On the nematode genus *Heterodorus* Altherr, 1952 (Dorylaimida: Nordiidae) with descriptions of three new species

I. ANDRÁSSY

Abstract. The genus *Heterodorus* Altherr, 1952 is analysed and redefined. Of the nominal species, four are synonymized, namely *H. magnificus* Altherr, 1952 and *H. thornei* (Baqri & Jairajpuri, 1974) with *H. arcuatus* (Thorne, 1939), *H. bongersi* (Mushtaq, Baniyamuddin & Ahmad, 2007) with *H. brevidentatus* (Thorne, 1939) and *H. satendri* (Baqri & Jairajpuri, 1974) with *H. constrictus* (Jairajpuri & Loof, 1968). Three species, new to science, are described. *Heterodorus unicus* sp. n. from Papua New Guinea is distinguished by its small body (on average 1.23 mm), continuous lip region, short odontostyle as long as lip region width, far posteriorly located D nucleus, greenish intestine, deep vulva, and by a single ventromedial supplement. *Heterodorus monticola* sp. n. from Peru is characterized by its short body (on average 1.36 mm), continuous lip region, short odontostyle as long as 1.1–1.2 lip region widths, far posteriorly widened pharynx, strongly swollen vagina, and by two or three ventromedial supplements. *Heterodorus alius* sp. n. from Papua New Guinea also belonging to the small species (on average 1.22 mm long) shows some atypical or marginal characters: a longer cylindrus, more anteriorly located D nucleus (54–57 %), more anteriorly posited vulva (39–41 %), longer vagina, longer spicula, and a row of six or seven ventromedial supplements beginning closer to the adanal pair as usual. A key to the identification of *Heterodorus* species is added. Finally, an *Enchodelus* species is transferred to *Papuadorus* Andrássy, 2009 as *P. coomansi* (Nicholas & Stewart, 1985) comb. n.

Keywords. Nematoda, Dorylaimida, *Heterodorus*, new species, key to the species.

In the second part of his classic paper on the nematode fauna of Swiss National Park, Altherr (1952) erected the genus *Heterodorus*, and described its type species, *Heterodorus magnificus* Altherr, 1952. He compared it with *Enchodelus* Thorne, 1939 and distinguished by the somewhat (apparently) different odontophore and the “peculiar” structure of the female gonad. In 1963, he reported on further specimens from Switzerland, and corrected the original description and measurements of *H. magnificus*. In the meantime, three excellent specialists of that time, M. Luc, J. B. Goodey and G. Thorne, checked the type specimens of *H. magnificus*, and unisono stated that they belonged to the genus *Enchodelus*. Both the structure of the odontostyle/odontophore and that of the genital organ corresponded to the usual types in *Enchodelus* species. Therefore, Altherr synonymized *Heterodorus* with *Enchodelus* and transferred the Swiss species to the latter genus as *Enchodelus magnificus* (Altherr, 1952) Altherr, 1963. Later, Siddiqi (1969) also studied Altherr’s specimens, and provided fine drawings of the anterior and pharyngeal region (Fig. 4 M–N). In that paper, Siddiqi revised the classification of Dorylaimoidea, and accepted *Heterodorus* as valid genus characterized by the position of the second pair of subventral pharyngeal gland nuclei (PS nuclei) lying “considerably anterior to the base of the oesophagus”.

Most of subsequent authors left Siddiqi’s opinion out of consideration, and regarded *Heterodorus* as junior synonym of *Enchodelus*. Ahmad and Jairajpuri (1980) revised the genus *Enchodelus* and grouped its species under five subgenera. Subgenus *Heterodorus* was one of them including the only species, *E. (H.) magnificus*. The above authors stressed that *Enchodelus* essentially consists of two main groups of species defined by tail shape, either rounded or conical. For the second group, they proposed the new subgenera *Nepalus* (with long odontostyle) and *Paraen-chodelus* (with shorter odontostyle). In their book (1992), Jairajpuri and Ahmad followed this classification.

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Recently, Andrássy (2009) expressed the opinion that the genus of Altherr can still be accepted as valid. It includes those *Enchodelus*-like species that have a conoid tail in both sexes, and ventromedial supplements few in number lying in their series at a distance from the adanal pair. Since the above mentioned two subgenera of Ahmad and Jairajpuri, *Nepalus* and *Paraenchodelus*, showed all the main structures of *Heterodorus*, he synonymized them with Altherr’s genus. At the same time, Andrássy transferred 24 conical-tailed species from *Enchodelus* to *Heterodorus*.

The genus *Heterodorus* is characterized and differentiated from *Enchodelus* as follows.

**Heterodorus Altherr, 1952**


**Diagnosis.** Nordiidae, Pungentinae. Body ranging in length from 1.0 to 2.8 mm. Cuticle smooth or finely, exceptionally coarsely transversely annulated. Lips amalgamated or slightly separated, lip region not or moderately separated from adjoining body. Odontostyle thin to very thin with small aperture, 10 to 70 µm, one to four times the labial diameter long; odontophore rod-like, lacking basal flanges. Guiding ring double, but thin. Basal expanded part (cylindrus) shorter than half a pharyngeal length, weakly muscular. Anterior pair of pharyngeal nuclei (AS) often inconspicuous, posterior pair (PS) distinct and lying far anterior to basal end of cylindrus, close to the middle of glandularium. Intestine often filled with green-coloured food rests. Prerectum medium long. Female genital system amphidelphic, with bipartite uterus, transverse vulva and occasionally highly developed vagina. Males known in nearly 60 % of the species. Spicula dorylaimoid. Ventromedial supplements one to nine, well spaced, posterior ones lying well anterior to the adanal pair. Tail in sexes similar, short, conoid, ventrally arcuate, with finely rounded tip.

