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[ESSAY]

Gilbert Rahm and the Status of Mesotardigrada Rahm, 1937

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The tardigrade class Mesotardigrada was erected on the basis of the description of *Thermozodium esakii* by Gilbert Rahm in 1937. In some characteristics, *T. esakii* is intermediate between members of the classes Eutardigrada and Heterotardigrada. The class Mesotardigrada is known only from Rahm's published drawings of *T. esakii*; no voucher specimens are known, and subsequent attempts to collect it at the *locus typicus* have been unsuccessful. Among the possible explanations for this situation are that Rahm may have collected specimens of a more typical tardigrade, but misinterpreted what he saw. Alternatively, changes in habitat in the area may have led to the tardigrade's extirpation. Perhaps *T. esakii* is a rare species, such that recent sampling efforts have been insufficient to rediscover it. Finally, Rahm's 1937 description may be an attempt at deception. Until physical evidence of *T. esakii* is found, the species, and by extension the class Mesotardigrada, should be considered *nomen dubium*.

Key words: hot spring, Mesotardigrada, *Thermozodium*, *nomen dubium*, Tardigrada

In 1937 Gilbert Rahm (Fig. 1), an invertebrate biologist and monk of the Order of Saint Benedict, finished his term as a visiting scholar in Fu-Jen University, Peking (Rahm, 1937a), and travelled through Japan, including Unzen (Rahm, 1937c, d), Kobe (Rahm, 1937b), Tokyo (Rahm, 1937c, d), and Sapporo (Zoological Society of Japan, 1938). Among his research interests were the meiofauna—particularly nematodes—of hot springs, an area of active investigation in Japan around this time (Okada, 1936). From Japan, Rahm simultaneously published two papers on hot-spring meiofauna. In these he described Mesotardigrada, a new order (now a class) within the phylum Tardigrada (Rahm, 1937c, d). He erected this taxon on the basis of his observations of a single new species, *Thermozodium esakii* Rahm, 1937, which he reported finding in the runoff from hot water springs in Unzen National Park (now Unzen-Amakusa National Park), Kyushu.

This new class is, in many characteristics, intermediate between the orders (now classes) Heterotardigrada and Eutardigrada. For instance Rahm reported *T. esakii* having cirri but no clava, with Heterotardigrada-like spines and claws, but Eutardigrada-like macroplacoids (Fig. 2, Table 1) (Rahm, 1937c, d). Its Eutardigrada-like features similarly include a mix of traits from the orders Apochela (i.e. peribuccal papillae) and Parachela (other features of the buccal apparatus). There is no indication that Rahm kept specimens of *T. esakii*, so only Rahm's original descriptions and drawings are available in support of this species. As no

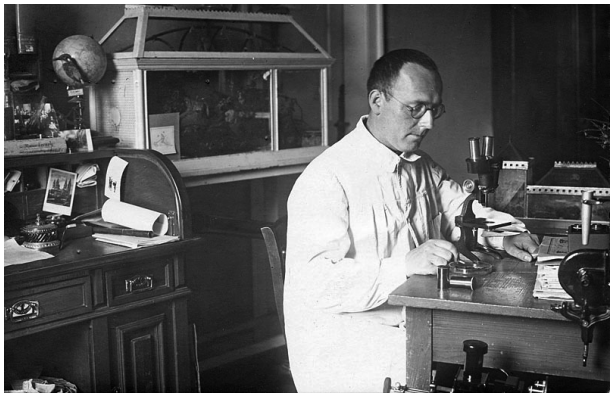

Fig. 1. Rahm, ca. 1930 (Mena, 2016, used with permission).

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other researchers have reported finding *Thermozodium*-like tardigrades anywhere in the world, these two simultaneous papers by Rahm remain the only reports for this species and this monotypic class.

