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Morphological ontogeny of *Melanozetes avachai* n. sp., a unique member of *Melanozetes* (Acari: Oribatida: Ceratozetidae)

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ABSTRACT — The morphological ontogeny of *Melanozetes avachai* n. sp. from Kamchatka Peninsula (Russia) is described and illustrated. The juveniles of this species have a humeral organ and a humeral macrosclerite, which occur in most Sphaerozetinae (Ceratozetidae), but in the larva seta *c*₁ inserts on microsclerite, rather than on the humeral macrosclerite, which is unique in *Melanozetes*. The larva lacks the gastronotal shield and the gastronotal setae are inserted on microsclerites, which is unique in *Melanozetes*; other species have these setae inserted on the gastronotal shield. The juveniles of *M. avachai* also differ from congeners by the length and shape of some gastronotal setae. All instars of *M. avachai* have femora I and II uniquely oval in cross section; in all other species of *Melanozetes* at least femur II is flattened, with a ventral carina. The adult of *M. avachai* differs from congeners by its larger body size and longer prodorsal seta *le*. The translamella is variable in *M. avachai*; usually it is absent, but may be incomplete, or present. The diagnosis of *Melanozetes* is modified and enlarged with the morphological characters of juveniles.

KEYWORDS — Oribatid mites; Sphaerozetinae; juveniles; leg setation; stage structure

INTRODUCTION

*Melanozetes* Hull, 1916 is a well defined genus, if we limit the number of notogastral setae of the adults to 14 pairs, including *c*₂ and *c*₃ (Seniczak *et al*. 2015). This genus is not rich in species. Subías (2015) listed 21 species and two subspecies in this genus, but according to Seniczak *et al*. (2015) this number is much lower mainly because of the nine species that are unrecognizable as nymphs. *Melanozetes* species differ from one another mainly by their body size, the length of the lamella and lamellar cusp, the shape of the sensillus, the length and shape of notogastral setae and the size of porose area *Aa* (Seniczak *et al*. 2015).

The juveniles of *Melanozetes* species are less well-known. Based on the catalogue of Norton and Ermilov (2014) and the publication of Seniczak *et al*. (2015), the full ontogeny of only four species of this genus is known:

(1) *Melanozetes azoricus*: Seniczak *et al*. (2015) described and illustrated the morphological ontogeny, including leg setae and solenidia.

(2) *Melanozetes interruptus* Willmann, 1953: Seniczak (1993d) described and illustrated the morphological ontogeny.

(3) *Melanozetes meridianus* Sellnick, 1928: Tuxen (1943) described and illustrated a nymph and
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Seniczak (1989a) described and illustrated the morphological ontogeny.

(4) Melanozetes molliconus (C. L. Koch, 1839): Michael (1884) described and illustrated a nymph, Hammenn (1952) described and illustrated a tritonymph and Shaldybina (1967) and Seniczak (1989a) described and illustrated the morphological ontogeny.

Our knowledge of juveniles of M. stagnatilis (Hull, 1914), Melanozetes sellnicki (Hammer, 1952) and Melanozetes crossleyi Behan-Pelletier, 2000 is incomplete in that only the adults and some nymphs of these species are known (Hull 1914; Behan-Pelletier 1985; Behan-Pelletier 2000, respectively).

The aim of this paper is to propose M. avachai n. sp. based on a collection from Kamchatka, and to describe and illustrate its morphological ontogeny, and then compare it and morphology of the adult with that of other species of Melanozetes.

**MATERIAL, METHODS AND TERMINOLOGY**

The juveniles and adults of M. avachai n. sp. used in this study were collected on 20 June 2014 in Nalychevo Nature Park, at the bottom of Avacha volcano in the Kamchatka Peninsula, Russia (53°13'98"N, 158°41'00"E, 548 m a. s. l.). Specimens were extracted from dense moss covering the floor of a deciduous forest, with alder (Alnus fruticosa Ruprecht) dominating, but also with some birch (Betula ermanii Gray). The morphological ontogeny of M. avachai is similar to that of M. azoricus Weigmann, 1976, as described by Seniczak et al. (2015). Therefore, the illustrations of instars are limited to the body regions of mites that show substantial differences, including the dorsal, lateral and some ventral regions of the larva, tritonymph and adult. The legs and palp of some instars are also illustrated, as well as the chelicera of the adult. Illustrations were prepared from individuals mounted temporarily on slides in lactic acid. We measured total length of the mites’ body (excluding chelicerae if extended) and maximum body width. All measurements are given in μm. In the text and figures we used the following abbreviations: rostral (ro), lamellar (le), interlamellar (in) and exobothridial (ex) setae, lamella (La), translamella (tr), bothridium (bo), sensillus (ss), pteromorph (ptm), tutorium (tut), genal tooth (gt), pedotectum (pd), notogastral or gastronotal setae (c-, d-, h-, p-series), anal and anal setae (ad-, an-series), aggenital seta (ag), epimeral setae (3a, 3b, 4a-c), lyrifissures or cupules (ia, im, ip, ih, ips, iad), humeral sclerite (hs), opisthonotal gland opening (glA), humeral organ (oh), subcapitular setae (a, m, h), axillary saccula of subcapitulum (sac), epimeral setae (1a-c, 2, 3a-c, 4a-c), leg solenidia (σ, ϕ, ω), famulus (e) and setae (bv, d, f, ft, tc, ti, p, u, a, s, pv, pl, v), and palp setae (sup, inf, l, d, cm, acm, it, vt, ul, su) and solenidion ω. Terminology used follows that of Grandjean (1939, 1949, 1953), Behan-Pelletier (1985, 1986) and Norton & Behan-Pelletier (2009). The species nomenclature follows Subías (2004, 2015) and Weigmann (2006).

