

A peer-reviewed version of this preprint was published in PeerJ on 6 October 2015.

[View the peer-reviewed version](https://peerj.com/articles/1307) (peerj.com/articles/1307), which is the preferred citable publication unless you specifically need to cite this preprint.

Boll PK, Rossi I, Amaral SV, Leal-Zanchet A. 2015. A taste for exotic food: Neotropical land planarians feeding on an invasive flatworm. PeerJ 3:e1307 <https://doi.org/10.7717/peerj.1307>

A taste for exotic food: Neotropical land planarians feeding on an invasive flatworm

Piter K Boll, Ilana Rossi, Silvana V Amaral, Ana Leal-Zanchet

Invasive species establish successfully in new habitats especially due to their generalist diet and release of natural enemies. However, native species may also adapt to use new elements in their ecosystem. The planarian *Endeavouria septemlineata*, first recorded in Hawaii, was later registered in Australia and Brazil. Recently we found it in human-disturbed areas in southern Brazil and here we investigate its interactions with other invertebrates both in the field and in the laboratory. We observed the species in the field during collecting activities and maintained some specimens alive in small terraria in the laboratory, where we offered different invertebrate species as potential prey and also put them in contact with native land planarians in order to examine their interaction. Both in the field and in the laboratory, *E. septemlineata* showed a gregarious behavior and was found feeding on woodlice, millipedes, earwigs and gastropods. In the laboratory, specimens did not attack live prey, but immediately approached dead specimens, indicating a scavenging behavior. Four native land planarians of the genus *Obama* and two of the genus *Paraba* attacked and consumed *E. septemlineata*, which, after the beginning of the attack, tried to escape by tumbling or using autotomy. As a scavenger, *E. septemlineata* would impact the populations of species used as food, but could possibly exclude native scavengers by competition. On the other hand, its consumption by native land planarians may control its spread and thus reduce its impact on the ecosystems.

2 **A taste for exotic food: Neotropical land planarians feeding on an invasive flatworm**

3

4 Piter K. Boll¹, Ilana Rossi¹, Silvana V. Amaral¹, Ana Maria Leal-Zanchet¹

5 ¹Instituto de Pesquisa de Planárias e Programa de Pós-Graduação em Biologia

6 Universidade do Vale do Rio dos Sinos – UNISINOS

7 São Leopoldo, RS, Brasil

8 Corresponding author: Ana Maria Leal-Zanchet, zanchet@unisinis.br

9

10 **Abstract**

11 Invasive species establish successfully in new habitats especially due to their generalist diet and
12 release of natural enemies. However, native species may also adapt to use new elements in their
13 ecosystem. The planarian *Endeavouria septemlineata*, first recorded in Hawaii, was later
14 registered in Australia and Brazil. Recently we found it in human-disturbed areas in southern
15 Brazil and here we investigate its interactions with other invertebrates both in the field and in the
16 laboratory. We observed the species in the field during collecting activities and maintained some
17 specimens alive in small terraria in the laboratory, where we offered different invertebrate
18 species as potential prey and also put them in contact with native land planarians in order to
19 examine their interaction. Both in the field and in the laboratory, *E. septemlineata* showed a
20 gregarious behavior and was found feeding on woodlice, millipedes, earwigs and gastropods. In
21 the laboratory, specimens did not attack live prey, but immediately approached dead specimens,
22 indicating a scavenging behavior. Four native land planarians of the genus *Obama* and two of the
23 genus *Paraba* attacked and consumed *E. septemlineata*, which, after the beginning of the attack,
24 tried to escape by tumbling or using autotomy. As a scavenger, *E. septemlineata* would impact

25 the populations of species used as food, but could possibly exclude native scavengers by
26 competition. On the other hand, its consumption by native land planarians may control its spread
27 and thus reduce its impact on the ecosystems.

