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A redefinition of the genus *Monhystrella* Cobb (Nematoda, Monhysteridae) with keys to the species

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The genus *Monhystrella* Cobb, 1918 is redefined and an up-to-date list of its species is given. Illustrated keys to both females and males of the species are provided, including the description of the most important characteristics for each species.

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Introduction

Cobb (1918) erected *Monhystrella* as a subgenus without indicating to which genus it belongs. He described *Monhystrella plectoides* as the type species and included *Monhystera bulbifera* de Man, 1880 in his subgenus. Steiner (1920) assigned *Monhystrella* to the genus *Monhystera* Bastian, 1865. *Monohystrella* as used by Micoletzky (1922) and subsequent authors is an invalid emendation. Micoletzky (1922) included *Monhystrella* within the genus *Terschellingia* de Man, 1880 because of the presence of a prominent pharyngeal bulb and four cervical setae in *Monhystera bulbifera*. This assignment is rejected because of the presence of only one ovary in *Monhystrella* but two ovaries in *Terschellingia*. In 1934 Filipjev raised *Monhystrella* to the genus level. Revisions of the genus *Monhystrella* have been conducted by Andrássy (1968, 1981), Gerlach & Riemann (1971, 1973–1974) and Timm (1964). In the present paper an up-to-date list of the *Monhystrella* species based on a re-evaluation of the most important characteristics is presented.

Within the Monhysteridae the species of the genus *Monhystrella* are characterised by a high temperature dependency (e.g. Heip *et al.* 1985: *M. parelegantula*), the capacity to withstand high osmotic stress conditions and the occurrence of parthenogenetic species in saline inland waters, which are in accordance with the geographical distribution of the genus.

Abbreviations used in the text (measurements in μm)

a	body length divided by greatest body width (♂) or by body width at the vulva (♀)
a.f.b.l.	distance between anterior body end and anterior margin of fovea apertures, measured along the central body axis
an.b.w.	anal body width
b	body length divided by pharynx length
c	body length divided by tail length
c.b.w.	body width at the pharyngo-cardial junction
Cl.	distance of cloaca from anterior body end as a percentage of body length
f.b.w.	body width at centres of foveae
f.d.	outer fovea aperture diameter measured parallel with body axis
G	distance between ovarium tip and vulva as percentage of body length
h.d.	head diameter = body width at cephalic setae measured perpendicular to central body axis
L	body length measured along central body axis
l.sp.l.	left spicule length measured along the arc
n.r.	distance between anterior body end and nerve ring as percentage of pharynx length
r.sp.l.	right spicule length measured along the arc
sp.l.	spicule length measured along the arc
T	distance between testis tip and cloacal orifice as percentage of body length
t.l.	tail length
V	distance of the vulva from the anterior body end as percentage of body length

Subclass Chromadoria Pearse, 1942
Order Monhysterida Filipjev, 1929
Suborder Monhysterina Filipjev, 1929
Superfamily Monhysteroidea de Man, 1876
Family Monhysteridae de Man, 1876
Subfamily Monhysterinae de Man, 1876

Monhystrella Cobb, 1918

Redefinition

The genus *Monhystrella* Cobb, 1918 may be redefined as follows.

Small nematodes, usually not longer than 0.5 mm, exceptionally reaching 0.77 mm. Cuticle finely striated, annulae smaller than 0.25 μm, generally bearing somatic setae. Six inner labial sensillae always papilliform; six outer labial sensillae unjointed, usually setiform but sometimes papilliform; four cephalic, unjointed setae always present. Setiform sensillae mostly arranged in one circle. Ocelli with red pigment sometimes present. Amphideal fovea cryptospiral, anterior margin of fovea aperture at least equal to, but usually two or more times, the head diameter behind the anterior body end. Cheilo-

stome small, tubiform, funnel-shaped or conoid; often well cuticularised. Stoma narrow; sometimes tube-like but mostly funnel-shaped. Prostome only exceptionally not surrounded by muscular pharyngeal tissue. Buccal ring present. A tooth-like protrusion sometimes present at the base of the stoma (second dental type according to Lorenzen 1978). Radial tubuli present in pharynx. Posterior part of pharynx generally swollen, sometimes weakly divided into two bulbs; without valvular apparatus, but sometimes with valvuloid muscular tissue surrounding the pharyngeal lumen at the bulbus centre. Ventral gland, when present, situated on the right or subventrally on the right side of the anterior part of the intestine. Progaster present, often prominent. Intestinal cells large. Rectum shorter than anal body width. Female reproductive system rather short, monodelphic, prodelphic, with ovary outstretched on right side of intestine, consisting of a few cells, mostly only one egg in uterus; vulva located near mid-body. Males rare in most species. Males monorchic, pro-orchic, with testis outstretched on right side of intestine. Spicules comparatively short and slender. Tail of both sexes usually long and attenuated. Three caudal glands opening through a common duct. Spinneret tube-like. Spinneret outlet, a cuticular protrusion of the excretion pore of the spinneret, always present.

Thalassic, athalassic saline water (Bayly 1967) and thermal freshwater; halophilic and thermophilic, often (extremely) euryhaline.