**Melanozetes avachai n. sp.**

Diagnosis — Adult relatively long (length of females 831 – 864, and males 717 – 799), with characters of Melanozetes (Shaldybina 1975). Lamellar cusp short, translamella usually absent, but may be present or incomplete. Seta le almost as long as in, sensillus clavate. Notogastral setae with barbs. Femora I and II oval in cross section, without ventral carina. Larva without gastronotal shield and seta c1 inserted on microsclerite, not on humeral macrosclerite, nymphs with uniform gastronotal shield bearing 10 pairs of smooth setae, c1 on humeral macrosclerite, c2, c3, p2 and p3 on microsclerites. Humeral organ present. Femora I and II oval in cross section, without ventral carina.

Description of adult — Body oval in dorsal aspect (Figure 1), females usually slightly larger than males. Measurements: length of holotype (female 799), mean of 30 females - 810.1 (range 831 – 864) and 30 males - 751.4 (range 717 – 799); notogaster width of holotype (455), mean of 30 females - 491.4 μm (range 462 – 546) and 30 males - 443.9 μm (range 423 – 468).

Integument — Posterior part of prodorsum, central part of notogaster and ventral plate microscopere, with light dots (Figure 1B), marginal parts of notogaster and pteromorphs microscopere and reticulate (Figure 1C), other parts of body microscopere.
FIGURE 1: *Melanozetes avachai* n. sp., adult: A – dorsal aspect, legs partially drawn, scale bar 100 μm; B – microporose notogaster, with light dots and seta *da*; C – reticulate pattern of pteromorph.
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Table 1: Measurements of some morphological characters of juvenile stages of Melanozetes avachai n. sp. (mean measurements of 3-10 specimens in µm).

<table>
<thead>
<tr>
<th>Morphological characters</th>
<th>Larva</th>
<th>Protonymph</th>
<th>Deutonymph</th>
<th>Tritonymph</th>
<th>Adult</th>
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<tbody>
<tr>
<td>Body length</td>
<td>340</td>
<td>423</td>
<td>501</td>
<td>689</td>
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<tr>
<td>Body width</td>
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<td>195</td>
<td>264</td>
<td>358</td>
<td>423</td>
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<tr>
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<td>125</td>
<td>139</td>
<td>156</td>
<td>191</td>
<td>190</td>
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<tr>
<td>Length of: sensillus</td>
<td>30</td>
<td>38</td>
<td>43</td>
<td>48</td>
<td>35</td>
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<tr>
<td>seta ro</td>
<td>32</td>
<td>34</td>
<td>37</td>
<td>40</td>
<td>91</td>
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<td>118</td>
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<tr>
<td>seta cx</td>
<td>8</td>
<td>11</td>
<td>19</td>
<td>21</td>
<td>46</td>
</tr>
<tr>
<td>seta c 1</td>
<td>18</td>
<td>18</td>
<td>32</td>
<td>33</td>
<td>Lost</td>
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<td>21</td>
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<td>22</td>
<td>22</td>
<td>69</td>
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<td>20</td>
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<td>21</td>
<td>65</td>
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<tr>
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<td>20</td>
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<td>22</td>
<td>22</td>
<td>67</td>
</tr>
<tr>
<td>seta h 1</td>
<td>23</td>
<td>21</td>
<td>22</td>
<td>22</td>
<td>69</td>
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<td>seta h 2</td>
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<td>21</td>
<td>21</td>
<td>21</td>
<td>67</td>
</tr>
<tr>
<td>seta h 3</td>
<td>5</td>
<td>21</td>
<td>22</td>
<td>22</td>
<td>69</td>
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<tr>
<td>seta p 1</td>
<td>Not developed</td>
<td>18</td>
<td>21</td>
<td>21</td>
<td>68</td>
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<tr>
<td>genital opening</td>
<td>Not developed</td>
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<td>51</td>
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<td>anal opening</td>
<td>68</td>
<td>79</td>
<td>100</td>
<td>136</td>
<td>129</td>
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</table>

Prodorsum — Subtriangular, rostrum rounded (Figure 1). Seta ro relatively long (Table 1), positioned laterally and barbed laterally. Seta le nearly as long as in, barbed, acuminate, seta cx short. Lamella (La) long (118 – 122), with longitudinal striae, translamella (tr) usually absent, but may be present or incomplete (Figure 2), lamellar cusp short (10) and rounded. Bothridium (bo) with well-developed medial and lateral scales; sensillus (ss) short (Table 1), clavate, with smooth stalk and barbed head. Humerosejugal porose area A1 oval.