28 **Keywords:** exotic prey, Geoplanidae, native predator, scavenger, invasive species

30 INTRODUCTION

31 Most invasive species establish successfully in new habitats because of their generalist
32 habits and the release from natural enemies (Colautti et al., 2004; Prior et al., 2014). However, as
33 easily as an introduced species may adapt to a new environment, native species may adapt to a
34 new element in their ecosystem. For example, native predators often adapt to exotic prey,
35 controlling their population (Carlsson, Sarnelle & Strayer, 2009). Conversely, an invasive
36 predator may benefit from the ineffective antipredator behavior of native species, thus increasing
37 its chances of capturing prey (Sih et al., 2010).

38 Land planarians are important predators of other invertebrates in the soil fauna in tropical
39 regions (Ogren, 1995; Sluys, 1999). Despite being sensitive to dehydration, high temperatures
40 and luminosity, some species are able to adapt to human-disturbed environments and become
41 invasive when colonizing areas outside their native range (Froehlich, 1955). The success of most
42 invasive land planarians is attributed to their generalist feeding habits, which gives them the
43 ability to adapt their diet to include local invertebrate species, thus leading to a quick dispersal
44 (Murchie, Moore & Walter, 2003). Furthermore, the naïveté of native species to respond
45 effectively to predation has been shown to increase the predation success of planarians (Fiore et
46 al., 2004). The possibility of natural enemies to control invasive planarians is usually not taken
47 into account because it is assumed that land planarians are top predators and therefore lack
48 predators (Sluys, 1999).

49 Currently, several land planarians of the subfamily Rhynchodeminae that are native from
50 Australasia are known as important invasive species (Winsor, Johns & Barker, 2004; Justine,
51 Thévenot & Winsor, 2014; Álvarez-Presas et al., 2014). In Hawaii, Mead (1963) found that a
52 rhynchodemid planarian from tribe Caenoplanini, *Endeavouria septemlineata*, is an effective

53 predator against the introduced giant African snail. He also observed the species feeding on
54 earthworms and small insects. Later, *E. septemlineata* was recorded for Brazil, although the
55 impact of its invasion over native species was not studied (Carbayo, Pedroni & Froehlich, 2008).
56 In addition, Carbayo, Pedroni & Froehlich (2008) also mentioned the occurrence of *E.*
57 *septemlineata* in Australia.

58 Recently, we found *E. septemlineata* in human-disturbed areas in southern Brazil. In
59 order to understand its impact over the ecosystem and its effectiveness as an invasive species, we
60 investigated its interactions with other invertebrates, both in the field and in the laboratory. Our
61 predictions are that, as an effective invader, *E. septemlineata* would feed on a wide range of
62 invertebrates. We also investigated whether or not native predators may use *E. septemlineata* as
63 an alternative food source.

64

65 MATERIAL AND METHODS

66 We found specimens of *E. septemlineata* in gardens in Montenegro (29°40'S, 51°28'W)
67 and Campo Bom (29°40'S, 51°3'W), and in the Porto Alegre Botanical Garden (30°03'S,
68 51°10'W), in Porto Alegre, Brazil. We documented occasional observations related to behavior
69 in the field during collecting activities in the city of Montenegro and captured several specimens,
70 taking them to the laboratory. We placed the planarians in plastic terraria with moist soil, leafs
71 and log fragments under a temperature of 20°C and a relative air humidity of 90%.

72 We killed nine specimens in hot water and fixed them in 10% buffered formalin. Later,
73 we processed these specimens histologically (following Froehlich and Leal-Zanchet, 2003) for
74 taxonomic identification through examination of the internal morphology and deposited them in

75 the reference collection of Museu de Zoologia da Universidade do Vale do Rio dos Sinos, São
76 Leopoldo, Rio Grande do Sul, Brazil.

