviews, the beer mat nematode, described by de Man in 1913 and 1914, is now considered to be the same as the library- or sour-paste nematode. In the absence of preserved specimens of early material, and with the inadequacy of early descriptions of the organisms, the unifying thread for the taxonomic lineage is the nature of the environments in which the nematodes have been found, primarily fermenting pastes and beer-soaked fibres that might provide substrate for yeasts. Consequently, despite the precise rules that have evolved for documenting changes in a binomial, and our ability to track those changes through the literature, there must remain lingering uncertainty that *Chaos redivivum* and *Panagrellus redivivus* are the same nematode.

Key words: *Chaos redivivum*, *Panagrellus redivivus*.

Resumen.- El linaje taxonómico del nematodo hasta ahora conocido como *Panagrellus redivivus* puede ser rastreado, a lo largo de numerosas asignaciones genéricas y sinonimias específicas, hasta el nematodo de la pasta de encuadernar, *Chaos revidivivum*, descrito por Linneo in 1767. En una sinonimia que ha sobrevivido a varias revisiones, el nematodo del esterillo de la cerveza, descrito por de Man en 1913 y 1914, se considera ahora el mismo que el de la pasta de encuadernar o pasta agria. Ante la ausencia de ejemplares conservados del material original, y la insuficiencia de las primeras descripciones de los organismos, el hilo conductor para establecer el linaje taxonómico es la naturaleza de los ambientes en que los nematodos han sido encontrados, principalmente pastas de fermentación y fibras empapadas de cerveza que pudieran proveer un sustrato para levaduras. Por consiguiente, a pesar de las estrictas reglas que se han desarrollado para documentar cambios en un binomen, y nuestra capacidad para seguir la pista de dichos cambios en la literatura, debe quedar una permanente incertidumbre acerca de que *Chaos redivivum* y *Panagrellus redivivus* sean la misma especie.

Palabras clave: *Chaos redivivum*, *Panagrellus redivivus*.

Carl von Linné (Linnaeus) developed the binomial system of organism nomenclature. The rules for using binomials and establishing types for genera and species, and for dealing with names for which there were antecedents, evolved thereafter and still engender debate among biologists. Among the organisms to which binomial nomenclature was applied by von Linné in the 12th Edition of his *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*, appeared in 1767, were protists, nematodes, and fungi, all within the genus *Chaos*.

In describing the diversity and abundance of nematodes, Cobb (1914) referred to a unique species occurring in "the felt mats on which the Germans are accustomed to set their mugs of beer, and has been found in no other habitat". Cobb did not provide a name for the nematode or a reference to the source of the information. Later, Cobb (1921) reported that he had found the same nematode in rotting peaches and used its name at that time, *Anguillula silesiae*, with the specific epithet an apparent misspelling of *silusiae* (see later). He surmised that the nematode is favored by acetic conditions. Cobb's beer mat quote, or one like it, has appeared frequently in the literature since that time. At the present time, *Panagrellus redivivus* is commonly referred to as the 'beer mat nematode' (e.g., Williamson *et al.*, 1991; McPartland *et al.*, 2006).

Thirteen species of *Panagrellus* are currently recognized: *P. pycnus* Thorne, 1938, the type species, and *P. ceylonensis* Hechler, 1971b, *P. dorsobidentatus* (Rühm, 1956) Baker, 1962, *P. dubius* Sanwal, 1960, *P. filiformis* (Sukul, 1971) Andrássy, 1984, *P. japonicus* (Yokoo & Ota, 1961) Andrássy, 1984, *P. leperisini* Massey, 1974 (Andrássy, 2005), *P. ludwigi* (de Man, 1910) Goodey, 1945, *P. nepenthicola* (Menzel, 1922) Goodey, 1945; *P. redivivoides* (Goodey, 1943) Goodey, 1945, *P. redivivus* (Linnaeus,1767) Goodey, 1945, *P. silusioides* Tsalolikhin, 1965, and *P. ventrodentatus* (Heindl-Mengert, 1956)

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Baker, 1962. There is confusion in the literature regarding the authorship of *P. ventrodentatus* with description of its predecessor, *Anguillula ventrodentata*, variously ascribed to Weingartner, 1954 (Andrássy, 1984; Stock & Nadler, 2006), which seems to be an incorrect citation, and to Heindl-Mengert (1956) (Goodey, 1963; Andrássy, 2005). Also, the transfer of *Anguillula dorsibidentata* Ruhm, 1956 and *A. ventrodentata* Heindl-Mengert, 1956 to *Panagrellus* has been ascribed to Goodey (1963) (Andrássy, 1984, 2005; Stock & Nadler, 2006). However, an earlier authorship of the new combinations *P. dorsibidentatus* and *P. ventrodentatus* appears to be Baker (1962).