Remarks

Important (re-)descriptions of *Monhystrella* species are given by Andrássy (1952, 1963, 1965, 1968), Bastian (1865), Cobb (1918), De Coninck (1943), De Coninck & Schuurmans Stekhoven (1933), de Man (1876, 1880, 1884, 1922), Filipjev (1931), Gerlach (1951), Gerlach & Riemann (1971), Harrington *et al.* (1967), Hoeppli & Chu (1932), Hopper (1969), Hopper & Meyers (1967), Jacobs (1987), Juget (1969), Khera (1966, 1971), Loof (1961, 1964), Lorenzen (1969, 1979), Meyl (1953, 1954*a, b*, 1955), Micoletzky (1922), Moorthy (1938), Paetzold (1958), Schiemer (1965, 1978), Schuurmans Stekhoven (1935), Schneider (1906), Steiner (1914), Timm (1952, 1963, 1964), Vranken *et al.* (1982) and Wu & Hoeppli (1929).

List of species

M. anolphthlama (Lorenzen, 1969) comb.n.
  Monhystera anolphthalma Lorenzen, 1969
M. fukienensis (Hoeppli & Chu, 1932) comb.n.
  Monhystera filiformis fukienensis Hoeppli & Chu, 1932
M. gracilis Khera, 1966
M. hastata Andrássy, 1968
M. inaequispiculum Lorenzen, 1979
M. iranica Schiemer, 1965
  Monhystrella marina iranica Schiemer, 1965
M. lepidura (Andrássy, 1963) Andrássy, 1968
  Monhystera lepidura Andrássy, 1963
  M. lepidura lepidura (Andrássy, 1963) Andrássy, 1968
  M. lepidura altherri Juget, 1969 new rank
    Monhystrella altherri Juget, 1969
    Monhystera lepidura sensu Andrássy, 1965 *nec* Andrássy, 1963
M. longistoma (Khera, 1971) Andrássy, 1981
  Monhystera longistoma Khera, 1971
M. macrura (de Man, 1880) Andrássy, 1981
  Monhystera macrura de Man, 1880
  Monhystera vulgaris var. *macrura* de Man, 1880; Micoletzky 1922
M. marina Timm, 1964
M. microphthalma (de Man, 1880) comb.n.
  Monhystera microphthalma de Man, 1880
  Monohystera macrura apud G. Steiner, 1916 *nec* de Man, 1880 syn.n.
M. paramacrura (Meyl, 1954) Andrássy, 1968
  Monhystera paramacrura Meyl, 1954
M. parelegantula (De Coninck, 1943) Andrássy, 1981
  Monhystera parelegantula De Coninck, 1943
  Monhystera filiformis var. *salina* Meyl, 1954
  Monhystera salina Meyl, 1954; Meyl 1960
  Monhystrella salina (Meyl, 1954) Andrássy, 1981
M. parvella (Filipjev, 1931) Jacobs, 1987
  Monhystera parvella Filipjev, 1931
  Monhystera filiformis sensu Gerlach, 1951 *nec* Bastian, 1865; Jacobs 1987
M. plectoides Cobb, 1918; type species
  Monhystera (Monhystrella) plectoides (Cobb, 1918) Steiner, 1920
  Terschellingia (Monhystrella) plectoides (Cobb, 1918) Micoletzky, 1922
M. spiralis (Wu & Hoeppli, 1929) Andrássy, 1981
  Monhystera spiralis Wu & Hoeppli, 1929
M. stewarti (Khera, 1971) Andrássy, 1981
  Monhystera stewarti Khera, 1971
M. thermophila (Meyl, 1953) Andrássy, 1981
  Monhystera thermophila Meyl, 1953

Species inquirendae

M. elegantula (Schuurmans Stekhoven, 1935) comb.n.
  Monhystera elegantula Schuurmans Stekhoven, 1935
M. bulbifera (de Man, 1880) Steiner, 1920
  Monhystera bulbifera de Man, 1880
  Monhystera (Monhystrella) bulbifera (de Man, 1880) Steiner, 1920
  Terschellingia (Monhystrella) bulbifera (de Man, 1880) Micoletzky, 1922

Species transferred to the genus Sinanema *Andrássy, 1960*

Sinanema godeti (Steiner, 1920) comb.n.
  Monhystera (Monhystrella) godeti Steiner, 1920
  Terschellingia (Monhystrella) godeti (Steiner, 1920) Micoletzky, 1922
  Monhystrella godeti (Steiner, 1920) Timm, 1964
Sinanema mysorensis (Moorthy, 1938) comb.n.
  Monhystrella mysorensis Moorthy, 1938

Discussion

In his descriptions of *Monhystera microphthalma*, de Man (1884, 1922) mentioned the presence of a 6.5 μm long, cylindrical outlet of the caudal glands (Fig. 2j). This is one of the most important characteristics of the genus *Monhystrella*, as are the relatively small and posteriad situated fovea, the position of the vulva at 50% of the body length and the long, mostly filiform tail which are present in *Monhystera microphthalma* (Figs. 1E, F, 2w, x). *Monhystera anophthalma*, which closely resembles *Monhystera microphthalma* (Lorenzen 1969), also has a mid-body situated vulva, a tubiform spinneret and a long tail (Fig. 1B). Both species are here transferred to the genus *Monhystrella*. The shape of the tail of the males and the spicular system of *Monhystrella anophthalma, M. macrura* and *M. microphthalma* are similar (Figs. 1A–F, K–P). In de Man's descriptions of *M. microphthalma* (de Man 1884), 1922; Figs. 1N, O) the spicules are shorter and more cuticularised than in the description given by De