77 In the laboratory, we performed two experiments of interaction. In the first one, we kept
78 groups of 10 to 20 individuals of *E. septemlineata* alive in small terraria and offered different
79 invertebrates as food, viz., land gastropods *Bradybaena similaris*, *Helix aspersa*, *Deroceras*
80 *leae* and *Sarasinula plebeia*; earthworms *Eisenia fetida*, *Amyntas gracilis* and *Metaphire*
81 *schmardae*; isopods *Atlantoscia floridana* and *Armadillidium vulgare*; termites *Nasutitermes* sp.;
82 millipedes *Rhinocricus* sp.; and unidentified earwigs. We put two different species of
83 invertebrates from different taxonomic groups in the terraria with the planarians and monitored
84 the terraria twice a week. If the planarians did not consume the invertebrates in two weeks, we
85 replaced the invertebrates with other species.

86 In the second experiment, we tested the possibility of predation on *E. septemlineata* by
87 native predators. Most known predators of land planarians in the Neotropical ecozone are other
88 land planarians (Froehlich 1955), especially from the genera *Obama* and *Paraba* (Froehlich,
89 1955; Hauser and Maurmann, 1959). Therefore, we examined the interaction of *E.*
90 *septemlineata* with native species of land planarians of these two genera, viz., *Obama*
91 *anthropophila*, *O. carrierei*, *O. ficki*, *O. josefi*, *O. ladislavii*, *O. marmorata*, *Paraba multicolor*
92 and *Paraba* sp. We put one specimen of the native planarian and one specimen of *E.*
93 *septemlineata* in a moistened Petri dish under low diffuse light and examined their interaction.

94

95 **RESULTS**

96 Both in the field and in the laboratory, specimens of *E. septemlineata* showed a
97 gregarious behavior, constantly gathering in groups ranging from a few to tens of individuals

98 (Fig. 1A). Specimens were often found in the field feeding in groups on *B. similaris* (Fig. 1B), *D.*
99 *laeve*, *A. vulgare* (Fig. 1C), *Rhinocricus* sp. (Fig. 1D), and earwigs, or individually on *A. vulgare*
100 and *Nasutitermes* sp. (I. Rossi, personal observation).

101 In the laboratory, we found the planarians consuming the woodlice *A. vulgare* and *A.*
102 *floridana* individually (Fig. 1E). When in groups of 10 to 20 specimens, *E. septemlineata*
103 consumed *B. similaris*. Despite being maintained in large groups with the invertebrates in the
104 terraria for several days, specimens of *E. septemlineata* were rarely found eating. In fact,
105 feeding was not very common. They also did not show interest in live prey species when put in
106 direct contact with them, but immediately approached dead specimens of *D. laeve* and *A.*
107 *floridana* and started to feed on them.

108 Specimens of the native land planarians *O. josefi* (Fig. 2A), *O. marmorata* (Fig. 2B), *O.*
109 *carrierei*, *O. anthropophila* (Fig. 2C), *Paraba multicolor* and *Paraba* sp. (Fig. 2D) reacted to the
110 encounter with *E. septemlineata* by capturing and consuming it. At the beginning of the attack by
111 the native planarians, individuals of *E. septemlineata* showed an escaping behavior by moving
112 quickly away from the predator. The most frequent strategies to avoid predation were tumbling
113 or, if the posterior end was trapped, autotomy of the posterior end. The planarian performed the
114 tumbling behavior by lifting the posterior end and bending it forward until touching the substrate
115 ahead of the anterior end (Fig. 3).

116 When in contact with native land planarians, individuals of *E. septemlineata* constantly
117 showed a non-aggressive approaching behavior, often crawling either onto the dorsum or to the
118 side of the individual of the other species and entering a resting position in a way similar to the
119 one showed towards conspecific individuals. They only started an escape response after the
120 native planarian initiated the attack.