This combination of circumstances has led to a decades-long debate over the tardigrade that Rahm actually found, if any. Some believe the species, and hence the class, is dubious (e.g., Noda, 1997; Nelson, 2002), or part of a hoax by Rahm (Noda, 1997), perhaps to discredit a research rival or boost his own standing among tardigrade biologists. We lament the lack of specimens, but look for other explanations for the lack of substantiating evidence. Unfortunately much of the debate results from incorrect or incomplete information, or lack of knowledge of Rahm's movements and dealings. Additionally, taxonomic investigation in the 1930s was not always rigorous in its standards of documentation.

Rahm (1937c, d) wrote a believably detailed description, and one that would have been possible using microscopes available in the 1930s. His description matches what would be expected from a "middle" class tardigrade. However the complete lack of specimens and documentation to support the published description, and the possibility that habitat at the type locality has changed, leads most to believe that the rediscovery of this class is unlikely; thus *T. esakii* remains an ongoing source of speculation.

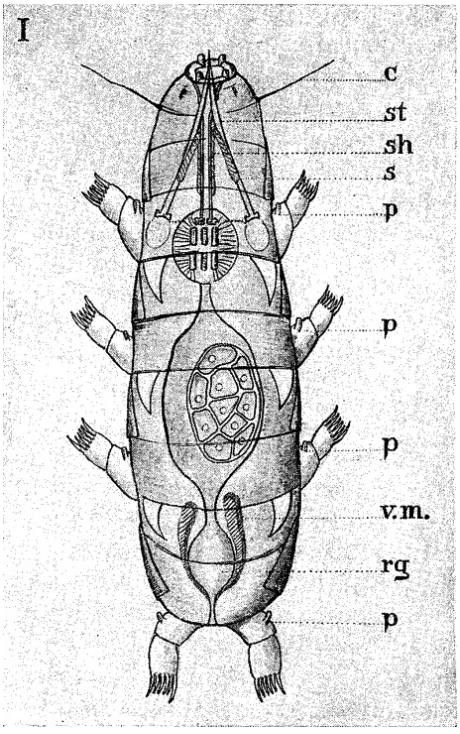

Fig. 2. Original *Thermozodium esakii* illustration from Rahm 1937c. c = cirrus lateralis, st = stylet, sh = sheathholder, s = sheath of the stylets, p = papillae, v.m. = vassa Malpighii, rg = rectal gland (Rahm 1937c, used with permission).

Apparent lack of specimens

Under the International Code of Zoological Nomenclature, since 1999 it is established practice to document the deposition of type specimens in the published description of new animal species (ICZN, 1999, art.16.4.2). Rahm (1937c, d) did not do that. However, this is consistent with Rahm's other descriptions of new animal species, where he did not mention deposition of specimens (e.g., Rahm, 1932, 1936a, b). Rahm must certainly have been aware of the importance of documenting the deposition of types, and he did specifically describe the deposition of moss specimens at herbariums (Rahm, 1937c). We note that this lapse is not unusual for reports of the time, when many authorities failed to document the deposition of type material (examples: de Barros, 1939; Bartoš, 1938; Marcus, 1930; Mathews, 1937; Mihelčič, 1938; but counterexamples: Iharos, 1936; Schulz, 1935).

It is possible that the lack of *T. esakii* specimens is a consequence of Rahm's ongoing travels; he worked in Europe, Japan, China, India, Palestine (Rahm, 1936b), Chile, Brazil, and the USA for extended periods (von Severus, 1990). During each of those stays he resided at abbeys and served as a visiting scholar at Catholic universities. Given his itinerant lifestyle, Rahm may have left his voucher specimens at hosting abbeys, or in local university collections. These specimens may have eventually degraded, or may have been disposed of many years after Rahm had moved on.

Rahm died in 1954 after spending his final years in Newark Abbey in New Jersey, USA. On our behalf, Augus-

Table 1. Some characteristics of the Tardigrada classes (Rahm 1937c, d).