The taxonomic history of *Panagrellus redivivus* is complex, but interpretation is aided by the work of Stiles and Hassall (1905). In attempting to designate the correct type species of nematode taxa in which many taxonomic revisions have occurred, they invoked the principle of "Type by Absolute Tautonymy" (A tautonym is a taxonomic binomial in which the generic name and specific epithet are alike; it is used in zoology to designate a common or typical form). Using the example given by Stiles and Hassall (1905), if the genus *X-us*, 1890 without designated type has species *albus*, *niger* and *x-us*, the species *x-us* becomes type of the genus *X-us* by absolute tautonymy.

Panagrellus redivivus (Fig. 1) seems to have its origin in the nematode described as C*haos redivivum* by Linnaeus in 1767. The specific epithet is from the Latin word meaning resuscitate. The type designation of this species was painstakingly unraveled by Stiles and Hassall (1905) and further revisions have occurred thereafter, as follows:

1. Otto Friedrich Müller (1773) proposed the name *Vibrio anguillula* to include nematodes found "*in glutine farinoso at alibi vulgarissimum*", which translates to "in flour paste and also common elsewhere". Included among the nematodes described as *Vibrio anguillula* was C*haos redivivum* Linnaeus, 1767. Linnaeus had used that name to describe nematodes "*in aceto et glutine bibliopegorum*" (in vinegar and library – or book- paste). Hence the use of the species name *anguillula* by Müller in 1773 is a renaming of *redivivum* used by Linnaeus in 1767 and therefore is not justified. Accordingly, the correct name for the species (*Vibrio*) *anguillula* should have been (*Vibrio*) *redivivum*.

2. Göze (1774) considered the vinegar eelworm different from the 'Kleisterälchen' (paste eelworm) but did not provide names for the species. In fact, the vinegar eelworm appears in the literature before the species designations by Linnaeus and Müller. For example, Miles (1742) reported, in a letter to the Royal Society of London, on the mouth and movement of the "anguille in vinegar". Müller (1783) concurred with Göze that the vinegar and paste eelworms were different and separated *Vibrio* into four species:

a. *Vibrio fluvialis*.
b. *Vibrio aceti* – the vinegar eelworm.
c. *Vibrio glutinis* – the paste eelworm**,** which was a redesignation of *Vibrio anguillula* Müller, 1773, which, in turn, was the same as C*haos redivivum* Linnaeus, 1767.
d. *Vibrio marinus*.

3. According to Gmelin (1790) and Sherborn (1902), Müller (1786) in *Animalcula Infusoria* proposed the genus *Anguillula* with four species:

a. *Anguillula aceti* Müller, 1786 (derived chronologically from *Vibrio aceti* Müller, 1783, *Vibrio anguillula* Müller, 1773, and C*haos redivivum* Linnaeus, 1767).
b. *Anguillula fluviatilis* Müller, 1786 (derived from *Vibrio fluvialis* Müller, 1783).
c. *Anguillula glutinis* (Müller, 1783) Müller, 1786 (derived from *Vibrio glutinis* Müller 1783, *Vibrio anguillula* Müller, 1773, C*haos redivivum* Linnaeus, 1767).
d. *Anguillula marina* (Müller, 1783) Müller, 1786 (derived from *Vibrio marinus* Müller 1783).

So, the species name *Anguillula glutinis* Müller, 1786 is a synonym of *Vibrio anguillula* Müller, 1773 and by the principle of absolute tautonymy, *Anguillula anguillula* is the type species of the genus. However, the species *A. anguillula* is actually *A. redivivum* from the original C*haos redivivum* Linnaeus, 1767. Therefore, as documented by Stiles and Hassall (1905), the type species of *Anguillula* can be fixed from the papers of Müller and the correct name for the paste eelworm in 1786 should have been *Anguillula rediviva* and, as corrected in 1905, was designated *Anguillula rediviva* (Linnaeus, 1767) Stiles & Hassall, 1905.