**Relationships.** *Heterodorus* shows a fairly constant morphological pattern. It is very similar to *Enchodelus* Thorne, 1939, but the simple odontophore (vs. basally flanged), bipartite uterus consisting of a proximal wider and a distal narrower section (vs. tripartite consisting of a proximal wider, an intermediate narrower and a distal spherical section), conoid and ventrally arcuate tail (vs. broadly rounded, not curved) and the low number (1–9 vs. 7–16) and arrangement of supplements (their row lying at a distance from the adanal pair, predominantly well outside the range of spicula vs. their row continuous with the adanal pair, and the posteriormost supplement(s) lying in spicular range) clearly distinguish it from its “sister” genus.


Currently, the following 25 species can be classified under *Heterodorus*.

*H. alius* sp. n.

*H. arcaucus* (Thorne, 1939) Andrássy, 2009

*Enchodelus arcaucus* Thorne, 1939

*Enchodelus (Paraenchodelus) arcaucus* Thorne, 1939 (Ahmad & Jairajpuri, 1980)

*Heterodorus magnificus* Altherr, 1952 **syn. n.**

*Enchodelus magnificus* (Altherr, 1952) Altherr, 1963


*Enchodelus thornei* Baqri & Jairajpuri, 1974 **syn. n.**

*Enchodelus (Paraenchodelus) thornei* Baqri & Jairajpuri, 1974 (Ahmad & Jairajpuri, 1980)

*Heterodorus thornei* (Baqri & Jairajpuri, 1974) Andrássy, 2009

*H. brevidentatus* (Thorne, 1939) Andrássy, 2009

*Enchodelus brevidentatus* Thorne, 1939

*Enchodelus (Paraenchodelus) brevidentatus* Thorne, 1939 (Ahmad & Jairajpuri, 1980)

*Enchodelus bongersi* Mushtaq, Baniyamuddin & Ahmad, 2007 **syn. n.**

*Heterodorus bongersi* (Mushtaq, Baniyamuddin & Ahmad, 2007) Andrássy, 2009
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H. conicaudatus (Ditlevsen, 1927) Andrássy, 2009  
Dorylaimus conicaudatus Ditlevsen, 1927  
Dorylaimellus conicaudatus (Ditlevsen, 1927) Thorne & Swanger, 1936  
Enchodelus conicaudatus (Ditlevsen, 1927) Thorne, 1939  
Enchodelus (Paraenchodelus) conicaudatus (Ditlevsen, 1927) Thorne, 1939 (Ahmad & Jairajpuri, 1980)

H. constrictus (Jairajpuri & Loof, 1968) Andrássy, 2009  
Enchodelus constrictus Jairajpuri & Loof, 1968  
Enchodelus satendri Baqri & Jairajpuri, 1974 syn. n.  
Enchodelus (Paraenchodelus) satendri Baqri & Jairajpuri, 1974 (Ahmad & Jairajpuri, 1980)  
Heterodorus satendri (Baqri & Jairajpuri, 1974) Andrássy, 2009

H. faeroensis (Ditlevsen, 1928) Andrássy, 2009  
Dorylaimus (Doryllium) faeroensis Ditlevsen, 1928  
Enchodelus faeroensis (Ditlevsen, 1928) Thorne, 1939  
Enchodelus (Paraenchodelus) faeroensis (Ditlevsen, 1928) Thorne, 1939 (Ahmad & Jairajpuri, 1980)

Enchodelus geraldi Winiszewska-Slipińska, 1987

Enchodelus irregularis Altherr, 1972  

Enchodelus liangi Ahmad, Wu & Shaheen, 2002

H. longidens (Jairajpuri & Loof, 1968) Andrássy, 2009  
Enchodelus longidens Jairajpuri & Loof, 1968  
Enchodelus (Paraenchodelus) longidens Jairajpuri & Loof, 1968 (Ahmad & Jairajpuri, 1980)

Enchodelus lushani Ahmad, Wu & Shaheen, 2002

H. maximus (Baqri & Jairajpuri, 1974) Andrássy, 2009  
Enchodelus maximus Baqri & Jairajpuri, 1974  
Enchodelus (Nepalus) maximus Baqri & Jairajpuri, 1974 (Jairajpuri & Ahmad, 1992)

H. meghalayensis (Mushtaq, Baniyamuddin & Ahmad, 2007) Andrássy, 2009  
Enchodelus meghalayensis Mushtaq, Baniyamuddin & Ahmad, 2007

H. monticola sp. n.

H. morgensis (Loof, 1989) Andrássy, 2009  
Enchodelus morgensis Loof, 1989

H. nepalensis (Zullini, 1973) Andrássy, 2009  
Enchodelus nepalensis Zullini, 1973  

H. porosus (Guerrero, Liébanas & Peña-Santiago, 2007) Andrássy, 2009  
Enchodelus porosus Guerrero, Liébanas & Peña-Santiago, 2007

H. rhaeticus (Altherr, 1952) Andrássy, 2009  
Enchodelus rhaeticus Altherr, 1952  
Enchodelus (Paraenchodelus) rhaeticus Altherr, 1952 (Ahmad & Jairajpuri, 1980)

H. southeyi (Jairajpuri & Ahmad, 1986) Andrássy, 2009  
Enchodelus (Paraenchodelus) southeyi Jairajpuri & Ahmad, 1986

H. striatus (Thorne, 1939) Andrássy, 2009  
Enchodelus striatus Thorne, 1939  
Enchodelus (Paraenchodelus) striatus Thorne, 1939 (Ahmad & Jairajpuri, 1980)

Enchodelus transsilvanicus Ciobanu, Popovici, Guerrero & Peña-Santiago, 2010

H. tropicus (Mushtaq, Baniyamuddin & Ahmad, 2007) Andrássy, 2009  
Enchodelus tropicus Mushtaq, Baniyamuddin & Ahmad, 2007

H. unicus sp. n.
H. veletensis (Guerrero, Liébanas & Peña-Santiago, 2007) Andréssy, 2009
Enchodelus veletensis Guerrero, Liébanas & Peña-Santiago, 2007

H. zonatus (Jairajpuri & Loof, 1968) Andréssy, 2009
Enchodelus zonatus Jairajpuri & Loof, 1968
Enchodelus (Paraenchodelus) zonatus Jairajpuri & Loof, 1968 (Ahmad & Jairajpuri, 1980)

REMARKS

Some species should be commented.