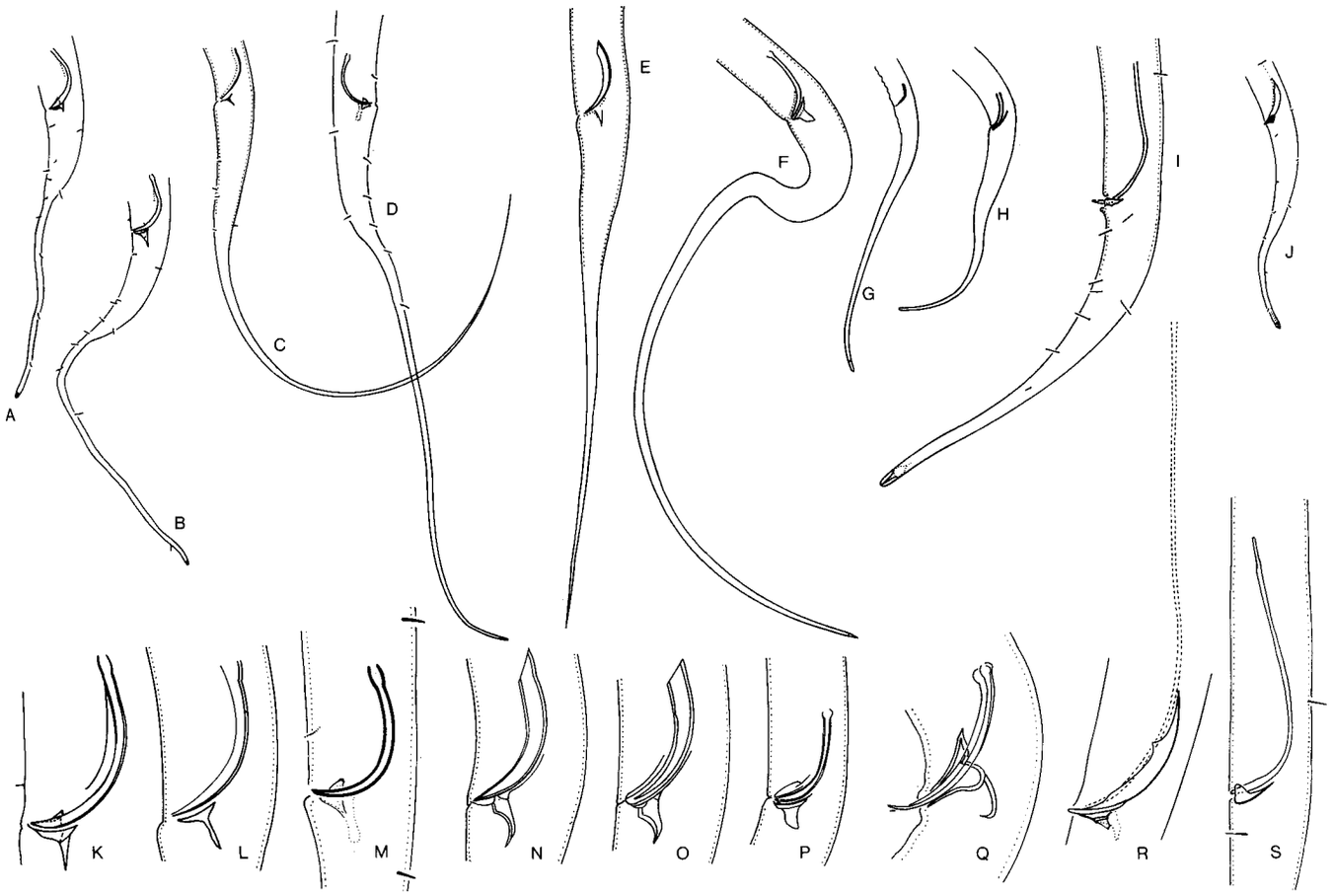


Fig. 1. The genus *Monhystrella* Cobb, 1918, ♂♂.—*A–J.* Tails of males.—*A. M. anophthalma*, after Lorenzen (1969).—*B. M. anophthalma*, after Lorenzen (1969).—*C. M. macrura*, after de Man (1884).—*D. M. macrura*, after Hopper (1969).—*E. M. microphthalma*, after de Man (1884).—*F. M. microphthalma*, after De Coninck & Schuurmans Stekhoven (1933).—*G. M. parelegantula*. after Paetzold (1958).—*H. M. parelegantula*, after Timm (1963).—*I. M. parelegantula*, after Vranken *et al.* (1982).—*J. M. inaequispiculum*, after Lorenzen (1979).—*K–S.* Lateral view of the spicular system.—*K. M. anophthalma*, after Lorenzen (1969).—*L. M. macrura*, after de Man (1884).—*M. M. macrura*, after Hopper (1969).—*N. M. microphthalma*, after de Man (1884).—*O. M. microphthalma*, after de Man (1922).—*P. M. microphthalma*, after De Coninck & Schuurmans Stekhoven (1933).—*Q. M. paramacrura*, after Meyl (1954).—*R. M. inaequispiculum*, after Lorenzen (1979).—*S. M. parelegantula*, after Vranken *et al.* (1982).