Notogaster — Longer (females 585 – 650, males 520 – 585) than wide (females 462 – 546, males 423 – 468), with well-developed, immovable pteromorphs. Notogastral setae (14 pairs, including c2 and c3) relatively long (Figures 1, 3A; Table 1) and barbed. lyrifissures ia, im, ip, ih, ips and opisthontal gland opening (gla) and porose areas (4 pairs) in normal position, Aa largest.

Gnathosoma — Subcapitular seta h longer (45) than m (41) and a (31); all smooth (Figure 4). Chelicera (length 209 – 212) with seta cha (64) barbed and chb (33) smooth (Figure 5D). Axillary saccula of subcapitulum (sac) short (16). Palp (length 126 – 129) with seta inf’ barbed, other setae smooth (Figures 5A-C). Formula of palp setae (trochanter to tarsus + solenidion ω): 0-2-1-3-9(1).

Epimeral and lateral regions — Central epimeral setae (1a, 2, 3a, 3b, 4a, 4b) short (18 – 22) and smooth (Figure 4), marginal setae longer (37 – 41), and finely barbed, 1b longest (51). Tutorium (tu) long (148 – 162) and narrow, and distally pointed. Humerosejugal porose areas Am and Ah and sublamellar porose are A1 present. Pedotectum I (pd1) large, oval (131 × 56), with longitudinal striae (Figure 3A). Genal tooth (gtl) long (38), narrow and pointed, custodium (cus) shorter (20), triangular and blunt. Discidium (dis) triangular. Circumpedal carina (cp) well-formed.
Figure 2: Melanozetes avachai n. sp., adult, prodorsum and part of notogaster, legs partially drawn, scale bar 50 µm: A, B – different individuals, showing variation in form of translamella.
Figure 3: *Melanocetes avachai* n. sp., adult, legs partially drawn, scale bars 100 µm: A – lateral aspect; B – anogenital region.
FIGURE 4: *Melanozetes avachai* n. sp., adult, anterior half of ventral side, legs removed, scale bar 50 µm.
FIGURE 5: Melanozetes avachai n. sp., antiaxial aspect, scale bars 20 µm: A, B, C – palps of adult, tritonymph and larva, respectively; D – chelicera of adult, a hole through the chelicera partially shows the Traghardt’s organ on the opposite side.
FIGURE 6: Melanozetes avachai n. sp., adult, leg segments, antiaxial aspect, setae on the opposite side are not illustrated (in brackets), scale bar 20 μm: A – leg I, femur (l’), genu (l’), tibia (v’), tarsus (p’); B – region of solenidia ω1 and ω2 on tarsus I; C – leg II, femur (l’), tibia (v’); D – leg III, tibia (v”); E – leg IV.
TABLE 2: Ontogeny of leg setae (Roman letters) and solenidia (Greek letters) in Melanozetes avachai n. sp.

<table>
<thead>
<tr>
<th>Leg</th>
<th>Trochanter</th>
<th>Femur</th>
<th>Genu</th>
<th>Tibia</th>
<th>Tarsus</th>
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</thead>
<tbody>
<tr>
<td>Larva</td>
<td>–</td>
<td>d, bo&quot;</td>
<td>(l), σ</td>
<td>(l), v’, ϕ₁</td>
<td>(ft’), (tc’), (p’), (u’), (a’), s, (pv’), (pl’), ε, ω₁</td>
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<td>Protonymph</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Deutonymph</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Tritonymph</td>
<td>v’</td>
<td>(l)</td>
<td>v’</td>
<td>v”</td>
<td>(ft’)</td>
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<tr>
<td>Adult</td>
<td>–</td>
<td>v’”</td>
<td>–</td>
<td>–</td>
<td>l”’, v’</td>
</tr>
<tr>
<td>Larva</td>
<td>–</td>
<td>d, bo’’</td>
<td>(l), σ</td>
<td>l’, v’, ϕ’</td>
<td>(ft’), (tc’), (p’), (u’), (a’), s, (pv’), ω₂</td>
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<tr>
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<tr>
<td>Deutonymph</td>
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<td>–</td>
<td>–</td>
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<tr>
<td>Tritonymph</td>
<td>v’</td>
<td>(l)</td>
<td>–</td>
<td>l”’, v”</td>
<td>(ft’)</td>
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<tr>
<td>Adult</td>
<td>–</td>
<td>v’”</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Larva</td>
<td>–</td>
<td>d, co’</td>
<td>l’, σ</td>
<td>v’, ϕ’</td>
<td>(ft’), (tc’), (p’), (u’), (a’), s, (pv’), ω₂</td>
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<td>–</td>
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<td>l’</td>
<td>–</td>
<td>–</td>
<td>(ft’)</td>
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<tr>
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<td>–</td>
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<td>d, v’</td>
<td>v’, ϕ’</td>
<td>(ft’), (tc’), (p’), (u’), s</td>
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<td>Tritonymph</td>
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<td>–</td>
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<td>l’’, v”</td>
<td>–</td>
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<td>Adult</td>
<td>–</td>
<td>–</td>
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</tbody>
</table>