Heterodorus magnificus. – When in 1963 corrected the description and measurements of Heterodorus magnificus, Altherr compared his species with Enchodelus arcuatus Thorne, 1939 as described by different authors and found a great similarity between them. Indeed, if these two taxa are compared, there is hardly doubt about it whatever they represent the same species. As may be seen in Table 1, the morphometric characters of the two species are practically identical. In addition, they are very similar in the finely striated cuticle, shape of the lip region, length of the cylindrical part. It can be concluded with good reason that the species of Altherr is the same as that of Thorne. Altherr’s magnificus should be considered a junior synonym of Thorne’s arcuatus.

Heterodorus thornei. – This species also cannot be differentiated from H. arcuatus. Their habitus, shape of the lip region, odontostyle, genital organ and tail are very similar. Ahmad and Jairajpuri (1980) separated them in their key by the dubious structure of the odontophore “with poorly developed basal flanges” in thornei, and “rod-like” in arcuatus. Table 1 shows how similar arcuatus and thornei are in their morphometrics as well.

Heterodorus bongersi. – In its morphometrics, this species completely agrees with Heterodorus brevidentatus as described by Thorne (1939) and redescribed by Guerrero and Peña-Santiago (2007) (see Tab. 2). Mushtaq, Baniyamuddin and Ahmad (2007) mentioned some very small differences between these species, of which the only real, maybe, the greater length of the prerectum. This latter as such is, however, not enough for accepting the validity of H. bongersi.

Heterodorus satendri. – This species seems to be the same as H. constrictus. In their key to conical-tailed species, Ahmad and Jairajpuri (1980) give the minor difference: odontophore “rod-like” in constrictus, and “with poorly developed basal flanges” in satendri. The descriptions and the morphometric data of the two specific taxa well correspond to each other (Tab. 3).

Heterodorus irregularis. – The systematic position of this species is somewhat uncertain. Altherr (1972) described it from Sweden on the basis of three female specimens. The tail shows a transition from the Enchodelus to the Heterodorus type, it is 1.0–1.2 anal body widths long, conoid-rounded, straight with bluntly rounded tip. Not knowing the male characters, this taxon should be classified with some reservations under the genus Heterodorus.

Enchodelus coomansi. – Nicholas and Stewart (1985) described this conoid-tailed species from mangrove forests on the coast of south-eastern Australia. After them, their species would key out to the subgenus Paraenchodelus. However, it differs from every species of this group (now: genus Heterodorus) as well as from all the species of Enchodelus (s. str.) by the large number (26–31) of contiguous medioventral supplements. On the other hand, the Australian species, just in the number and arrangement of the supplements, resembles another enchodelid (nordiid) species, Papuadorus amplus Andréssy, 2009. Papuadorus also has an Enchodelus-like habitus and organization, differs however both from Enchodelus and Heterodorus in having a longitudinal vulva and a great number of contiguous supplements. Although the species of Nicholas and Stewart has a transverse vulva, it fits in other morphological respects, especially in the male characters, well into Papuadorus. E. coomansi should herewith be transferred to the Papuan genus as Papuadorus.
Table 1. Comparison of some main morphometric characters of Heterodorus magnificus Altherr, 1952, H. thornei (Baqri & Jairajpuri, 1974) and H. arcuatus (Thorne, 1939)

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<tr>
<td>L (mm)</td>
<td>1.45–1.73</td>
<td>1.28–1.67</td>
<td>1.50–1.99</td>
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<tr>
<td>a</td>
<td>26–32</td>
<td>30–35</td>
<td>25–30</td>
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<tr>
<td>b</td>
<td>4.8–6.0</td>
<td>4.8–5.3</td>
<td>5.2–5.9</td>
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<td>c</td>
<td>21–32</td>
<td>23–29</td>
<td>24–25</td>
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<tr>
<td>c’</td>
<td>2.0–2.5</td>
<td>2.0–2.4</td>
<td>2.0–2.2</td>
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<tr>
<td>V (%)</td>
<td>52–55</td>
<td>48–57</td>
<td>50–54</td>
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<tr>
<td>Lip region width (µm)</td>
<td>12–13</td>
<td>11–12</td>
<td>12–14</td>
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<tr>
<td>Odontostyle length (µm)</td>
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<td>17–18</td>
<td>18–22</td>
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<tr>
<td>Odontostyle / lip width</td>
<td>1.4–1.5</td>
<td>1.4</td>
<td>1.5–1.6</td>
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<tr>
<td>Pharynx enlarged at (%)</td>
<td>60</td>
<td>60</td>
<td>58–62</td>
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<tr>
<td>Tail length</td>
<td>60–80</td>
<td>55–65</td>
<td>62–80</td>
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Heterodorus unicus sp. n. (Figs. 1–2)

Holotype female: L = 1.28 mm; a = 31; b = 5.2; c = 35; c’ = 1.3; V = 50 %.