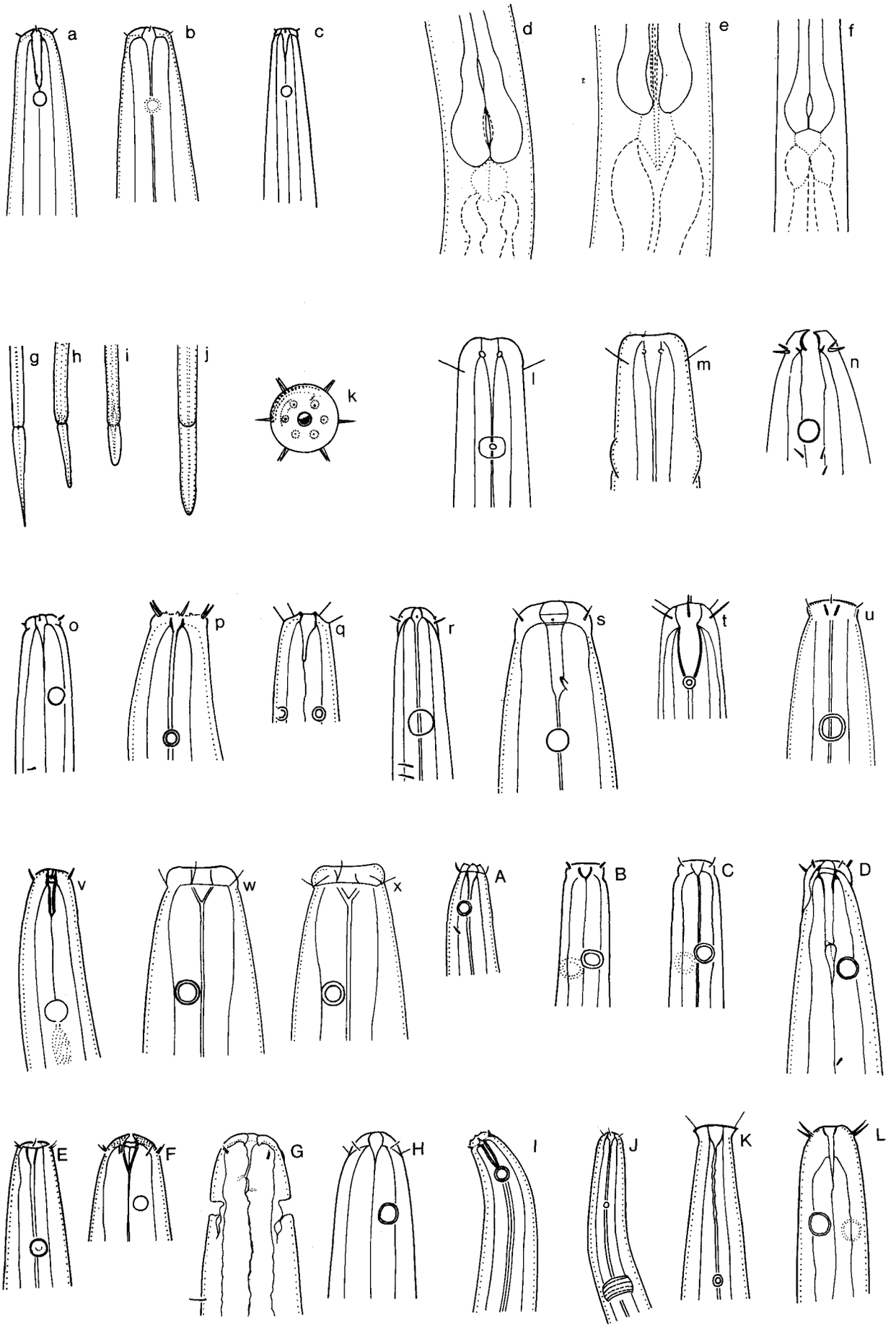
Coninck & Schuurmans Stekhoven (1933; Fig. 1P). This difference can be attributed to the sometimes weak cuticularisation of the proximal end of the spicula and the latters' sometimes superimposed position parallel to the lumen of the intestine. A similar situation is well documented by Vranken *et al.* (1982) in *Monhystrella parelegantula* (Figs. 1G–I, S).

Monhystera filiformis fukienensis differs from *Monhystera f. filiformis* in the following features: total length less than 0.5 mm; cheilostome not cylindrical and only weakly cuticularised (Fig. 2p); position of 6 + 4 cervical setae more anteriad (Fig. 2p); position of fovea more posteriad; fovea smaller in relation to the corresponding body diameter; vulva on mid-body instead of 60–65% of the body length; tail longer, 2/3 filiform and spinneret with tubular outlet. *Monhystera filiformis fukienensis* is transferred to *Monhystrella* because of the position of the vulva, the shape of the tail, the presence of the typical spinneret outlet and the presence of a relatively small fovea (Fig. 2p).