Note: structures are indicated where they are first added and are present through the rest of ontogeny; pairs of setae in parentheses, dash indicates no additions.

Anogenital region — Genital setae (six pairs) about equally as long (15 – 18) as aggenital (one pair), adanal (three pairs) and anal (two pairs) setae (Figure 4). Lyrifissures iad short, located close to anterior end of anal opening. Postanal porose present.

Legs — Femora I and II oval in cross section, without ventral carina. Porose areas present on paraxial side of femora I-IV and trochanters III and IV. Solenidion ω₂ on tarsus I longer than ω₁, and located anterolateral to ω₁; famulus c short, seta ft” minute (Figure 6); solenidia ω₁ and ω₂ on tarsus II of similar size. Seta l” on genua I and II and seta d on femora III and IV thicker than other leg setae. Formulae of leg setae [trochanter to tarsus (+ solenidia)]: I - 1-5-3(1)-4(2)-20(2); II - 1-5-3(1)-4(1)-15(2); III - 2-3-1(1)-3(1)-15; IV - 1-2-2-3(1)-12 (Table 2).

Description of juveniles — Larva oval in dorsal view (Figure 7), main body unpigmented, except light brown sclerites and legs. Prodorsum triangular, with setae ro and le of medium size, in long (Table 1) and ex short; all barbed. Mutual distance of setae ro> mutual distance le > greater than mutual distance in; pair le inserted approximately in midway between pairs ro and in. Opening of bothridium rounded, sensillus clavate with barbed head. Lateral depression present above leg I. Prodorsum porose, porosity denser posteriorly.

Gastronotum of larva (Figures 7, 8A) unsclerotized, except for three pairs of glabrous, aligned macrosclerites (well-formed humeral macrosclerite and two elongated lateral macrosclerites), and 12 pairs of setae, including h₃ inserted lateral to middle part of anal valves. Gastronotal setae (12 pairs) short and barbed, except smooth h₂ and minute h₃, inserted lateral to middle of anal valves; all on microsclerites, except h₃; other microsclerites present in central part of gastronotum. Cupule ia posteroverentral to seta c₃, cupule im posterior to seta lm,
FIGURE 7: *Melanozetes avachai* n. sp., larva: A – Dorsal aspect, legs partially drawn, scale bar 50 µm; B – gastronotal seta $c_1$. 
FIGURE 8: *Melanocotes avachai* n. sp., lateral aspect, legs partially drawn, scale bars 50 μm: A – larva; B – tritonymph.
Figure 9: Melanozetes avachai n. sp., lateral aspect, legs partially drawn, scale bars 50 µm: A – larva; B – tritonymph.
Figure 10: *Melanozetes avachai* n. sp., legs partially drawn, anogenital region, scale bars 50 μm: A – deutonymph; B – tritonymph.
FIGURE 11: *Melanozetes avachai* n. sp., tritonymph: A – Dorsal aspect, legs partially drawn, scale bar 100 µm; B – part of gastronotum with seta *c₂*; C – part of gastronotum with seta *da*.
cupule ip lateral to seta h2, cupule ih lateral to anterior end of anal opening; opisthonotal gland opening gla on microsclerite, lateral to ih and humeral organ (oh) located anterolateral to seta c3. Paraproctal valves (segment PS) glabrous.