Character	Heterotardigrada	Eutardigrada	Mesotardigrada
Cirrus A	present	absent	present
Clavae	generally present	absent	absent
Lateral spines	variable	absent	3 pairs of short, broad spines
Peribuccal papillae	absent	only in order Apochela	present
Macroplacoids	absent	generally present	present
Microplacoids	absent	variable	absent
Claws	equal, number variable	two per leg, occasionally reduced/absent	outermost and innermost distinctly longer. 6–10 claws per leg
Claw branches	separate	primary & secondary branches joined (except *Milnesium* spp.)	separate
Leg papillae	variable	absent	present on all legs
Eye color, where present	most red, few black	black	black
vasa malpighii	absent	present	present

tine Curley, the archivist at that abbey, searched unsuccessfully for journals, papers, microscope slides, and scientific equipment that belonged to Rahm. The archivist suggested, however, that since Rahm was only a visiting monk, it is more likely that his effects would have been sent to his home abbey.

At our request, Dr. Hartmut Grevin contacted Rahm's home abbey, the Abbey of Maria Laach. A search of their archives turned up some biographical information, but no natural history artifacts, manuscripts, or relevant field note books.

Rahm named *T. esakii* after Professor Dr. Esaki of Kyushu Imperial University (now Kyushu University) in Japan. He also acknowledged the assistance of Professor Dr. N. Yatsu of Tokyo Imperial University (now The University of Tokyo). Inquiries and searches by ACS, HK, and others at these institutions, including Dr. Kunieda of The University of Tokyo, have not located any material deposited by Rahm in the collections of either university.

Rahm (1937c, d) thanked the R. Fth. J. Schmerbach O.S.B., then in Tonogaoka Shudoin near Chigasaki, Kanagawa prefecture, for assistance with the published drawings of *T. esakii*. This suggests that one other person may have seen Rahm's Mesotardigrada specimens. However, it is also possible that Schmerbach prepared final drawings based on Rahm's first drafts or on his written descriptions. No record of such reference specimens has been found, nor has any mention by Schmerbach of *T. esakii*.

Lack of reliability

Those who doubt the veracity of *T. esakii* have suggested that Rahm was primarily a nematologist who only occasionally dabbled in tardigrades, and have pointed out that some of his taxonomic work has been declared invalid (Noda, 1997; Dastych et al., 1998). Some of this doubt comes from oft-repeated incorrect information. In terms of his commitment to the study of tardigrades, for much of his early research career (mid to late 1920s), Rahm was very active in this discipline, writing a textbook chapter on tardigrades (Rahm, 1927) and publishing extensively on cryptobiosis in the group (Rahm, 1925). He later completed additional tardigrade surveys (Rahm, 1932, 1936a, b). It was only later in his career, while living in South America, and then the United States, that Rahm's research focused narrowly on nematodes. At that time research grants supported Rahm's studies of the economic impact of nematodes on agriculture.

As with Rahm, the taxonomic work of many early tardigrade specialists has been subsequently re-examined, using better microscopes and with the benefit of a more thorough understanding of the group. These re-examinations have resulted in substantial taxonomic revision. Revision is not unique to Rahm, and does not imply that his research was substandard. Furthermore, Rahm's (1921) pioneering work on animal cryptobiosis is still highly regarded and frequently cited, indicating his abilities as a research biologist.

It is, however, noteworthy that Rahm's identification of tardigrades of genus *Oreella*, arguably the most similar genus in general appearance to *T. esakii* (but compare *Carphania fluviatilis* Binda, 1978), are all regarded as "extremely" or "very dubious" (Ramazzotti and Maucci, 1983; Binda and Kristensen, 1986) or *nomen dubium* (Dastych et al., 1998). Again, this confusion is not unique to Rahm (Dastych et al., 1998), but it does support the suggestion that Rahm may have over-interpreted aberrant heterotardigrades as novel species, or misinterpreted observed characteristics or preparation artifacts (Dastych et al., 1998; Suzuki, 2016). Without corroboration, it is plausible that *T. esakii* may not be as Rahm described it, and may represent a misinterpretation of a species within one of the two established classes of Tardigrada, such as the Heterotardigrada genus *Carphania* or *Oreella*.