Wheat paste (also known as potato paste, flour paste, rice paste, Marxist glue, or simply as paste) is a liquid adhesive used since ancient times for various arts and crafts such as book binding, decoupage, collage, and papier-mâché. It is also made for the purpose of adhering paper posters to walls and other surfaces. Closely resembling wallpaper paste, it is made by mixing roughly equal portions of flour and water (some argue for using more water or more flour), and heating it until it thickens. Clearly the paste could become a substrate for bacteria and yeasts that would provide food for nematodes.

4. Further taxonomic changes by Oken (1815), Bory (1824), Hemprich and Ehrenberg (1828), Ehrenberg (1838), Dujardin (1845) and Bastian (1865) confused the nematode name issue.

a. *Anguillula aceti* was transferred to *Gordius* by Oken (1815).
b. Bory (1824) listed *Vibrio anguillula* of Müller (1773) as four subspecies, apparently in disagreement with the changes by Müller (1786):
    i. *Vibrio anguillula aceti* (Müller, 1783) Bory, 1824.
    ii. *Vibrio anguillula fluviatilis* (Müller, 1786) Bory, 1824.
    iii. *Vibrio anguillula glutinis* (Müller, 1783) Bory, 1824.

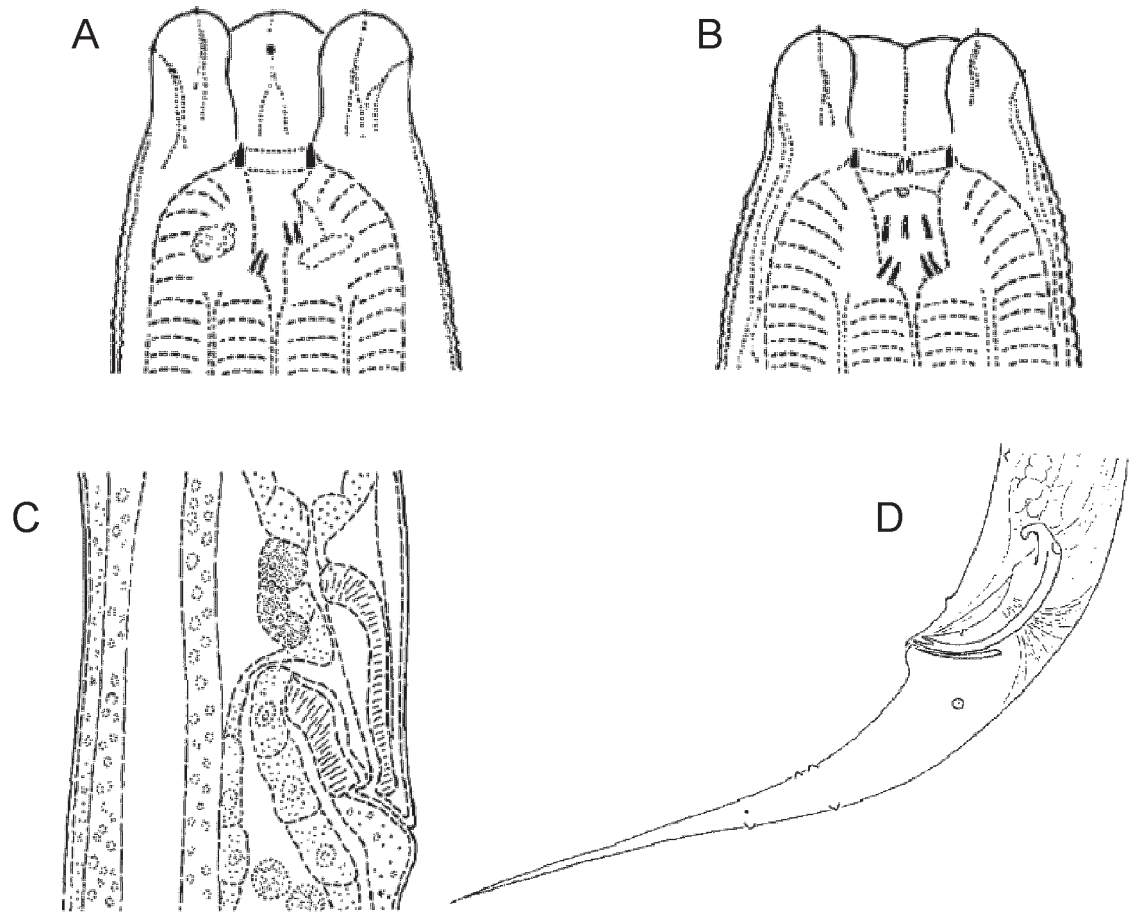

FIGURE. **1.** ***Panagrellus redivivus*** **(Linnaeus, 1967) Goodey, 1945**. A: Head, lateral view. B: Head, dorsoventral view. C: Female, vulva region. D: Male, tail. (Modified from Hechler, 1971a).