Andrássy (1981) synonymised *Monhystrella altherri* (Figs. 2c, f) with *Monhystrella hastata* (Figs. 2a, d, g). *Monhystrella lepidura* and *M. altherri* are very closely related to *M. hastata*, but differ from *M. hastata* by the absence of a denticle near the base of the stoma (Figs. 2a–c); the absence of a double pharyngeal bulb (Figs. 2d–f); a c value higher than 3; tail shorter than 1.5 times the distance between vulva and anus; the spinneret outlet blunt and smaller than 8 times the spinneret basis (Figs. 2*g–i*). The description of *Monhystrella lepidura* from Ghana (Andrássy 1965) agrees well with the description of *M. altherri* (Lake Leman; Juget 1969) and both differ from the original description of *M. lepidura* from Argentina (Andrássy 1963) by their lesser total length (L < 0.5 mm) and the presence of a larger and more posteriorly situated fovea (f.d. > 0.2 f.b.w.; a.f.b.l. > 2 h.d.; Figs. 2b, c). Therefore, both *Monhystrella altherri* and *M. lepidura sensu* Andrássy, 1965 are regarded as *Monhystrella lepidura altherri* new rank.

Monhystera elegantula is transferred to the genus *Monhystrella* because of the equatorial position of the vulva, the long and slender tail and the position of the fovea (a.f.b.l. = 2.2 h.d.; De Coninck 1934, p. 209), but its systematical position still remains unclear due to its poor description.

In the descriptions of *Monhystrella godeti* and *M. mysoriensis* Steiner (1920) and Moorthy (1938), respectively, mentioned the presence of a reflexed ovary. Therefore, both species are here transferred to the genus *Sinanema* Andrássy, 1960.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Key to females

1.a. Distance between vulva and anus less than twice length of tail . 2
b. Distance between vulva and anus more than twice length of tail ..... ***M. bulbifera***
Prominent bulbus at pharynx end; buccal ring present (Figs. 2l, m); cervical setae longer than 40% of head diameter; L = 300–450 μm. a = 21–25, b = 5.1–6.0, c = 6.5–7.0, V = 50.9%, G = 28.4%; ♂♂ unknown; wet dune soil and freshwater, moss.

2.a. Diameter of the fovea aperture less than 20% of corresponding body diameter 3
b. Diameter of fovea aperture as large or larger than 20% of corresponding body diameter 7

3.a. Head not offset or offset like a cap 4
b. Head atypical, umbrella-like appearance (Fig. 2K) .. ***M. stewarti***
Tail very long, filiform and about 20 times anal body width; anterior margin of fovea aperture situated at 4.6 times head diameter from anterior body end; cervical setae almost 50% of head diameter; L = 350–420 μm, a = 31–34, b = 6.3–6.5, c = 2.5–2.9, V = 42–44%, G = 13.0%, n.r. = 43.0–43.5%; ♂♂ unknown; freshwater, stagnant water.

4.a. Tail longer than distance between vulva and anus 5
b. Tail as long as or shorter than distance between vulva and anus ..... ***M. longistoma***
Cervical setae almost 50% of head diameter; stoma elongate, bi-lobed and cuticularised (Fig. 2t); L = 400–520 μm, a = 24–30, b = 5.3–5.6, c = 4.0–4.3, V = 47–50%, G = 17.5%, n.r. = 43.8%; ♂♂ unknown; freshwater, stagnant water.

5.a. Anterior margin of fovea aperture situated at more than 2 times head diameter from anterior body end 6
b. Anterior margin of fovea aperture situated at less than 2 times head diameter from anterior body end (Fig. 2b) ..... ***M. lepidura lepidura***
Cervical setae very small, their length about 1/6 of head diameter (Fig. 2b); cardia pentagonal (Fig. 2e); spinneret outlet clearly visible, 6.5 μm long, 3.5–5 times as long as tail diameter at outlet base (Fig. 2h); L = 530–580 μm, a = 25–27, b = 5.3–6.1, c = 3.7–4.2, V = 50.0–53.1%; ♂♂ unknown; freshwater.

6.a. Nerve ring situated at middle of pharynx; anterior margin of fovea aperture situated at about 2 (1.75–2.25) times head diameter from the anterior body end (Fig. 2p) ..... ***M. fukeniensis***
Fovea at 1/3 of distance between nerve ring and anterior body end; L = 460 & 480 μm, a = 31 & 32, b = 5.5 & 6.1, c = 3.6, V = 50.5%, G = 24.5%, n.r. = 51%; ♂♂ unknown; hot water well.
b. Nerve ring situated at 60% of pharynx length; anterior margin of fovea aperture situated at about 4 times head diameter from anterior body end (Fig. 2J) ..... ***M. spiralis***
Fovea located halfway between nerve ring and anterior body end; L = 320–540 μm, a = 23–27, b = 4.7–5.4, c = 3.3–3.7, V = 51%, G = 23%, n.r. = 59.2%; ♂♂ unknown; freshwater.

7.a. Head offset like a cap (Figs. 2n, s, u, w–D) 8
b. Head not or inconspicuously offset (Figs. 2a–c, x, E–H, L) ... 12

8.a. Anterior margin of fovea aperture situated at less than 2 times head diameter from anterior body end 9
b. Anterior margin of fovea aperture situated at more than 2 times head diameter from anterior body end 11

9.a. Tail longer than 10 times anal body width; at least one somatic seta present just behind fovea aperture; ♂♂ very common (Fig. 2n) 10
b. Tail as long as 9–10 times anal body width; post foveal setae absent; ♂♂ unknown ..... ***M. iranica***
Denticle well visible and situated at base of stoma, at 6.5 μm of anterior body end (Fig. 2s); cervical setae longer than 20% of head diameter; pharynx with double bulb; spinneret outlet 6.5–9.5 μm long, about 6 times as long as its base; L = 430–570 μm, a = 23–33, b = 5.1–6.2, c = 3.3–4.0, V = 48–53%, G = 21%, n.r. = 60%; ♂♂ unknown; athalassic saline water.