By highlighting a particular case where he has drawn only what could be observed, where the anatomic status of certain elements was unclear in previous work, Rahm (1937d) implies that some of his illustrations may include features not directly observed but rather assumed. Noda (1997) and Dastych et al. (1998) voiced their suspicion that Rahm may have partly based his illustrations on existing drawings of related species. If correct, this would argue against an over-reliance on Rahm's figures, without corroboration, in support of his identification of *T. esakii*. However, his care in observation is supported by illustrations of *Milnesium tardigradum trispinosa*, which show fine details present in some *M. tardigradum* specimens, and not seen in earlier illustrations by other authors (Suzuki, 2016). In that case, Rahm's illustrations clearly show what is, in fact, a subtle preparation artifact. For this reason, while *M. tardigradum trispinosa* should no longer be considered a valid taxon, and Rahm may be criticized for over-interpreting a small detail in support of the declaration of a new subspecies, at the same time this demonstrates the care and originality possible in Rahm's observations and illustrations.

Possibility of attempted deception

Was the description of *T. esakii* a deception, intended to increase Rahm's stature among Far East tardigradologists, as proposed by Noda (1997)? G.B. Mathews and Rahm were both visiting professors at Fu-Jen University in the winter of 1936–1937, and knew each other. In the same papers in which he described *T. esakii*, Rahm (1937c, d) criticized the work of Mathews, and particularly his publications concerning the tardigrades of Japan. Rahm claimed that Mathews repeatedly ignored information from him, presented wildly unlikely sampling prowess, and consistently misidentified tardigrade samples. The tone and sharpness of his statements might suggest a strong concern for professional reputation, or even a personal vendetta against Mathews.

The idea that Rahm fabricated *T. esakii* to increase his own professional standing seems improbable. His publications concerning tardigrades and other meiofauna before 1937 were considerable, and it is not clear how he might have accrued benefit from the two Mesotardigrada papers. Additionally, as noted above, Rahm thanked Schmerbach, a monk of the Arch abbey of St. Martin, Beuron, for assistance in drawing the figures for his *T. esakii* paper; this involvement of a colleague in a deception appears to add unnecessary risk, both professionally and within Rahm's religious order.

Failure of subsequent searches to find mesotardigrades

Rahm (1937c, d) did not unequivocally specify the locality from which he collected *T. esakii*. He wrote: "The temperature was found to be 39.8°C to 41.7°C...[t]he animalcules are living in the algae in the little overflowing stream of the hot spring, where the minerals have produced some incrustations...[t]he 'Enryakuyu' which is not very far from the point where we collected the algae, is a acid hydrogen sulphide vitriol spring" (Rahm, 1937c); Rahm also reported that the spring was at 65°C according to a Japanese Government Railways guide-book he used.

Attempts to study *T. esakii* are further complicated by the study area's proximity to an active volcano. It has been suggested that the area, including the spring sampled by Rahm, has been altered or destroyed since 1937 by earthquakes (Ramazzotti and Maucci, 1983; Nelson, 2002). However, we have found no evidence of such destruction of the site described by Rahm (1937c, d).

Fugendake volcano has been intermittently active, and erupted in 1663, 1792, and 1990–1995 (Hoshizumi et al., 1999). Pyroclastic flows and block-and-ash flows generated from the most recent eruption descended the northeastern to the southeastern slopes of the volcano (Ui et al., 1999; Fujii and Nakada, 1999), not affecting the area around the *locus typicus* located in the southwest of the volcano. Two notable earthquake swarms were recorded around Unzen since 1937, in 1968–1974 and 1984–1991, but these were of relatively low magnitudes (Umakoshi et al., 2001), and associated above-ground destruction was not recorded (Japan Meteorological Agency, 2016).