iv. *Vibrio anguillula marina* (Müller, 1783) Bory, 1824.

c. Hemprich and Ehrenberg (1828) proposed a new genus *Anguillula* containing the species:
   i. *Anguillula fluviatilis* (Müller, 1786) Hemprich & Ehrenberg, 1828 – derived from *Vibrio fluvialis* Müller, 1783.
   ii. *Anguillula inflexa* Hemprich & Ehrenberg, 1828.
   iii. *Anguillula coluber* (Müller, 1786) Hemprich & Ehrenberg, 1828 – derived from *Vibrio coluber* Müller, 1786.
   iv. *Anguillula recticauda* Hemprich & Ehrenberg, 1828.
   v. *Anguillula dongalana* Hemprich & Ehrenberg, 1828.

d. Ehrenberg (1838) added, among others, the following species to the genus *Anguillula*:
   i. *Anguillula aceti* Müller, 1786.
   ii. *Anguillula glutinis* (Müller, 1783) Müller, 1786 = *A. rediviva* (Linnaeus, 1767) Stiles & Hassall, 1905, the type species of the genus.

e. Dujardin (1845) proposed that the genus *Rhabditis* included *R. aceti* (= *Anguillula aceti* = *Vibrio aceti*) and *R. glutinis* (= *Anguillula rediviva*, type species of *Anguillula* Müller, 1786 which = *Vibrio glutinis* by the above taxonomic genealogy), *R. terricola* and *R. tritici*.

f. Diesing (1851) returned *Rhabditis aceti*, *R. glutinis* and *R. tritici* to the genus *Anguillula*.

g. Since the genus *Rhabditis* Dujardin, 1845 included *R. glutinis* (= *A. rediviva*), the type of an earlier genus, *R. glutinis* should have become the "type by inclusion" of *Rhabditis* (Stiles & Hassall, 1905) However, Bastian (1865) designated *Rhabditis terricola* as the type species of *Rhabditis*, which only partially solves the

problem of Diesing (1851) having returned *R. glutinis* to the genus *Anguillula* because he also moved *R. terricola* to the genus *Angiostomum*! Of the original species designated for *Rhabditis* by Dujardin (1845), Bastian (1865) retained only *R. terricola*.

h. Schneider (1866) placed the vinegar eel in the genus *Leptodera* as *L. aceti* (Müller, 1783) Schneider, 1866. In the same paper, he described another species, *Leptodera oxophila*, which was later synonymized with *A. aceti*. According to Minot (1876), as quoted by Stiles and Hassall (1905), "the true name of the vinegar eel is *Leptodera oxophila* but most authors still call them *Anguillula aceti*" and "the same worm apparently appears in fermenting starch paste, although the starch worm has received a different specific name, *L. glutinis*." The genus name *Leptodera* does not seem to have been generally accepted.

5. Dutch nematologist and carcinologist Johannes (Jan) de Man visited Germany quite frequently to confer with colleagues on matters of nematological interest. He described (de Man, 1910) the 'Schleimflussälchen' (*Anguillula ludwigi* de Man, 1910) in pulp from oak trees that he received from Professor Ludwig. Among the interests of Professor Ludwig was the flora and fauna of so-called damp beer mats which, at that time, were thicker than beer mats in use today and made from oak pulp. One of Ludwig's students, Carl Jahn, discovered nematodes in damp beer mats in the German town Schleusingen (translated as Silusia in Latin). De Man (1913, 1914) described the nematode discovered by Jahn as the "Bierfilzälchen or beer felt nematode**",** *Anguillula silusiae*, speculating that it originated from oak trees (Karssen, 2006; Gerrit Karrsen, personal communication).

6. In 1922, Goodey wrote of the eelworm of paper-hanger's paste and confirmed the usage *Anguillula rediviva* (Linnaeus 1767) Stiles & Hassall, 1905.

7. In 1927, Peters erected the genus *Turbatrix* and transferred *A. aceti* into the genus as the type species, *T. aceti* (Müller, 1783) Peters, 1927, and *A. rediviva* as *Turbatrix rediviva* (Linnaeus, 1767) Peters, 1927.