Paratype females (n = 5): L = 1.07–1.30 mm; a = 26–34; b = 5.1–5.6; c = 31–35; c’ = 1.2–1.4; V = 50–55 %.

Paratype male: L = 1.09 mm; a = 27; b = 5.1; c = 35; c’ = 1.1.

General characters. Small nematodes. Body ventrally curved, C- or G-shaped, 40–47 µm wide at mid-region. Cuticle smooth (under optical microscopy), 1.5–2.0 µm thick. Labial region rounded, practically not separated from adjacent neck, 10–11 µm wide, lips amalgamated with very small papillae. Body at posterior end of pharynx 3.2–3.6 times as wide as labial region. Amphid aperture occupying about half of corresponding body width.

Odontostyle very thin and delicate, 10–11 µm long, as long as labial region width; aperture very small, hardly discernible. Odontophore rod-like without basal swelling, 18–20 µm long. Guiding ring double but thin. Pharynx weakly muscled, 210–245 µm long, gradually expanded at its 62–66 %; cylindrus weak. Distance between posterior end of pharynx and vulva 1.6–1.9 times as
Figure 1. *Heterodorus unicus* sp. n. A: anterior end; B: posterior pharyngeal region; C: vulval region; D: anterior female gonad. (Scale bars = 20 µm)
Figure 2. *Heterodorus unicus* sp. n. A–C: variations of female posterior end; D: male posterior end. (Scale bar = 20 µm)
### Table 2. Comparison of some main morphometric characters of *Heterodorus bongersi* (Mushtaq et al., 2007) and *H. brevidentatus* (Thorne, 1939)

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<td>c</td>
<td>24–32</td>
<td>24–34</td>
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<tr>
<td>c’</td>
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<td>1.5–2.4</td>
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<tr>
<td>V (%)</td>
<td>49–54</td>
<td>47–54</td>
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<tr>
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<td>12–16</td>
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<td>Odontostyle / lip width</td>
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<td>1.1–1.4</td>
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<tr>
<td>Pharynx enlarged at (%)</td>
<td>58–64</td>
<td>54–65</td>
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<tr>
<td>Tail length (µm)</td>
<td>49–65</td>
<td>50–70</td>
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### Table 3. Comparison of some main morphometric characters of *Heterodorus satendri* (Baqri & Jairajpuri, 1974) and *H. constrictus* (Jairajpuri & Loof, 1968)

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<td>c</td>
<td>23–35</td>
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<tr>
<td>c’</td>
<td>1.5–1.9</td>
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<td>V (%)</td>
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<td>51</td>
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<td>10–13</td>
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<td>Odontostyle length (µm)</td>
<td>24–29</td>
<td>23–25</td>
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<tr>
<td>Odontostyle / lip width</td>
<td>1.9–2.1</td>
<td>2.0–2.5</td>
</tr>
<tr>
<td>Pharynx enlarged at (%)</td>
<td>63–66</td>
<td>60–65</td>
</tr>
<tr>
<td>Spicula (µm)</td>
<td>42–52</td>
<td>40–48</td>
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<tr>
<td>Ventromed. supplements</td>
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long as pharynx. Dorsal pharyngeal nucleus (D) at 73–75 % of pharyngeal length, or 13–14 % of entire length of body. AS nuclei minute, PS nuclei distinct, located at 56–59 % of glandularium. The latter 60–62 µm long. Cardia conoid-rounded. Intestine either in its total length or in its posterior half filled with green-coloured food (probably moss) rests.

**Female.** Genital apparatus amphidelphic. Each branch equally developed, 3.8–4.8 body diameters long or occupying 12–15 % of body length. Ovaries reflexed midway to vulva. Vulva a deep transverse slit, vagina 18–22 µm long, extending inwards 38–48 % of corresponding body width. Sphincter between oviduct and uterus present. Each uterus branch consisting of a proximal wider and a distal narrower portion; the former packed with sperms. Three females possess one thick-walled uterine egg each, 95–104×35–38 µm, 2.2–2.5 times the body width long. Rectum 0.6–1.2, prerectum 1.8–2.5 times as long as anal body width. Vulva–anus distance equal to 13–16 tail lengths. Tail 35–40 µm long or 2.8–3.2 % of total body length, ventrally curved with rather bluntly rounded tip.

**Male.** Similar in general morphology to female. Testes two, opposed, spermatozoa fusiform, 4–5 µm long. Spicula dorylaimoid, 38 µm long. Adanal pair of supplements at 12 µm from cloaca. Only a single ventromedial supplement present, situated at 60 µm from cloacal opening. Prerectum longer than the former distance. Tail 36 µm long, 2.8 % of entire length of body, ventrally curved, similar to that of female.

**Diagnosis and relationships.** A small and rather robust member of Heterodorus, with body on average 1.23 mm long, continuous lip region, short and delicate odontostyle, well posterior to its middle expanded pharynx, far posteriorly located D nucleus, but anteriorly located PS nuclei, greenish intestine, deep vulva, paired gonads, thick-walled eggs, only one ventromedial supplement, and with short, ventrally curved tail.