While the geologic activity in the Shimabara area has apparently not destroyed the aboveground locality, it may have altered the underground flow of spring water (Tabata, 1961), perhaps altering the ecology of Rahm's original sampling site. The source of hot spring water in the Unzen region is groundwater in the upstream region, believed to move down through two main streams, Furu-yu and Shin-yu, with possible multiple secondary streams joining to these (Tabata, 1961). Even if the small spring-overflow stream sampled by Rahm has changed in terms of spring flow or local habitat, other nearby springs were undoubtedly connected to these same underground water sources (Tabata, 1961; Noda, 1997); it is possible that *T. esakii* existed in these. It may also be that the tardigrades collected by Rahm came not from the hot spring he described, but from elsewhere in the environment, and were found by Rahm in that particular location by happenstance.

Although it has been reported that researchers tried without success to recover *T. esakii* from the Unzen area (Noda, 1997), the only published account of such an attempt is a footnote in Morikawa (1967). This reference does not provide sufficient detail about which areas were searched, nor how extensively. Morikawa (1967) described artificial modification of the type locality, and explained that his research could thus not confirm the presence of *T. esakii*. However, it is unclear whether any sampling was carried out in Unzen by Morikawa, or whether his effort was abandoned because of the modifications observed. The spring referred to by Rahm was incorporated into a public bath site in 1653, and so at least some of the modifications occurred before Rahm's visit (Yamaguchi, 1982).

The Unzen hot springs are located in the special zone of Unzen-Amakusa National Park. As such, meiobenthic sampling in the area requires permits from three government agencies. There remain no records of official collecting permits being issued for Unzen-Amakusa National Park for tardigrades. It is possible that Morikawa obtained permits for sampling in the mid-1960s but if so, the records would have been discarded after the preservation period of thirty years; there remains no record of this or any subsequent application for permission to sample the hot springs for tardigrades prior to our application in 2012 (see below). Thus, the nature of any attempts to "rediscover" *T. esakii* before that date are largely unknown, despite the common assumption that repeated efforts had been made, unsuccessfully. Although not specifically searching for *T. esakii*, Okada and Ito (1938) did sample thermal waters in the Unzen area up to 68.0°C, and found shore flies (*Scatella* sp.) and chironomids (*Chironomus thummi*) at temperatures in the 32°C–34.4°C range, but no tardigrades.

In an effort to relocate *T. esakii*, and to provide a formal account of the methods used in searching for this species, we spent three days at Unzen National Park, exactly 75 years after Rahm's original work "in the end of May" 1937 (Rahm, 1937c). Additional sampling was carried out the following year by ACS and HK (see Suzuki et al., in this volume). The cluster of hot springs in Unzen, including the now-almost-inactive Enryaku-yu, is still an active resort with multiple active springs. We found water temperatures in the range reported by Rahm (1937c) in run-off from multiple springs, and pH measurements in these samples are comparable to what would be expected from a spring conforming to the chemical analysis reported by Rahm (1937c, d). Although Rahm (1937c) reported finding tardigrades among nematodes, and the present study recovered numerous nematodes from environments similar to those described by Rahm (Suzuki et al., this volume), no tardigrades of any species were collected in 2012 or 2013.

We consider three possible explanations for the failure of subsequent searches to find mesotardigrades. First, Rahm may have collected *T. esakii* in the circumstances that he described in his 1937 publications, but the species is no longer found at the *locus typicus*. Rahm implied that he found mesotardigrades in only one sample site, which could reflect either an extremely limited distribution of the species, or limited resources for sampling at the time. If the former is correct, then *T. esakii* may have been vulnerable to environmental change. Substantial changes to the habitat since Rahm's investigation might have destroyed all suitable habitat for this species. In particular, the most likely hot spring matching Rahm's description has suffered greatly reduced flow. Similar habitat remains in the locality, with likely connection to the same underground water sources, but no tardigrades have been collected from any of these sites. Tardigrade distribution does often appear very patchy, and other species have resisted rediscovery efforts after their first, solitary report (*e.g. C. fluviatilis*, O. Lisi, personal communication), even in their *locus typicus* and by their original discoverers as experienced by CJ (*Oreella chugachii*).