8. Thorne (1938) described *Panagrellus pycnus* from slime exuding from a cottonwood tree, *Populus sargentii* Dode in Utah. The genus name is a diminutive of *Panagrolaimus* in recognition of the panagrolaimoid pharynx and the species name from the Greek meaning "thick".

9. In 1943, Goodey erected the genus *Turbator* to share the subfamily Turbatricinae of the Cephalobidae with *Turbatrix*. He designated *Turbator redivivus* (Linnaeus, 1767) Goodey, 1943 the type species of the genus (descended from *Chaos redivivum* Linnaeus, 1767, *Vibrio anguillula* Müller, 1773, *Vibrio glutinis* Müller, 1783, *Anguillula glutinis*, Müller, 1786, *Anguillula rediviva* (Linnaeus, 1767) Stiles & Hassall, 1905, and *Turbatrix rediviva* (Linnaeus, 1767) Peters, 1927).

10. Goodey (1943) transferred *Anguillula silusiae* de Man, 1913 to *Turbator silusiae* (de Man, 1913) Goodey, 1943. He described the nematode as being from "so-called beer felts in Germany and Alsace". At the sane time, he transferred four other species to *Turbator*, including *P. pycnus* Thorne, 1938 and described an additional species. Later, after correspondence with Thorne, Goodey (1945) conceded that the name *Turbator* was invalid as it was predated by *Panagrellus* Thorne, 1938. The species *P. pycnus* Thorne, 1938 had the same genus characteristics of the seven species that Goodey had assigned to *Turbator* Hence, the valid name of the nematode by then designated the "sour paste eelworm" became *Panagrellus redivivus* (Linnaeus, 1767) Goodey, 1945.

11. At the same time, Goodey (1945) created a new combination, *Panagrellus silusiae* (de Man, 1913) Goodey, 1945 which he described as being from "so-called beer felts in Germany and France".

12. Rühm (1956), in describing nematodes associated with bark beetles (*Ips*), proposed the synonymy of *P. pycnus* Thorne, 1938, *P. leucocephalus* (Steiner, 1936) Goodey 1945, *P. silusiae* (de Man, 1913) Goodey, 1945 and *Panagrellus redivivus* (Linnaeus, 1767) Goodey, 1945 as a redescribed *Anguillula rediviva*. However, Sanwal (1960) rejected the synonymy and pointed out that the description of *A. rediviva* by Rühm differed from that of *P. redivivus* by Goodey with regard to tooth-like processes in the buccal cavity and the morphology of the spicules and gubernaculum.

13. Hechler (1971a,b) noted that among the few morphological features available to separate species of *Panagrellus* are the size and shape of the spicules and the structure of the vulva and stoma. She made detailed measurements of spicules and stoma and commented that variations in body size of the nematodes appeared to be associated with nutritional status. She concurred with the synonymies proposed by Rühm (1956) and listed the following synonyms of *Panagrellus redivivus* (Linnaeus, 1767) Goodey, 1945:

Chaos redivivum Linnaeus, 1767.
Vibrio anguillula Müller, 1773.
Vibrio glutinis MüIler, 1783.
Anguillula rediviva (Linnaeus, 1767) Stiles & Hassall, 1905.
Turbatrix rediviva (Linnaeus, 1767) Peters, 1927.
Turbator redivivus (Linnaeus, 1767) Goodey, 1945.
Gordius glutinis Oken, 1815.
Rhabditis glutinis Dujardin, 1845.
Leptodera oxophila Schneider, 1866 (in part).