In having a small body, narrow lip region, short and very thin odontostyle, Heterodorus unicus sp. n. comes closest to H. liangi (Ahmad, Wu & Shaheen, 2002) Andrássy, 2009 described from China and H. meghalayensis (Mushtaq, Baniamuddin & Ahmad, 2007) Andrássy, 2009 described from India. It differs from H. liangi by the shorter odontostyle (10–11 vs. 13 µm, or 1.0 vs. 1.3–1.4 lip region widths long), normal dorsal pharyngeal nucleus (vs. unusually large), strongly swollen vagina (vs. not or slightly swollen), much shorter prerectum (1.8–2.5 vs. 6–8 anal body widths long), and by the more strongly ventrally curved and narrowly tipped tail (vs. almost stright and more broadly rounded). Unfortunately, the male is unknown in H. liangi. The new species differs from H. meghalayensis by the somewhat shorter odontostyle (10–11 vs. 12–13 µm), shorter tail (1.2–1.4 vs. 2.0–2.1 anal body widths, or 35–40 vs. 50–53 µm long), more rounded tail tip (vs. sharply tipped), and especially by the presence of a single ventromedial supplement (vs. 4–6 in H. meghalayensis). In the latter respect, Heterodorus unicus sp. n. is unique within the genus. Where males have been described (in 13 other species), they are provided with 2 to 9 ventromedial supplements.

**Type specimens.** Holotype female on slide No. H-13607. Paratypes: five females, one male and two juveniles. They are deposited in the Department of Systematic Zoology and Ecology of the ELTE University, Budapest.

**Type habitat and locality.** Mosses from a fallen trunk in a rainforest lowland at Kiunga, a port town on the Fly River in the Western Province of Papua New Guinea; collected in July 1969 by J. Balogh.

**Etymology.** The species epithet unicus comes from the Latin and means: alone-standing or unique, referring to the single ventral supplement.

**Heterodorus monticola** sp. n. (Figs. 3–4)

Holotype female: L = 1.32 mm; a = 38; b = 4.9; c = 38; c’ = 1.5; V = 57 %. 

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Figure 3. *Heterodorus monticola* sp. n. A: anterior end; B: posterior pharyngeal region; C: vulval region; D: anterior female gonad. (Scale bars = 20 µm )
**Figure 4.** *Heterodorus monticola* sp. n. A: Female posterior end; B–C: male posterior ends. (Scale bar = 20 µm)
Paratype females (n = 2): L = 1.30–1.45 mm; a = 32–35; b = 5.0–5.4; c = 31–32; c’ = 1.5–1.9; V = 54–55 %.

Paratype males (n = 3): L = 1.26–1.46 mm; a = 37–40; b = 4.6–5.6; c = 33–40; c’ = 1.2–1.3.

**General characters.** Body strongly curved, G-shaped after fixation, 34–41 µm wide at mid-region. Cuticle smooth under light microscope, 1.5–2.0 thick on most part of body. Lip region 12–13 µm wide, practically confluent with adjacent neck, lips amalgamated, rounded. Body at posterior end of pharynx 2.6–2.8 times as wide as lip region. Amphids caliciform with aperture occupying half the corresponding body width.

**Female.** Genital system amphidelphic, each branch 4–6 times as long as mid-body diameter, occupying 12–15 % of body length. Vulva transverse, not sclerotized. Vagina strongly developed, 15 µm broad at its swollen in distal part, 20–22 µm long, extending inwards 52–54 % of corresponding body width. Ovaries reflexed about midway to vulva. Each uterine branch consisting of a proximal wider and a distal narrower section. Uterine eggs not observed. Distance between posterior end of pharynx and vulva 1.7–1.9 times as long as pharynx. Rectum 1.0–1.2 times, prerectum 2.6–2.8 times the anal body width long. Vulva–anus distance equal to 13–14 tail lengths. Tail 35–48 µm long, 2.6–3.3 % of total body length, conoid, ventrally curved with rounded tip.

**Male.** In most respects similar to female. Testes two, opposed, spermatozoa fusiform. Spicula dorylaimoid, 44–46 µm, nearly as long as tail. Adanal pair of supplements located at a distance of 13–14 µm from cloaca. Ventromedial supplements two in two males and three in one male, situated at 66–68, 84–86 and 102 µm from cloaca, respectively. Prerectum longer than the series of supplements. Tail similar to that of female, 38–42 µm long or occupying 2.5–3.1 % of total length of body.

**Diagnosis and relationships.** This new species belongs to the smaller representatives of the genus *Heterodorus*. It is distinguished by its body on average 1.36 mm long, lip region continuous, narrow, odontostyle short, slightly longer than lip region width, pharynx far posteriorly widened, D and PS nuclei large, the former far posterior, the latter in the middle of glandularium, intestine uncoloured, genital system paired, vulva transverse, vagina strongly swollen, two or three ventromedial supplements, and by a short, conical, ventrally curved tail.

In length of the body, the small odontostyle (as long as or only slightly longer than lip region width) and the very posterior location of the D nucleus (at 77–82 % of pharyngeal length), *Heterodorus monticola* sp. n. resembles *H. morgensis* (Loof, 1989) Andrássy, 2009. In comparing the present new species with the descriptions of *H. morgensis* by Loof (1989) from Switzerland, and Guerrero, Liébanas and Peña-Santiago (2007) from the Iberian Peninsula as well as with the paratype specimens (one female and two males) kindly sent by Loof to the present author, it differs by the shorter and plumper tail (35–48 vs. 44–84 µm, c’ = 1.5–1.9 vs. 2.0–2.9; tail in *H. morgensis* sharply tipped), the shorter hyaline portion on tail tip, and especially by the lower number of ventromedial supplements (2–3 vs. 4–7).