10.a. Ocelli, red–violet coloured, situated near amphideal fusus; tail smooth, without setae ..... ***M. microphthalma***
Ocelli very distinct and only occasionally absent in live material, but inconspicuous in fixed material; one seta just behind fovea (Fig. 2A); pharynx with single bulb; ventral gland present; L = 323–770 μm, a = 24–40, b = 4.7–6.7, c = 3.15–4.12, V = 48.0–58.7%, G = 22.8–29.7%, n.r. = 66.9–76.2%; ♂♂ common; thalassic water.
b. Ocelli not present; 3 pairs of setae on the tail ... ***M. anophthalma***
Cheilostome well cuticularised; at least 2 setae just behind fovea (Fig. 2n); spinneret outlet short, 2 μm long; L = 505–665 μm, a = 25–29, b = 5.6–6.7, c = 3.3–4.4, V = 47–53%, n.r. = 55%; ♂♂ common; thalassic inland water.

11.a. Spinneret outlet well visible, 10.5 μm long; denticle in stoma situated at 7.5 μm of anterior body end (Fig. 2D); tail shorter than 1.7 times pharyngeal length ..... ***M. paramacrura***
Pharynx with single bulb; tail narrowing gradually; ventral gland present; L = 314–487 μm, a = 20–35, b = 5.0–6.3, c = 3.0–4.0, V = 47.0–52.5%, G = 19.0–23.5%, n.r. = 60–72%; ♂♂ rare; freshwater and hot springs.
b. Spinneret outlet short, 3.5–4 μm long; tail longer than 1.7 times pharyngeal length; tail very fine, elongated, often 2/3 of tail bent in a ventral oblique position ..... ***M. macrura***
Anterior end of body, conoid between fovea and cervical setae (Fig. 2u); pharynx with single bulb; L = 415–770 μm, a = 23–45, b = 5.0–6.7, c = 2.5–3.8, V = 45–55%, G = 19.4–26.2%; ♂♂ very common; athalassic water and wet soil.

12.a. Tail longer than 1.5 times distance between vulva and anus; c less than 3 13
b. Tail shorter than 1.5 times distance between vulva and anus; c more than 3 17

13.a. Anterior margin of fovea aperture situated at more than 1.8 times head diameter from anterior body end 14
b. Anterior margin of fovea aperture situated at less than 1.8 times head diameter from anterior body end (Fig. 2I) ... ***M. plectoides***
Tail narrowing gradually; spinneret outlet short, 1.5 μm long; 10 intestinal cells between vulva and rectum; L = 430 μm, a = 28, b = 5.9, c = 2.86, V = 44%, G = 16%, n.r. = 59%; ♂♂ unknown; freshwater.

14.a. Distance between anterior margin of muscular tissue of pharynx and anterior body end less than 0.5 times head diameter; cardia clearly visible; cervical setae not longer than 1/4 of head diameter 15
b. Distance between anterior margin of muscular tissue of pharynx and anterior body end about 0.7 times head diameter; cardia faint; cervical setae longer than 1/3 of head diameter (Fig. 2L) ..... ***M. thermophila***
1/7 of tail conoid, 6/7 filiform; L = 368–475 μm, a = 27–37, b = 5.3–6.4, c = 2.2–2.6, V = 40.0–43.8%, G = 16.3–22.3%; ♂♂ unknown; hot springs.

15.a. Pharyngeal bulbus well developed, frequently divided into a double bulb (Fig. 2d); stoma clearly visible and cuticularised; spinneret outlet relatively long, at least 5 times as long as tail diameter at outlet base 16

Fig. 2. The genus *Monhystrella* Cobb, 1918, ♀♀.—*a–c.* Lateral view of the anterior body end.—*a. M. hastata*, after Andrássy (1968).—*b. M. lepidura lepidura*, after Andrássy (1963).—*c. M. lepidura altherri*, after Juget (1969).—*d–e.* Lateral view of the cardial region.—*d. M. hastata*, after Andrássy (1968).—*e. M. lepidura lepidura*, after Andrássy (1963).—*f. M. lepidura altherri*, after Juget (1969).—*g–j.* Tail end with spinneret outlet.—*g. M. hastata*, after Andrássy (1968).—*h. M. lepidura altherri*, after Andrássy (1965).—*i. M. lepidura lepidura*, after Andrássy (1963).—*j. M. microphthalma*, after de Man (1922).—*k.* Frontal view on the anterior body end of *M. fukienensis*, after Hoeppli & Chu (1932).—*l–m.* Anterior end of *M. bulbifera*, after de Man (1984).—*l.* Lateral view.—*m.* Ventral view.—*n–x, A–F.* Lateral view on the anterior body end.—*n. M. anophthalma*, after Lorenzen (1969).—*o. M. elegantula*, after Schuurmans Stekhoven (1935).—*p. M. fukienensis*, after Hoeppli & Chu (1932).—*q. M. gracilis*, after Khera (1966).—*r. M. inaequispiculum*, after Lorenzen (1979).—*s. M. iranica*, after Schiemer (1965).—*t. M. longistoma*, after Khera (1971).—*u. M. macrura*, after de Man (1884).—*v. M. marina*, after Timm (1964).—*w. M. microphthalma*, after de Man (1884).—*x. M. microphthalma*, after de Man (1922).—*A. M. microphthalma*, after De Coninck & Schuurmans Stekhoven (1933).—*B. M. paramacrura*, after Meyl (1954*a*).—*C. M. paramacrura*, after Meyl (1954*b*).—*D. M. paramacrura*, after Gerlach & Riemann (1971).—*E. M. parelegantula*, after Vranken *et al.* (1982).—*F. M. parvella*, after Filipjev (1931).—*G.* Ventral view of the anterior body end of *M. parvella*, after Jacobs (1987).—*H–L.* Lateral view of the anterior body end.—*H. M. parvella* Black Sea form, after Gerlach (1951).—*I. M. plectoides*, after Cobb (1918).—*J. M. spiralis*, after Wu & Hoeppli (1929).—*K. M. stewarti*, after Khera (1971).—*L. M. thermophila*, after Meyl (1953).