Main body of protonymph and legs light brown. Compared to larva, prodorsum relatively shorter, setae slightly longer (Table 1), and sensillus relatively slimmer. Gastronotum with 15 pairs of setae due to appearance of p-series (Figure 9A), which are retained by subsequent nymphs (Figures 10A, B); all setae smooth, except barbed which are retained by subsequent nymphs (Figures 10B). Gastronotal macroscel erite uniform, reticulate, with 10 pairs of setae (d-, l-, h-series and p1); setae p2 and p3 on microsclerites. In protonymph one pair of genital setae on genital valves, and two pairs are added in both deutonymph and tritonymph. Opisthonotal gland opening gla lateral to seta ip, with dark, porose sclerite, humeral organ oh located anterolateral to seta c3. Deutonymph with one pair of aggenital setae and three pairs of adanal setae (Figure 10A), remaining in subsequent instars; all short and smooth. Tritonymph with two pairs anal setae on anal valves (Figure 10B). Prodorsum of tritonymph relatively shorter (Figure 10; Table 1) than in other nymphs, but setae similar. Lateral integument with five macroscleerites, four elongated and one smaller (Figure 8B). Cupules ia and im placed as in larva, cupule ip between setae p1 and p2, cupule iad lateral to anterior part of anal valves, cupules ips and ih displaced posterolateral to iad. Setae of p-series (three pairs) longer than ad-series (three pairs) and an-series (two pairs); all smooth, p2 and p3 on microsclerites (Figure 10B). Genital setae (five pairs) and aggenital setae (one pair) short and smooth. Femora I and II oval in cross section, without ventral carina. Location and shape of solenidia on tarsus I of tritonymph (Figure 11) similar as in adult, but some setae on leg segments (d on femora I and II and genu IV, l’ on genua I and II and tibia II, l’ on genu and tibia III and tibia IV, v’ on tibia III and IV) thicker.

Summary of ontogenetic transformations — Setae ro and le are of medium size, in is long and ex is short in all juveniles, whereas in the adult ro and le are long, but cx remains short. The sensillus is relatively thicker in the larva than in the nymphs and adult. The larva has 12 pairs of gastronotal setae, including h3, the nymphs have 15 pairs. A humeral macroscleerite is present in all juvenile instars, but in the larva it is glabrous and in the nymphs it bears seta c1. Gastronotal macroscleerite is absent in the larva and is well-formed in the nymphs. The nogaaster of adult loses seta c1. The number of leg setae and solenidia increases during the ontogeny (Table 2), but some setae of tritonymph are thicker than in the adult.

Ecology and biology — We found M. avachai n. sp. in one sample (1 dm3) in dense moss in the floor of deciduous forest, with alder dominating and some birch. Density of oribatid mites was 345 individuals per 500 cm3, with M. avachai the dominant oribatid mite (59.8 %). In M. avachai, the adults dominated (67 % of all individuals), and the stage structure of this species was the following: 22 larvae, 38 protonymphs, 3 deutonymphs, 6 tritonymphs and 137 adults. The mean sex ratio (females to males) was 1:1.5. Most females (87 %) were gravid and carried 4-5 large eggs.

Type deposition — The holotype and 6 paratypes (in 70 % ethanol) are deposited in the University Museum of Bergen (Norway) and 6 paratypes are deposited in the Department of Evolutionary Biology, Kazimierz Wielki University, Bydgoszcz, Poland.

Etymology — The species epithet avachai refers to the Avacha volcano (Kamchatka, Russia), the type locality.

Comparison of ontogeny among species of Melanozetes

We compare the morphological ontogeny of M. avachai n. sp. with that of other species of Melanozetes with known ontogeny, namely M. azoricus investigated by Seniczak et al. (2015), M. meridianus and M. mollicomus studied by Seniczak (1989a) and M. interruptus investigated by Seniczak (1993d). We also used the morphology of the nymphs and adults of M. sellnicki and M. crosleyi studied by Behan-Pelletier (1985) and Behan-Pelletier (2000),
Table 3: Selected morphological characters of Melanozetes avachai n. sp., M. azoricus Weigmann, 1976, M. interruptus Willmann, 1953, M. meridianus Sellnick, 1928 and M. mollicomus (C.L. Koch, 1839).