121

122 **DISCUSSION**

123 We observed specimens of *E. septemlineata* from southern Brazil feeding on a great
124 range of invertebrates, including mollusks and arthropods. In Hawaii, the invasive giant African
125 snail became a greatly available food source for *E. septemlineata* (Mead, 1963). This led to a
126 boost in the population and, consequently, the predation impact over native land snails increased.
127 According to Mead (1963), the low density of native land snails in the island makes them
128 unlikely to be the main prey of the planarian. Our results corroborate this hypothesis of a diet
129 including more than only gastropods. Such feeding habits, including both gastropods and
130 arthropods, has been reported for other species of Caenoplanini, such as *Caenoplana coerulea*
131 and *Parakontikia ventrolineata* (Winsor, Johns & Barker, 2004; Breugelmans et al. 2012), the
132 latter also known to feed in groups (Barker, 1989).

133 Despite the fact that we find groups of *E. septemlineata* feeding on several invertebrates
134 in the field, the specimens rarely eat in the laboratory, ignoring prey species frequently. Mead
135 (1963) reports feeding observations in the laboratory that included the capture of live snails, but
136 gives no details about the conditions in which the planarians were maintained. Carbayo, Pedroni
137 & Froehlich (2008) reported that, under laboratory conditions, *E. septemlineata* accepted snails
138 and smashed slugs, but they also did not present details about the observations. In experiments
139 with native species of *Microplana* in the United Kingdom, McDonald and Jones (2007) found
140 that the planarians eat live prey less frequently in the laboratory than in the field, although they
141 accepted dead animals rather well. This may indicate that those species are more scavengers than
142 predators. A species closely related to *E. septemlineata* that shows a similar gregarious behavior
143 is *P. ventrolineata*. It has been reported to attack live prey actively in the field (Barker, 1989),

144 but recent observations also indicate a scavenging behavior (Justine, Thévenot & Winsor, 2014).
145 Our observations suggest that *E. septemlineata* most likely is also a scavenger.

146 As an obligate or facultative scavenger, *E. septemlineata* would have little effect on the
147 population of most invertebrates it uses as food, since it would not decrease significantly the
148 population size of those species. Nevertheless, it would decrease the number of dead material
149 available for native scavengers, leading to competition and, if having advantage over the
150 resources, the invasive species may dislodge a native scavenger or force it to change its diet
151 (Wilson and Wolkovich, 2011).

152 Nevertheless, despite this considerably wide occurrence of *E. septemlineata* in Brazil
153 (Carbayo, Pedroni & Froehlich, 2008), its impact over the populations of native species may be
154 under control due to its predation by native land planarians. In our study, which was restricted to
155 southern Brazil, six native land planarians fed on *E. septemlineata*. When considering the range
156 of distribution of this invasive species, it is likely that more predator species exist.

157 The control of invasive land planarians by predators has always seemed unlikely to
158 succeed, as few natural predators are known (Justine et al., 2014). Besides beetles (Gibson,
159 Cosens & Buchanan, 1997) and one snail species (Lemos, Canello & Leal-Zanchet, 2012), no
160 other organisms have been reported to feed on introduced land planarians prior to the present
161 work. Vertebrates do not accept land planarians as food as they seem to find them unpalatable
162 (Ducey et al., 1999).

163 Europe is the continent most affected by invasive land planarians (Álvarez-Presas et al.
164 2014; Justine, Thévenot & Winsor, 2014), but has also a very small number of native species.
165 Thus, native European animals are unlikely to predate land planarians, since land planarians
166 compose a rare group in this continent and therefore are not available as a significant food

167 resource. On the other hand, South America has a high richness of land planarians and effective
168 predators are very likely to exist. One such predator, the land snail *Rectartemon depressus*,
169 which consumes various native species of land flatworms, has been identified recently (Lemos,
170 Canello & Leal-Zanchet, 2012). The consumption of the invasive *E. septemlineata* by native land
171 planarians, including species common in urban environments, may be an important factor in
172 controlling the dispersal of introduced land planarians in South America.