b. Pharynx cylindrical with faint terminal swelling; stoma weakly sclerotised (Fig. 2E); spinneret outlet relatively short, about 2 times as long as tail diameter at outlet base .... ***M. parelegantula***
Tail narrowing gradually, with 1 postanal seta present at about 7 μm from anus and 2 other setae with variable position, the latter occasionally absent; spinneret outlet 6–7 μm long; L = 364–455 μm, a = 17–37, b = 5.1–6.3, c = 2.9–3.9, V = 43–55%, G = 16.5%, n.r. = 59.7–62.4%; ♂♂ rare; thalassic water, euryhaline.

16.a. Amphideal fusus distinct, about twice as long as fovea aperture (Fig. 2v); anterior margin of fovea aperture situated at more than 2.3 times head diameter from anterior body end; posterior end of spinneret outlet blunt ..... ***M. marina***
Tail not narrowing gradually; 1 pair of subventral setae situated just behind anus and 1 pair of subdorsal setae situated just in front of anus; spinneret outlet 7 μm long, 4.5–5 times as long as tail diameter at outlet base; ventral gland present; L = 340–400 μm, a = 25–34, b = 5.0–5.8, c = 2.9–3.1, V = 46.3–49.8%, G = 20.5%, n.r. = 52–58%; ♂♂ unknown; marine.

b. Amphideal fusus not distinct; anterior margin of fovea aperture situated at less than 2.3 times head diameter from anterior body end (Fig. 2a); spinneret outlet lancet-shaped (Fig. 2g) ***M. hastata***
Pharynx with double bulb (Fig. 2d); tail narrowing gradually; spinneret outlet 10–15 μm long, 9–14 times as long as tail diameter at outlet base (Fig. 2g); a tooth-like projection can be observed at 80% of stoma (Fig. 2a); L = 350–370 μm, a = 31–36, b = 5.3–5.4, c = 2.5–3.0, V = 42%, G = 15%; ♂♂ unknown; freshwater.

17.a. Fovea diameter larger than 20% of corresponding body diameter 18

b. Fovea diameter smaller than 20% of corresponding body diameter (Fig. 2q) ..... ***M. gracilis***
Cervical setae 38% of head diameter (Fig. 2q); tail narrowing gradually; ventral gland present; L = 380–440 μm, a = 31–42, b = 5.4–5.7, c = 3.5–4.0, V = 52.1–54.0%, G = 17.5–18.0%, n. r. = 42.5%; ♂♂ unknown; athalassic saline water.

18.a. Tail longer than 8 times anal body width 19

b. Tail shorter than 8 times anal body width ***M. parvella sensu stricto***
Cheilostome well cuticularised (Figs. 2F, G); anterior margin of fovea aperture situated at 0.9–1.4 times head diameter from anterior body end; spinneret outlet short, 2.4–4.8 μm long, 1.1–2.5 times as long as tail diameter at outlet base; 8–9 intestinal cells between vulva and rectum; L = 396–486 μm, a = 15–24, b = 4.6–5.7, c = 4.1–5.3, V = 50–59%, G = 17–29%, n.r. = 51.0–66.7%; ♂♂ unknown; athalassic saline water and thermal water.

19.a. Fovea diameter smaller than 45% of corresponding body diameter; cervical setae shorter than 33% of head diameter 20

b. Fovea diameter about 50% of corresponding body diameter; cervical setae longer than 33% of head diameter (Fig. 2r) ..... ***M. inaequispiculum***
6 labial papillae and 4 cephalic setae (Fig. 2r); stoma with a tooth-like projection, situated at about 8 μm from anterior body end; 2 setae situated closely behind fovea (Fig. 2r); about 2/3 of tail conoid and 1/3 filiform; spinneret outlet short; L = 650 μm, a = 30, b = 5.4, c = 5.2, V = 55%, G = 24.3%; ♂♂ common; thalassic.

20.a. Tail shorter than 11 times anal body width 21

b. tail longer than 12 times anal body width ... **M. lepidura altherri**
Cardia pentagonal; progaster prominent (Fig. 2f); subdorsal seta at 1/5 of tail length from posterior body end; L = 380–440 μm, a = 24–32, b = 4.9–5.8, c = 3.0–3.9, V = 46–51%, G = 19–25%; ♂♂ unknown; freshwater.