By having a small body, narrow lip region and short odontostyle, *Heterodorus monticola* sp. n. can also be compared with *H. liangi* (Ahmad, Wu & Shaheen, 2002) Andrássy, 2009, *H. meghalayensis* (Mushtaq, Baniyamuddin & Ahmad, 2007) Andrássy, 2009 and *H. unicus* sp. n. From *Heterodorus liangi* it differs by the broader lip region (12–13 vs. 9–10 µm), far posteriorly located D nucleus of normal size (77–82 vs. 64–67 %, and exceptionally large), shorter prerectum.
Andrásy: On the genus Heterodorus

(2.6–2.8 vs. 6–8 anal body widths long, and by the longer tail (35–48 vs. 26–30 µm). From H. meghalayensis it differs by the more posteriorly located D nucleus (77–82 vs. 71–72 %), tail with rounded tip (vs. sharply tipped), and by the lower number of medioventral supplements (2–3 vs. 4–6). From Heterodorus unicus it differs by the somewhat longer odontostyle (13–15 vs. 10–11 µm), uncoloured intestine, longer spicula (44–46 vs. 38 µm), and by the number of ventral supplements (2–3 vs. 1).

Type specimens. Holotype female on slide No. H-13661. Paratypes: two females, three males and one juvenile; all deposited in the Department of Systematic Zoology and Ecology of the ELTE University, Budapest.

Type habitat and locality. Soil and detritus from a rainforest (high jungle) at 2600 m above sea level, Oxapampa, Selva Alta Natural Park, eastern side of Pasco Region, Peru; collected in July 1999 by J. Farkas.

Etymology. Latin monticola (a noun) means: a mountain inhabitant, referring to the high altitude level where this species was collected.

Heterodorus alius sp. n.

(Figs. 5–6)

Holotype female: L = 1.14 mm; a = 27; b = 5.1; c = 41; c’ = 1.2; V = 41 %.

Paratype females (n = 2): L = 1.16–1.25 mm; a = 28–33; b = 5.2–5.3; c = 38–40; c’ = 1.3–1.4; V = 39–41 %.

Paratype males (n = 2): L = 1.26–1.30 mm; a = 33–38; b = 5.3–5.5; c = 40–44; c’ = 1.1–1.2.

General characters. Body ventrally curved after fixation, more in posterior half, 35–41 µm wide at mid-region. Cuticle smooth and thin, 1.5 µm thick on most body. Lip region slightly separated, 11–12 µm wide, lips amalgamated. Body at posterior end of pharynx 3.0–3.5 times as wide as lip region. Amphids caliciform, nearly half as wide as corresponding body.

Odontostyle very thin, 13–14 µm long, only 1.1–1.2 times longer than lip region width. Odontophore simple, 20–24 µm long. Guiding ring thin. Pharynx 210–235 µm long, weakly muscular, enlarged at 52–55 % of its length. Dorsal nucleus less conspicuous, at 54–57 % of pharyngeal length or 10–11 % of total body length. AS nuclei inconspicuous, PS nuclei located at 55–57 % of glandularium. Glandularium 95–103 µm long. Cardia hemispherical. Intestine light green.

Female. Reproductive system amphidelphic, anterior genital branch 3.7–4.6 body diameters long, occupying 13–17 % of body length, posterior branch 4.2–5.0 body diameters long, occupying 15–18 % of body length. Ovaries short, reflexed. Each uterus branch with a proximal wider and a distal narrower part. Uterus–oviduct junction with sphincter. Vulva a transverse deep oval slit, its inner lips not sclerotized. Vagina highly developed, strongly swollen distally, 30–34 µm long, occupying 70–75 % of corresponding body diameter. Uterine eggs not observed. Distance between posterior end of pharynx and vulva only slightly longer (1.1 times) than pharynx. Rectum 1.2–1.4, prerectum 2.5–3.2 anal body widths long. Vulva–anus distance equal to 22–23 tail lengths. Tail 28–31 µm long, occupying 2.4–2.5 % of entire length of body, conoid, slightly bent ventrally with finely rounded tip.

Male. In most respects similar to female. Testes two, spermatozoa fusiform. Spicula 50–52 µm long, much longer than tail. Adanal pair of supplements at 8–10 µm from cloaca. Ventromedial supplements six or seven, the posteriormost being with the anterior end of spicula, at 36–38 µm from cloaca, the anteriormost at 150–160 µm from cloacal opening. Tail similar to that of female, slightly ventrally curved, 27–29 µm long, occupying 2.2–2.3 % of entire length of body.

Diagnosis and relationships. Body short, on average 1.22 µm long, lip region slightly offset,
Figure 5. *Heterodorus alius* sp. n. A: anterior end; B: posterior pharyngeal region; C: vulval region; D: detail of the female gonad. (Scale bars = 20 µm)
Figure 6. *Heterodorus alius* sp. n. A–C: female posterior ends; D: male posterior end. (Scale bar = 20 μm)
Andrássy: On the genus Heterodorus

odontostyle thin and scarcely longer than lip region width, pharynx widened slightly posterior to its middle, D nucleus anteriorly located, PS nuclei in the middle of glandularium, genital system paired, vulva transverse, not sclerotized, anterior to the middle of body, vagina very strongly developed, spicula unusually large, male ventral supplements six or seven, the posteriormost at level of proximal end of spicula, and tail short, conoid, slightly ventrally curved with finely rounded tip.

Heterodorus alius sp. n. is an interesting taxon within the genus showing a number of marginal values in its morphological characters. Thus, it differs from the general pattern of Heterodorus in having a longer and stronger cylindrus (pharynx enlarged at 52–55 % vs. 56–75 % in other species), a more anteriorly located dorsal pharyngeal nucleus (D = 54–57 vs. 57–82 %), more anteriorly posited vulva (39–41 vs. 41–58 %), very long vagina (70–75 vs. 36–60 % of body diameter), spicula much longer than tail (vs. as long as or shorter than tail, with one exception), and in having the row of ventromedial supplements closer to the adanal pair than usual.

**Type specimens.** Holotype female on slide No. H-13028. Paratypes: two females, two males and two juveniles. Deposited in the collection of Department of Systematic Zoology and Ecology of the ELTE University, Budapest.