173 The inclusion of exotic prey in the diet of a native predator, sometimes even leading it to
174 switch from a native to an exotic species as a main food source, is not uncommon (Carlsson,
175 Sarnelle & Strayer, 2009), although it seems to vary considerably depending on the type of
176 ecosystem and the trophic level (Prior et al., 2014). *Obama anthropophila*, *O. carrierei* and *O.*
177 *josefi* seem to have other native land planarians as their main prey (P. Boll, personal observation)
178 and thus may recognize *E. septemlineata* as a suitable species to replace native prey. The
179 consequences of such interaction over the populations of both predator and prey depend on the
180 responsive capacities of both species, including rapid adaptive change of individuals by learning
181 or changes in morphology and behavior within a population due to natural selection (Carlsson,
182 Sarnelle & Strayer, 2009).

183 Our results suggest that, as primarily a scavenger, *E. septemlineata* may not have
184 significant effects over native species it feeds on, and its spread may be under control by native
185 predators (Carlsson, Sarnelle & Strayer, 2009). However, it is possible that its presence
186 significantly affects the trophic web structure by dislodging native scavengers or altering the
187 predation pressure over native preys by native predators.

188

189 **ACKNOWLEDGMENTS**

190 We gratefully acknowledge the Conselho Nacional de Desenvolvimento Científico e
191 Tecnológico (CNPq), the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior
192 (CAPES) and the Fundação de Amparo à Pesquisa do Rio Grande do Sul (FAPERGS) for
193 research grants and fellowships in support of this study. We thank Elisa von Groll, João Braccini,
194 Lucas Schwambach, Márcio Sasamori and Victor Sawa for helping in the capture of land
195 planarians; Ignacio Agudo, Marie Bartz and Patrícia Rodrigues for the help in identifying
196 invertebrate species. We acknowledge MSc. Edward Benya for the English review of the text.
197 The work was conducted under the collection permits and licenses granted by Instituto Chico
198 Mendes de Conservação da Biodiversidade (permit numbers 24357 and 26683).

199

200

201 REFERENCES

202 Álvarez-Presas M, Mateos E, Tudó A, Jones H, Riutort M (2014) Diversity of introduced
203 terrestrial flatworms in the Iberian Peninsula: a cautionary tale. PeerJ 2:e430. doi:
204 10.7717/peerj.430

205 Barker GM (1989) Flatworm predation of terrestrial molluscs in New Zealand, and a brief
206 review of previous records. N Z Entomol 12:75-79. doi: 10.1080/00779962.1989.9722571

207 Breugelmans K, Cardona JQ, Artois T, Jordaens K, Blackeljou T (2012) First report of the exotic
208 blue land planarian, *Caenoplana coerulea* (Platyhelminthes, Geoplanidae), on Menorca
209 (Balearic Islands, Spain). ZooKeys 199:91-105. doi: 10.3897/zookeys.199.3215

210 Carbayo F, Pedroni J, Froehlich EM (2008) Colonization and extinction of land planarians
211 (Platyhelminthes, Tricladida) in a Brazilian Atlantic Forest regrowth remnant. Biol
212 Invasions 10:1131-1134. doi: 10.1007/s10530-007-9190-1