<table>
<thead>
<tr>
<th>Morphological characters</th>
<th>M. avachai</th>
<th>M. azoricus</th>
<th>M. interruptus</th>
<th>M. meridianus</th>
<th>M. mollicomus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body length/width</td>
<td>1.060</td>
<td>1.063</td>
<td>1.066</td>
<td>1.067</td>
<td>1.059</td>
</tr>
<tr>
<td>Lamellar cusp</td>
<td>Short</td>
<td>Medium sized</td>
<td>Medium sized</td>
<td>Medium sized</td>
<td>Medium sized</td>
</tr>
<tr>
<td>Presence of translammella</td>
<td>Present/absent</td>
<td>Present/absent</td>
<td>Absent</td>
<td>Present</td>
<td>Absent</td>
</tr>
<tr>
<td>Shape of sensillus</td>
<td>Clavate</td>
<td>Fusiform</td>
<td>Fusiform</td>
<td>Fusiform</td>
<td>Fusiform</td>
</tr>
<tr>
<td>Length of seta in</td>
<td>Neatly</td>
<td>Clearly</td>
<td>Clearly</td>
<td>Clearly</td>
<td>Clearly</td>
</tr>
<tr>
<td></td>
<td>as long as</td>
<td>as short as</td>
<td>as short as</td>
<td>as short as</td>
<td>as short as</td>
</tr>
<tr>
<td>Length of seta c3</td>
<td>As long as</td>
<td>c3</td>
<td>c3</td>
<td>c3</td>
<td>c3</td>
</tr>
<tr>
<td>Barbs on most notogastral setae</td>
<td>Present</td>
<td>Present</td>
<td>Absent</td>
<td>Absent</td>
<td>Present</td>
</tr>
<tr>
<td>Juvenile: shape of sensillus</td>
<td>Clavate</td>
<td>Clavate</td>
<td>Fusiform</td>
<td>Fusiform</td>
<td>Fusiform</td>
</tr>
<tr>
<td>Nymphic: length of seta c1</td>
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<td>c1</td>
<td>As short as c1</td>
<td>Longer than c1</td>
<td>As short as</td>
</tr>
<tr>
<td>Microsclerites at setae c2 and c3</td>
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<td>Absent</td>
<td>Present</td>
<td>Present</td>
<td>Present</td>
</tr>
<tr>
<td>Barbs on most gastronotal setae</td>
<td>Absent</td>
<td>Present</td>
<td>Absent</td>
<td>Present</td>
<td>Present</td>
</tr>
<tr>
<td>Microsclerites at setae p2 and p3</td>
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<td>Absent</td>
<td>Present</td>
<td>Absent</td>
<td>Present</td>
</tr>
<tr>
<td>Larva: seta c1, located</td>
<td>Outside hs</td>
<td>On hs</td>
<td>On hs</td>
<td>On hs</td>
<td>On hs</td>
</tr>
<tr>
<td>Microsclerites at setae c2 and c3</td>
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<td>Absent</td>
<td>Present</td>
<td>Present</td>
<td>Absent</td>
</tr>
<tr>
<td>Gastronotal shield</td>
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<td>Present</td>
<td>Present</td>
<td>Present</td>
<td>Present</td>
</tr>
<tr>
<td>Most gastronotal setae inserted on</td>
<td>Microsclerites</td>
<td>Gastronotal shield</td>
<td>Gastronotal shield</td>
<td>Gastronotal shield</td>
<td>Gastronotal shield</td>
</tr>
<tr>
<td>Shape of seta dp</td>
<td>Barbed</td>
<td>Barbed</td>
<td>Smooth</td>
<td>Smooth</td>
<td>Smooth</td>
</tr>
<tr>
<td>Barbs on most gastronotal setae</td>
<td>Present</td>
<td>Present</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
</tr>
</tbody>
</table>

* – according to Seniczak et al. (2015); † – according to Seniczak (1993d); ‡ – according to Seniczak (1989a).

respectively. The morphology of the adult of M. avachai was compared with that of M. orientalis Shaldybina, 1969 and M. altaicus Shaldybina, 1969 described by (Shaldybina 1969), M. tanana Behan-Pelletier, 1986 studied by Behan-Pelletier (1986) and M. exobothridialis Bayartogtokh and Aoki, 1998 described by Bayartogtokh and Aoki (1998).

It is evident that the juveniles of M. avachai have several morphological characters that are typical of Melanozetes (Table 3), but the larval lack a gastronotal shield, and seta c1 located on a microsclerite, outside the humeral macrosclerite, are unique character states in Melanozetes; in other species the gastronotal shield is present and c1 is inserted on the humeral macrosclerite. The tritonymphs of M. sellnicki and M. crossleyi have a clavate sensillus and seta c1 inserted on the humeral macrosclerite, but in the former species other setae of the c-series are placed on microsclerites, as in M. avachai, whereas in the latter species they are on un sclerotized integument, as in M. azoricus.

The juveniles of M. avachai have femora I and II oval in cross section and clearly slimmer than those of M. azoricus, and without ventral carina (Figure 12), whereas in the latter species these femora are wide, flattened, with a large, ventral carina. The tritonymph of M. sellnicki and M. crossleyi also have femora I and II flattened, with ventral carina. The nymphs of M. avachai have solenidion ω2 on tarsus I longer than ω1 and located anterolateral to solenidion ω1, as in those of M. azoricus.

The adult of M. avachai differs distinctly from M. azoricus, M. meridianus and M. mollicomus by larger body size (Table 3), and from M. interruptus it differs mainly by shorter lamella and lamellar cusp, larger porose area Aa and a clavate sensillus; in M. interruptus the sensillus is fusiform.

Considering the shape of lamellar cusp, M. avachai is most similar to M. tanana, but the latter species is distinctly smaller and more stocky (females - mean length 553, mean width 353; males - mean length 545, mean width 351) than M. avachai. Additionally, in M. tanana the lamellar cusps are thicker and closer together (Behan-Pelletier 1986) than in M. avachai, porose area Aa is smaller and the clavate sensillus has longer barbs than M. avachai.