21.a. Tail as long as or longer than distance between vulva and anus; anterior half of tail attentuating gradually, posterior half filiform ..... ***M. parvella*** Black Sea form
Head rounded (Fig. 2H); L = 430–570 μm, a = 23–33, b = 6.0–6.3, c = 3.3–4.0, V = 48–52%; ♂♂ unknown; athalassic saline water.

b. Tail shorter than distance between vulva and anus; anterior two thirds of tail attenuating gradually, posterior third filiform; tail tip blunt ..... ***M. elegantula***
One seta present behind fovea (Fig. 2g); ventral gland present; L = 391–624 μm, a = 26–36, b = 4.8–5.9, c = 3.6–4.4, V = 51.0–52.4%; ♂♂ unknown; marine, thalassic saline water and freshwater.

Key to males

1.a. Spicular system symmetrical 2

b. Spicular system asymmetrical (Fig. 1J, R) .. ***M. inaequispiculum***
At least 2 setae just behind fovea; L = 550–580 μm, a = 26–31, b = 4.8–5.0, c = 5.3–5.8, T = 53.4%, Cl. = 81.8–82.8%, l.sp.l. = 71–75 μm = 5.5–6.1 an.b.w., r.sp.l. = 26–28 μm = 1.9–2.1 an.b.w., t.l. = 1.33–1.40 l.sp.l = 3.57–3.95 r.sp.l.; ♂♂ very common; thalassic water.

2.a. Head offset like cap, tail longer than 2.5 times spicule length; gubernaculum with caudally directed apophyses 3

b. Head not offset like cap (Fig. 2E); tail shorter than 2.5 times spicule length (Fig. 1I), spicule capitulum very slightly cuticularised; gubernaculum without caudally directed apophyses (Fig. 1S) ..... ***M. parelegantula***
Very small tooth-like differentiation on lateral side of distal end of spicule (Fig. 1I); L = 330–469 μm, a = 25–38, b = 4.9–5.4, c = 3.2–4.7, T = 53.1%, Cl. = 68.8–77.0%, n.r. = 61–62%; sp.l. = 34–42 μm = 3–3.6 an.b.w., t.l. = 2.14–2.35 sp.l.; ♂♂ very rare; thalassic saline water, euryhaline.

3.a. Proximal part, about 1/3, of tail conoid, distal part, about 2/3, filiform; tail often with several setae; tail longer than 5 times spicule length 4

b. Tail narrowing gradually, without somatic setae; spicules narrow with spheroid capitulum (Fig. 1Q); tail shorter than 5 times spicule length ..... ***M. paramacrura***
Maximum spicule shaft diameter 3.3% of spicule length (Fig. 1Q); L = 455–487 μm, a = 28–35, b = 5.1–5.3, c = 5.3–6.3, Cl. = 81.5–84.1%, n.r. = 65%, sp.l. = 17–22 μm = 1.75 an.b.w., t.l. = 3.4–4.8 sp.l.; ♂ : ♀ < 1 : 100; freshwater and hot springs.

4.a. Caudally directed gubernaculum apophyses weakly cuticularised and not arcuated; maximal spicule shaft diameter 5–6.7% of spicule length; setae on tail 5

b. Gubernaculum and caudally directed apophyses well cuticularised, trigger-like arcuated end bent in ventral direction (Figs. 1N–P); maximum spicule shaft diameter 6.7–13.5% of spicule length; tail devoid of setae (Figs. 1E, F) ..... ***M. microphthalma***
Ocelli red-violet coloured and very distant in live material, situated near the amphideal fusus, only occasionally absent, ocelli inconspicuous in fixed material; anterior margin of fovea situated at less than 2 times head diameter from the anterior body end; ventral gland present; spinneret outlet 2–3 times as long as tail diameter at outlet base; L = 361–856 μm, a = 33.3–53.3, b = 4.3–6.7, c = 3.82–4.18, T = 17.4–58.9%, Cl. = 71.4–73.8%, n.r. = 56.3–72.7%, sp.l. = 22.6 μm = 1.5–1.9 & 2.25 an.b.w., t.l. = 5.0–10.1 sp.l.; ♂♂ common; thalassic.

5.a. 7 pairs of setae present on conical part of tail (Figs. 1A, B); 1 seta situated 5–6 μm anterior to cloacal orifice (Fig. 1B); tail shorter than 1.8 times pharyngeal length ..... ***M. anophthalma***
Cheilostome well cuticularised; at least 2 setae situated closely behind fovea; ocelli not present; L = 675 μm, a = 29, b = 6.4, c = 4.8, Cl. = 70.6–79.3%, n.r. = 55%, sp.l. = 20–26 μm = 1.44 an.b.w., t.l. = 5.38 sp.l.; ♂♂ very common; thalassic.

b. 5 pairs of setae present on conical part of tail (Figs. 1C, D); 1 seta situated 5–6 μm anterior to cloacal orifice (Fig. 1D); tail longer than 1.8 times pharyngeal length ..... ***M. macrura***
Ocelli absent; anterior margin of fovea aperture situated at more than 2 times head diameter from anterior body end; spinneret outlets short, 3.5–4.0 μm long, 2–3 times as long as tail diameter at its base; L = 710–770 μm, a = 30–45, b = 5–7, c = 2.5–3.3, T = 48.25%, Cl. = 63.6–69.7%, sp.l. = 28 μm = 1.7–1.8 an.b.w., t.l. = 8.3–10.6 sp.l.; ♂♂ very common; terrestrial and freshwater.

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