- 213 Carlsson NO, Sarnelle O, Strayer DL (2009) Native predators on exotic prey – an acquired taste?
214 Front Ecol Environ 7:525-532. doi: 10.1890/080093
- 215 Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by
216 the enemy release hypothesis? Ecol Lett 7:721-733. doi: 10.1111/j.1461-0248.2004.00616.x
- 217 Ducey PK, Messere M, Lapoint K, Noce S (1999) Lumbricid prey and potential herpetofaunal
218 predators of the invading terrestrial flatworm *Bipalium adventitium* (Turbellaria: Tricladida:
219 Terricola). Am Midl Nat 141:305-314.
- 220 Fiore C, Tull JL, Zehner S, Ducey PK (2004) Tracking and predation on earthworms by the
221 invasive terrestrial planarian *Bipalium adventitium* (Tricladida, Platyhelminthes). Behav
222 Process 67:327-334. doi:10.1016/j.beproc.2004.06.001
- 223 Froehlich CG (1955) On the biology of land planarians. Bol Fac Filos Ciênc Let Univ São Paulo
224 Sér Zool 20:263-271.
- 225 Froehlich EM, Leal-Zanchet AM (2003) A new species of terrestrial planarian of the genus
226 *Notogynaphallia* Ogren & Kawakatsu (Platyhelminthes, Tricladida, Terricola) from south
227 Brazil and some comments on the genus. Rev Bras Zool 20:745-753. doi: 10.1590/S0101-
228 81752003000400030
- 229 Gibson PH, Cosens D, Buchanan K (1997) A chance field observation and pilot laboratory
230 studies of predation of the New Zealand flatworm by the larvae and adults of carabid and
231 staphylinid beetles. Ann Appl Biol 130:581-585. doi: 10.1111/j.1744-7348.1997.tb07684.x
- 232 Hauser J, Maurmann E (1959) Studien über die Bewegungen des Genus *Geoplana*. Pesquisas
233 3:631-646.
- 234 Hyman L (1939) Land planarians from the Hawaiian Islands. Archiv Zool Exp Gen 80:116-124.

- 235 Justine J-L, Thévenot J, Winsor L (2014) Les sept plathelminthes invasifs introduits en France.
236 *Phytoma* 674:28-32.
- 237 Justine J-L, Winsor L, Gey D, Gros P, Thévenot J (2014) The invasive New Guinea flatworm
238 *Platydemus manokwari* in France, the first record for Europe: time for action is now. PeerJ
239 2:e297. doi: 10.7717/peerj.297
- 240 Lemos VS, Canello R, Leal-Zanchet AM (2012) Carnivore mollusks as natural enemies of
241 invasive land flatworms. *Ann Appl Biol* 161:127-131. doi: 10.1111/j.1744-
242 7348.2012.00556.x
- 243 McDonald JC, Jones HD (2007) Abundance, reproduction, and feeding of three species of
244 British terrestrial planarians: observations over 4 years. *J Nat Hist* 41:293-312. doi:
245 10.1080/00222930701219149
- 246 Mead AR (1963) A flatworm predator of the giant African snail *Achatina fulica* in Hawaii.
247 *Malacologia* 1:305-309.
- 248 Murchie AK, Moore JP, Walters KFA (2003) Invasion of agricultural land by the earthworm
249 predator *Arthurdendyus triangulatus* (Dendy). *Pedobiologia* 47:920-923. doi: 10.1078/0031-
250 4056-00281
- 251 Ogren, RE (1995) Predation behavior of land planarians. *Hydrobiologia* 205:105-111. doi:
252 10.1007/BF00036370
- 253 Prior KM, Powell THQ, Joseph AL, Hellmann JJ (2014) Insights from community ecology into
254 the role of enemy release causing invasion success: the importance of native enemy effects.
255 *Biol Invasions*. doi: 10.1007/s10530-014-0800-4.

256 Santoro G, Jones HD (2001) Comparison of the earthworm population of a garden infested with
257 the Australian land flatworm (*Australoplana sanguinea alba*) with that of non-infested
258 garden. *Pedobiologia* 45:313-328. doi: 10.1078/0031-4056-00089

259 Sih A, Bolnick DI, Luttbeg B, Orrock JL, Peacor SD, Pintor LM, Preisser E, Rehage JS, Vonesh
260 JR (2010) Predator-prey naïveté, antipredator behavior, and the ecology of predator
261 invasions. *Oikos* 119:610-621. doi: 10.1111/j.1600-0706.2009.18039.x

262 Sluys R (1999) Global diversity of land planarians (Platyhelminthes, Tricladida, Terricola): a
263 new indicator-taxon in biodiversity and conservation studies. *Biodivers Conserv* 8:1663-
264 1681. doi: 10.1023/A:1008994925673

265 Sugiura S (2009) Seasonal fluctuation of invasive flatworm predation pressure on land snails:
266 implications for the range expansion and impacts of invasive species. *Biol Conserv*
267 142:3013-3019. doi: 10.1016/j.biocon.2009.07.032