Other species of Melanozetes are also smaller than M. avachai. The body length of females and males of M. sellnicki is 421 – 473 and 421 – 447, respectively, that of M. crossleyi is 600 – 624 and 557 – 596, respectively), and both species have distinctly longer lamella and lamellar cusp than M.
FIGURE 12: *Melanozetes avachai* n. sp., tritonymph, leg segments, antiaxial aspect, setae on the opposite side are not illustrated (in brackets), scale bar 20 μm: A – leg I, femur (l’), tibia (l’), tarsus (p’); B – leg II, femur (l’), tibia (p’); C – region of solenidia ω₁ and ω₂ on tarsus I; D – leg III, tibia (v’); E – leg IV, tibia (v’).
avachai. The length of *M. altaicus* is 537 – 559 and *M. orientalis* is 516 – 602, and the former species has smaller area porose *Aa* and distinctly longer lamella and lamellar cusp than *M. avachai*, whereas the latter species has distinctly shorter notogastral setae than *M. avachai*. *Melanozetes exobothridialis* is smaller (length 616 – 688) than *M. avachai*, and has longer lamella and lamellar cusp and seta *ex* than *M. avachai*, but the shape of translamella also varies in it (can be absent or incomplete), as in *M. avachai*.

The leg femora I and II of adult of *M. avachai* are slimmer than in *M. azoricus*, and have no ventral carina, whereas the latter species has these femora flattened, and with ventral carina. Flattened femora I and II are also observed in *M. sellnicki*, *M. tanana* and *M. crossleyi*, whereas in *Melanozetes meridianus* Sellnick, 1928 sensu Behan-Pelletier (1986) only femur II is flattened, with ventral carina. The adult of *M. azoricus* has the solenidion *ω*₂ on tarsus I longer than *ω₁*, and located anterolateral to solenidion *ω₁*, as in *M. azoricus*. Similar shape and location of these solenidia was observed in other species of *Melanozetes* studied by Behan-Pelletier (1985, 1986, 2000).

**DISCUSSION**

*Melanozetes avachai* n. sp. is an interesting member of *Melanozetes* because the larva lacks the gastronotal shield, which is present in other species of *Melanozetes* with known ontogeny (Seniczak 1989a; Seniczak 1993d; Seniczak et al. 2015). The larva of *M. avachai* has seta *c₁* inserted on a microsclerite, whereas in other species of *Melanozetes* it is located on a humeral microsclerite.

Considering the larva of *M. avachai*, it seems to be more similar to that of *Fuscozetes fuscipes* (C. L. Koch, 1841) than to other species of *Melanozetes*. The larvae of both species have a humeral macrosclerite with no seta *c₁* and in both species the gastronotal shield is absent and gastronotal setae are inserted on microsclerites (Seniczak 1989b). In some species of *Fuscozetes* we observe reduction of gastronotal shield size in the larvae. For example, in *F. setosus* (C. L. Koch, 1941) this shield is uniform (Seniczak 1989b), in *F. tatricus* Seniczak, 1993 it is divided in two parts (Seniczak 1993c), whereas in *F. fuscipes* the gastronotal shield is reduced to three pairs of medium sized macrosclerites (Seniczak 1993d). In the larvae of *Sphaerozetes*, the gastronotal shield can be present (Seniczak et al. 2016a) or absent (Seniczak et al. 2016b). In Trichoribatinae sensu Shaldybina (1975) the gastronotal shield is usually absent (Behan-Pelletier 1985; Seniczak 1980a, d, 1993a, b; Seniczak & Solhøy 1987), but in some species is present (Seniczak 1993d). In Ceratozetinae sensu Shaldybina (1975), the gastronotal shield of juveniles is reduced in size, especially in the larvae, and in some species only microsclerites remain on the larval gastronotum, some with gastronotal setae (Behan-Pelletier 1984). All these observations indicate that the presence or absence of gastronotal shield in the larvae of Sphaerozetinae has specific value.

In all instars of *M. avachai* femora I and II are slimmer than in those of *M. azoricus*, especially in the juveniles, and without ventral carina, which is unique in *Melanozetes*, and more similar to those of *Fuscozetes setosus* than *Melanozetes* (Seniczak et al. 2015). The shape of femora I and II of juveniles of other species of *Melanozetes* is poorly known, but in the adults these femora are wide, flattened, and with ventral carina (Behan-Pelletier 1985, 1986), and flattened femur II with ventral carina was considered typical of *Melanozetes* (Behan-Pelletier 1985).