**Type habitat and locality.** Soil with fallen leaves around Styphelia suaveolens (a kind of shrubs of the family Epacridaceae), 4000 m above sea level, Mt. Wilhelm, highest mountain in Papua New Guinea; collected in September 1968 by J. Balogh.

**Etymology.** Latin alius means: different or other, referring to the special structures of this new species.

**Key to species of Heterodorus**

1 Odontostyle 40 µm or longer (to 70 µm) ....... 2
   – Odontostyle 35 µm or shorter (to 10 µm) ....... 6

2 Body 2.5–2.8 mm long ........................... 3
   – Body 1.5–2.0 mm long ........................... 4

3 Tail 25 µm, as long as anal body diameter ....
   ........................................ faeroensis (Ditlevsen, 1928)
   – Tail 60 µm, nearly twice as long as anal body diameter ... maximus (Baquir & Jairajpuri, 1974)

4 Odontostyle 65–70 µm long ........................................ nepalensis (Zullini, 1973)
   – Odontostyle 40–48 µm long ........................... 5

5 Odontostyle as long as 3–4 labial diameters;
   tail tip sharp ........................................ longidens (Jairajpuri & Loof, 1968)
   – Odontostyle as long as 2–3 labial diameters;
   tail tip rounded ........................................ geraldii (Winiszewskia-Slipińska, 1987)

6 Odontostyle longer, 25–35 µm ...................... 7
   – Odontostyle shorter, 10–22 µm ........................ 12

7 Tail 25–50 µm long ........................................ 8
   – Tail 50–80 µm long ........................................ 9

8 Tail tip sharp; male supplements 4–6 .............. constrictus (Jairajpuri & Loof, 1968)
   – Tail tip rounded; male supplements 6–8 ............. transsilvanicus (Ciobanu et al., 2010)

9 Shorter species, 1.1–1.4 mm ........................... southeyi (Jairajpuri & Ahmad, 1986)
   – Longer species, 1.6–2.0 mm ........................... 10

10 Tail 70–80 µm long ........................................ veletensis (Guerrero et al., 2007)
    – Tail 50–60 µm long ..................................... 11

11 Lip region 16–18 µm broad; ventral supplements three . zonatus (Jairajpuri & Loof, 1968)
   – Lip region 12–14 µm broad; ventral supplements six to nine ....... striatus (Thorne, 1939)

12 Tail straight ................................................. 13
   – Tail ventrally arcuate ................................... 14

13 Tail cuticle with numerous “bubbles” ...........
   .................................................... irregularis (Altherr, 1972)
   – Tail cuticle simple, without “bubbles” .......... conicaudatus (Ditlevsen, 1927)

14 Two rows of ring-like lateral body pores present .......... porosus (Guerrero et al., 2007)
   – Lateral body pores absent or inconspicuous ...... 15
15 Labial diameter 16–17 μm ............................. 15
   Labial diameter 9–14 μm .................................. 16
16 Odontostyle 18–22 μm long ......................... 17
   Odontostyle 10–16 μm long .......................... 18
17 Tail short, 28–32 μm, 1.0–1.1 anal body diameter .................... 17
   Tail longer, 55–80 μm, 2.0–2.5 anal body diameters ...........................
   rhaeticus (Altherr, 1952)
18 Dorsal pharyngeal nucleus unusually large ..........................
   liangi (Ahmad et al., 2002)
19 Tail shorter, 1.1–1.4 anal body width long ........................
   Body 1.6–1.9 mm long ...................................... 22
   Body 1.1–1.5 mm long ...................................... 22
20 Odontostyle 15–16 μm long ............................. 21
   Odontostyle 10–14 μm long .......................... 21
21 Spicula 50 μm, much longer than tail; supplements 6–7
   Spicula 38 μm, as long as tail; supplement 1 ........................
   unicus sp. n. .................................................... 24
22 Dorsal pharyngeal nucleus at 78–82 %; tail terminus slightly ventrally arcuate
   Dorsal pharyngeal nucleus at 71–72 %; tail terminus strongly ventrally bent
   brevidentatus (Thorne, 1939)
   morgensis (Loof, 1989)
23 Tail tip rounded; supplements 2–3 ...........................
   Tail tip sharp; supplements 4–7 ........................ 23
24 Dorsal pharyngeal nucleus at 78–82 %; tail terminus slightly ventrally arcuate
   Dorsal pharyngeal nucleus at 71–72 %; tail terminus strongly ventrally bent
   morgensis (Loof, 1989)
   meghalayensis (Mushtaq et al., 2007)

REFERENCES


NICHOLAS, W. L. & STEWART, A. (1985): Criconemella avicenniae n. sp. (Nematoda: Criconematidae) and
Table 4. Main morphometric characters of *Heterodorus* species. (In the de Manian ratios, up: females, down: males)