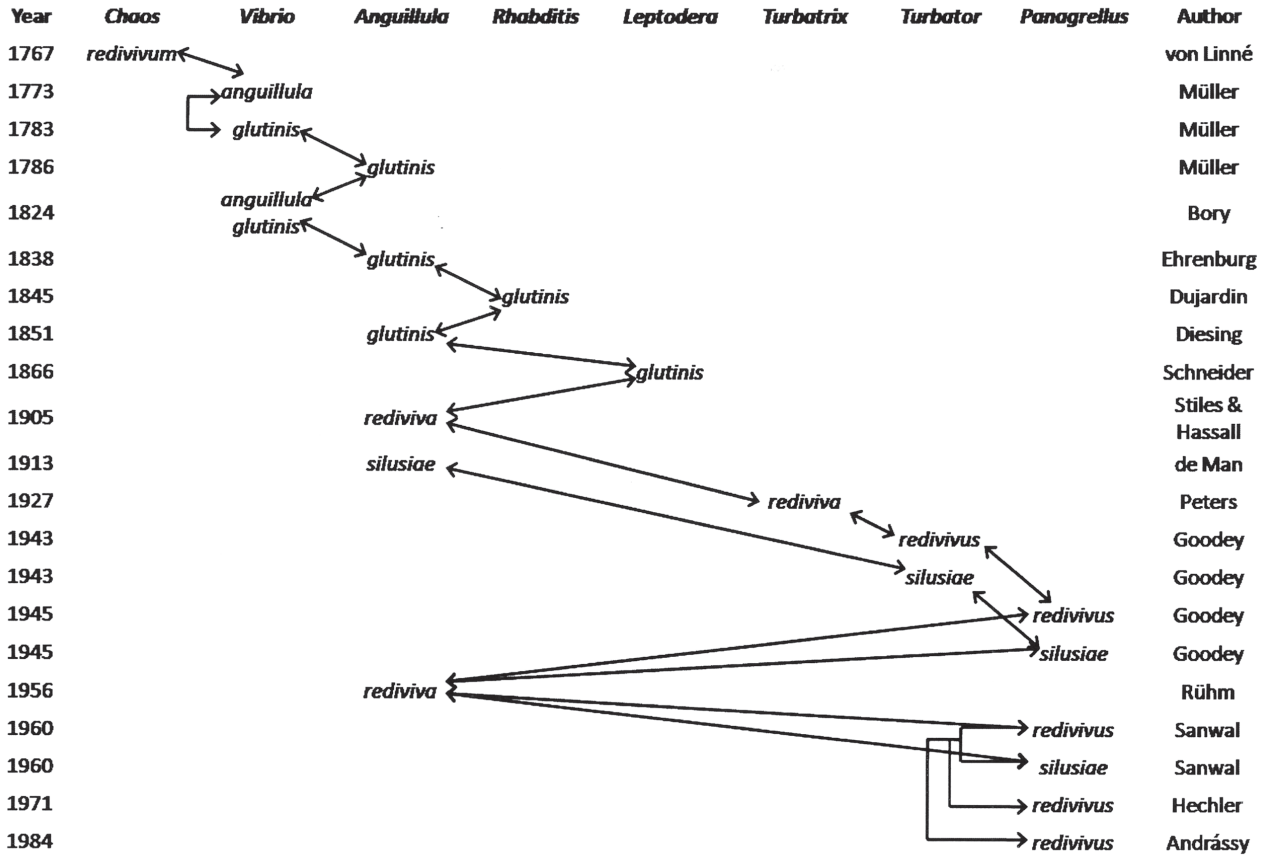

Figure **2**. Genealogical schematic for *Panagrellus redivivus* (Linnaeus, 1967) Goodey, 1945.

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.

In her list, Hechler (1971a) consistently used "glutinus" rather than "glutinis" but I can find no justification for that in her paper or in earlier literature. I assume that the usage was in error.

In 1984, Andrássy accepted and enumerated the synonyms of *Panagrellus redivivus* (Linnaeus, 1967) Goodey, 1945 including *Panagrellus silusiae* (de Man, 1913) Goodey, 1945 among them.

The various habitats described for species of *Panagrellus* (beer mats, insect frass, slime from tree wounds, wheat paste) are all consistent with reports of their association with various species of yeast (Kerrigan *et al.*, 2001, 2003, 2004; Smith *et al.*, 1992). The characteristics of the stoma, approximately 6 µm diameter and 16 µm long from drawings and data of Hechler (1971a), with three dorsal teeth and two pairs of subventral teeth, are consistent with ingestion of yeast cells. *Panagrellus redivivus* is cultured as food for newly-hatched fish and crustaceans. The culture media include oatmeal and bread, usually with inclusion of a small quantity of yeast (Schlechtriem *et al.*, 2004).

In conclusion, *Panagrellus redivivus*, traceable back to *Chaos redivivum* Linnaeus, 1767, is currently correctly recognized as the beer mat nematode! However, the genealogy (Fig. 2) may not yet be complete since cross-hybridization studies among four isolates of *P. redivivus* did not all produce viable offspring and phylogenetic analysis of rDNA suggested that the isolates did not

represent a single species (Stock & Nadler, 2006). While I have traced, hopefully with accuracy, the evolution of the *Panagrellus redivivus* binomial from *Chaos redivivum*, the original description by Linnaeus (1767) was minimal and there are no preserved type specimens from that era. The unifying thread is that nematodes have been described from various pastes over the last 2.5 centuries. Might these have included other species of *Panagrellus* or even related genera?

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