Secondly, the creatures collected by Rahm may remain at the original location, but subsequent searches failed to recover them. Rahm implied that he collected at least eight

specimens and one discarded cuticle, but did not indicate how comprehensive his sampling effort was (Rahm, 1937d, e). It is, therefore, not possible to know their abundance. If *T. esakii* is extremely rare, then it is possible that Rahm was fortunate in finding it, and that subsequent researchers have been less fortunate. Rahm may have reported the *locus typicus* incorrectly, such that later collecting efforts were in the wrong locations; his description included at least some errors, such as using names applied to large areas when referring to specific hot springs. Further, it is possible that the specimens collected by Rahm were not normal inhabitants of hot-spring runoff, but had been transported into that habitat by unknown circumstances. Only Rahm has ever claimed to have observed any sort of tardigrade from hot-spring runoff at the temperatures and acidity he described, although there were previous reports of *Macrobiotus* sp. in hot-springs runoff at 32–37°C (Ciofalo, 1927), and again of *Macrobiotus* sp., and later of *Macrobiotus intermedius*, in hot springs at 36–38°C and pH 6.7–7.4 (Okada et al., 1938; Uyemura, 1938). However, sampling efforts in 2012 and 2013 were extensive, focusing on the type of habitat described by Rahm, including all of the accessible hot springs near Rahm's presumed sites (see Suzuki et al., in this volume).

Finally, it is possible that mesotardigrades, as described by Rahm, do not exist. Perhaps Rahm intended to deceive others with his description of *T. esakii*, an animal for which no physical evidence has been found. There is, however, no obvious motivation for such a fabrication. In that case, Rahm may have misinterpreted samples collected in Unzen. Even though he made errors in his description and interpretation of similar tardigrade species, Rahm was experienced in collecting and interpreting meiofauna. If Rahm erred in his description of *T. esakii* based on observation of another, more typical tardigrade, this still suggests that some tardigrade was present in this unusual environment, which is a noteworthy finding.

The tardigrade described by Rahm (1937c, d) has an odd combination of characteristics not typically found together (Table 1). In using the word "Mesotardigrada," Rahm clearly recognized the intermediate nature of its characteristics between those of Heterotardigada and Eutardigrada. If legitimate, Rahm's report of *T. esakii* is all the more noteworthy, and with considerable significance for studies of the phylogeny of this phylum. Other unusual characteristics of *T. esakii* include a unique pattern of dorsal spines (Noda, 1997), nearly-identical papillae on all four pairs of legs, and basal spines on all claws, a feature noted in Rahm's description, but not in the accompanying illustrations. Noda (1997) noted that the illustrations in Rahm (1937c, d) show apparently bending leg-joints, which would be a unique feature among tardigrades.

Conclusion

Rahm's (1937c, d) reports of *T. esakii*, if legitimate, describe an extraordinary member of an ever-surprising group of animals. The hot-spring habitat described by Rahm is extreme, both in terms of temperature and pH. Regrettably, no one corroborated *T. esakii* at the time, no voucher specimens have been found, and subsequent attempts to find the species at the type locality have failed. Although further searches of hot-springs habitat for tardigrades may prove rewarding, the taxonomic status of *nomen dubium* should apply to *T. esakii*, and so to the class Mesotardigrada.

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COMPETING INTERESTS

The authors have no competing interests to declare.

AUTHOR CONTRIBUTIONS

GG, CJ, GC, and ACS conducted historical research. HK and ACS performed most translations, GTG did minor translation work. GTG wrote the paper, with major contributions by CJ, GC, ACS, and significant contributions by HK and MT. All authors discussed and contributed to interpretations and conclusions. All authors read and approved the final manuscript.

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