<table>
<thead>
<tr>
<th>Species</th>
<th>L (mm)</th>
<th>a</th>
<th>b</th>
<th>c</th>
<th>c’</th>
<th>V</th>
<th>Lip w. (µm)</th>
<th>Odont. (µm/lip w.)</th>
<th>Tail (µm)</th>
<th>Spicula (µm)</th>
<th>Suppl.</th>
</tr>
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<td><em>altius</em> sp. n.</td>
<td>1.1-1.2</td>
<td>27-33</td>
<td>5.1-5.3</td>
<td>38-41</td>
<td>1.2-1.4</td>
<td>39-41</td>
<td>11-12</td>
<td>13-14 (1.1-1.2)</td>
<td>28-31</td>
<td>50-52</td>
<td>6-7</td>
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<tr>
<td><em>arctatus</em> (Thorne, 1939)</td>
<td>1.4-2.0</td>
<td>25-35</td>
<td>4.8-6.0</td>
<td>21-32</td>
<td>2.0-2.5</td>
<td>48-57</td>
<td>12-14</td>
<td>18-22 (1.5-1.6)</td>
<td>50-80</td>
<td>42</td>
<td>6</td>
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<tr>
<td><em>brevidentatus</em> (Thorne, 1939)</td>
<td>1.6-1.9</td>
<td>28-38</td>
<td>4.6-6.5</td>
<td>24-34</td>
<td>1.5-2.4</td>
<td>47-54</td>
<td>11-14</td>
<td>12-16 (1.1-1.4)</td>
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<tr>
<td><em>conicaudatus</em> (Ditlevsen, 1927)</td>
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<td>30</td>
<td>6.1</td>
<td>30</td>
<td>1.4-2.2</td>
<td>42</td>
<td>12</td>
<td>18 (1.4)</td>
<td>36-50</td>
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<td><em>constrictus</em> (Jairajpuri &amp; Loof, 1968)</td>
<td>1.2-1.9</td>
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<td>4.3-5.5</td>
<td>23-36</td>
<td>1.5-1.9</td>
<td>49-58</td>
<td>10-14</td>
<td>25-29 (2.0-2.5)</td>
<td>25-50</td>
<td>40-53</td>
<td>4-6</td>
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<tr>
<td><em>faeroensis</em> (Ditlevsen, 1928)</td>
<td>2.8</td>
<td>26</td>
<td>6</td>
<td>28</td>
<td>1.0</td>
<td>41</td>
<td>16</td>
<td>65 (3.0)</td>
<td>25</td>
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<tr>
<td><em>geraldi</em> (Winiszewska-SL, 1987)</td>
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<td>27-38</td>
<td>4.5-5.8</td>
<td>30-38</td>
<td>1.5-2.0</td>
<td>49-52</td>
<td>14-16</td>
<td>39-45 (2.7-3.2)</td>
<td>52-58</td>
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<td>–</td>
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<tr>
<td><em>irregularis</em> (Altherr, 1972)</td>
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<td>7.0-7.3</td>
<td>55-60</td>
<td>1.0-1.2</td>
<td>41-45</td>
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<td>33-34</td>
<td>–</td>
<td>–</td>
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<td><em>liangi</em> (Ahmad et al., 2002)</td>
<td>1.1-1.3</td>
<td>28-38</td>
<td>4.1-5.2</td>
<td>43-49</td>
<td>1.2-1.4</td>
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<td><em>longidens</em> (Jairajpuri &amp; Loof, 1968)</td>
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<td>30-35</td>
<td>1.3-1.8</td>
<td>48-51</td>
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<td>40-48 (3.0-4.0)</td>
<td>45-50</td>
<td>50-56</td>
<td>7-8</td>
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<tr>
<td><em>lushani</em> (Ahmad et al., 2002)</td>
<td>1.3-1.5</td>
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<td>4.6-5.0</td>
<td>47-49</td>
<td>1.0-1.1</td>
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<td>28-32</td>
<td>–</td>
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<td>5.8-6.0</td>
<td>41-43</td>
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<td>60-62</td>
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<td>5.2-5.8</td>
<td>22-24</td>
<td>2.0-2.1</td>
<td>43-46</td>
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<td>12-13 (1.0-1.2)</td>
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<td>40-46</td>
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Table 4. (continued)

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<th>L</th>
<th>a</th>
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<th>c</th>
<th>c'</th>
<th>V</th>
<th>Lip w.</th>
<th>Odontost.</th>
<th>Tail</th>
<th>Spicula</th>
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<td>35–48</td>
<td>44–46</td>
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<td>2.0–2.9</td>
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<td>40–48</td>
<td>39–45</td>
<td>4–6</td>
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<td>1.6–1.7</td>
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<td>50</td>
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<td><em>transilvanicus</em> (Czoba et al., 2010)</td>
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<td>22–30</td>
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<td>28–36</td>
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<td>42–47</td>
<td>47–50</td>
<td>6–8</td>
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<td><em>tropicus</em> (Mushitaq et al., 2007)</td>
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<td>26–29</td>
<td>3.5–3.8</td>
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<td><em>unicus</em> sp. n.</td>
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</tr>
<tr>
<td><em>veletensis</em> (Guerreiro et al., 2007)</td>
<td>1.8–2.0</td>
<td>34–36</td>
<td>4.9–5.3</td>
<td>23–26</td>
<td>2.3–2.6</td>
<td>48–52</td>
<td>16–18</td>
<td>29–31 (1.6–1.9)</td>
<td>72–78</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><em>zonatus</em> (Jairajpuri &amp; Loof, 1968)</td>
<td>1.6–2.0</td>
<td>35–39</td>
<td>4.6–5.8</td>
<td>28–36</td>
<td>1.9–2.2</td>
<td>46–50</td>
<td>16–18</td>
<td>34–35 (2.0)</td>
<td>54–62</td>
<td>52</td>
<td>3</td>
</tr>
<tr>
<td>From – to (range)</td>
<td>1.0–2.8</td>
<td>21–50</td>
<td>3.5–7.2</td>
<td>18–49</td>
<td>1.0–2.9</td>
<td>40–58</td>
<td>9–18</td>
<td>10–70 (1.0–4.3)</td>
<td>24–84</td>
<td>38–60</td>
<td>1–9</td>
</tr>
</tbody>
</table>
Andrássy: On the genus Heterodorus

Enchodelus coomansi n. sp. (Nematoda: Nordiidae) associated with the roots of the mangrove Avicennia marina (Forsk.) Vierh. Nematologica, 30: 429–436.