Some similarities of the larva of *M. avachai* to that of *F. fuscipes*, and similar shape of femora I and II to those of *F. setosus* may raise a question if *M. avachai* belongs to *Melanozetes*. Our answer is positive because this species has three morphological characters of generic value:

1. the adult has 14 pairs of notogastral setae, including *c₂* and *c₃*, as other species of *Melanozetes*;
2. the nymphs have notogastral macrosclerite with seta *c₁*, as other species of *Melanozetes*;
3. the nymphs and adult have solenidion *ω₂* on tarsus I longer than *ω₁* and located anterolateral to solenidion *ω₁*, as other species of *Melanozetes* (Seniczak et al. 2015). *Melanozetes* is sometimes confused with *Fuscozetes*, but latter genus has 10-13 pairs of notogastral setae in the adult, including *c₂*, and the nymphs and adult have solenidion *ω₂* on
tarsus I shorter than $\omega_1$ and located posterolateral to solenidion $\omega_1$ (Seniczak et al. 2015).

According to Grandjean (1939, 1949, 1953), Shaldybina (1972) and Seniczak et al. (1990, 2015), the number of notogastral setae of adults is important because it is helpful in explaining the phylogeny of Ceratozetidae. For example, the adult of \textit{Ghilarovizetes} Shaldybina, 1969 has 15 pairs of notogastral setae, retaining all setae in this region from the tritonymph, \textit{Melanozetes} loses one seta of c-series ($c_1$) and 14 pairs of notogastral setae remains (Shaldybina 1975; Seniczak et al. 1990; Pavlichenko 1994), \textit{Fuscozetes} Sellnick, 1928 loses two setae of c-series ($c_1$ and $c_3$), and sometimes some or all setae of d-series, such that 10-13 pairs on notogastral setae remain, including $c_2$ (Seniczak 1989b, 1993c, Seniczak et al. 1991), whereas \textit{Edwardzetes} Berlese, 1914 loses two setae of c-series ($c_1$ and $c_3$) and all setae of d-series, such that 10 pairs on notogastral setae remain (Seniczak et al. 1990, 2016a). \textit{Sphaerozetes} Berlese, 1885 has the same setal count (11 pairs of notogastral setae) as some species of \textit{Fuscozetes}, but the pattern of notogastral setae is different: it retains $c_2$ and $c_3$, but no setae of the d-series (Seniczak et al. 1990, 2016a, b), whereas \textit{Fuscozetes} retains $c_2$ (but not $c_3$) and dp. \textit{Melanozetes} and \textit{Ghilarovizetes} differ from other genera of Sphaerozetinae sensu Shaldybina (1975) by the location and length of solenidion $\omega_2$ on tarsus I in the nymphs and adult (Seniczak et al. 2015, 2016a). In \textit{Melanozetes} and \textit{Ghilarovizetes} solenidion $\omega_2$ is inserted anterolateral to solenidion $\omega_1$ and is longer than $\omega_1$, whereas in \textit{Fuscozetes}, \textit{Edwardzetes} and \textit{Sphaerozetes} solenidion $\omega_2$ is inserted posterolateral to solenidion $\omega_1$ and is shorter and thinner than $\omega_1$.

It is interesting to compare \textit{M. avachai} and other species from the Asian Far East with those from Western North America because these regions were connected during the Pleistocene and subsequently separated by the Bering Strait. The general morphology of adults of these species is similar, but the shape of the translamella of adults varies in \textit{M. avachai} and \textit{M. azoricus} from Kamchatka and in \textit{M. exobothridialis} from Mongolia (Bayartogtokh and Aoki 1998), whereas the \textit{M. tanana} from the western North American arctic has no translamella (Behan-Pelletier 1986). Further research on juveniles of species from these regions may provide clarification on species relationships.

Seniczak et al. (2015) modified the diagnosis for adults of \textit{Melanozetes} given by Behan-Pelletier (1985), but in the light of our observations this diagnosis needs the further modification: the adults have femora I and II with or without ventral carina.

We enlarge the diagnosis of \textit{Melanozetes} by including the following morphological characters of juveniles. Juveniles oval in dorsal view, unscleritized, with brown sclerites and legs. Humeral organ and humeral macro sclerite present. Larva with 12 pairs of gastronotal setae, including $h_3$, nymphs with 15 pairs. Seta $c_1$ on humeral macro sclerite, but in larva can be on micro sclerite or unsclerotized integument; other setae of c-series on unsclerotized integument or micro sclerites. Gastronotal shield of larva present or absent, in nymphs present, with 10 pairs of setae; $p_2$ and $p_3$ on unsclerotized integument, macro sclerite or micro sclerites. In nymphs solenidion $\omega_2$ on tarsus I longer than $\omega_1$, and located anterolateral to solenidion $\omega_1$. Femora I and II with or without ventral carina.

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This study on \textit{Melanozetes avachai n. sp.} was possible due to Dr Sergey Chalov (Lomonosov Moscow State University, Russia) who kindly invited the second author to participate in an international scientific expedition to Kamchatka (Russia) under the EU FP - 7 IRSES Project (Flumen Grant Agreement No 318969). We thank two anonymous reviewers for helpful suggestions that considerably improved the scientific value of this paper.

**REFERENCES**


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