268 Sugiura S (2010) Prey-preference and gregarious attacks by the invasive flatworm *Platydemus*
269 *manokwari*. *Biol Invasions* 12:1499-1507. doi: 10.1007/s10530-009-9562-9

270 Wilson EE, Wolkovich EM (2011) Scavenging: how carnivores and carrion structure
271 communities. *Trends Ecol Evol* 26:129-135. doi: 10.1016/j.tree.2010.12.011

272 Winsor L, Johns PM, Barker GM (2004) Terrestrial planarians (Platyhelminthes: Tricladida:
273 Terricola) predaceous on terrestrial gastropods. In: Barker GM (ed) *Natural enemies of*
274 *terrestrial molluscs*. CAB International, Wallingford, pp 227-278.

275
276

Figure 1 (on next page)

Figure 1 Behavior of *Endeavouria septemlineata*.

Figure 1 Behavior of *Endeavouria septemlineata*: (A) Specimens of *Endeavouria septemlineata* gathering in a group of many individuals in the field; (B-D) Specimens feeding on *Bradybaena similaris* (B), *Armadillidium vulgare* (C) and *Rhinocricus* sp. (D) in the field; (E) A single specimen feeding on *Atlantoscia floridana* in the laboratory.



10 mm

A



10 mm

B



10 mm

C



10 mm

D



10 mm

E

Figure 2 (on next page)

Figure 2 Native land planarians consuming *Endeavouria septemlineata* in experiments in the laboratory.

Figure 2 Native land planarians consuming *Endeavouria septemlineata* in experiments in the laboratory : (A) *Obamajosefi* in ventral view; (B) *Obama marmorata* in ventral view; (C) *Obama anthropophila* in dorsal view; and (D) *Paraba* sp. in dorsal view. Arrows indicate the pharynx of the predators; double arrows show parts of the body of a preyed specimen of *E. septemlineata* in the intestine.

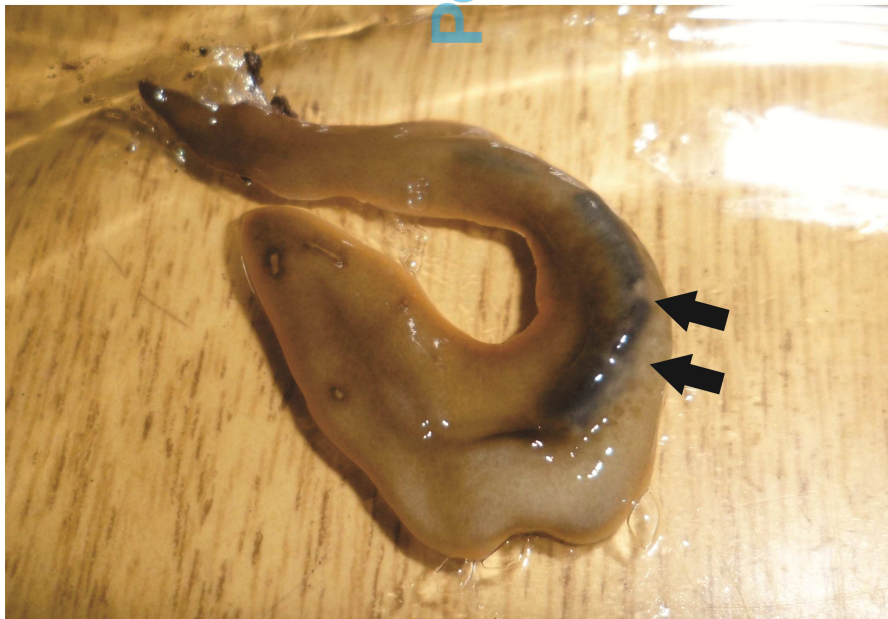


10 mm



A 10 mm

B



10 mm

C



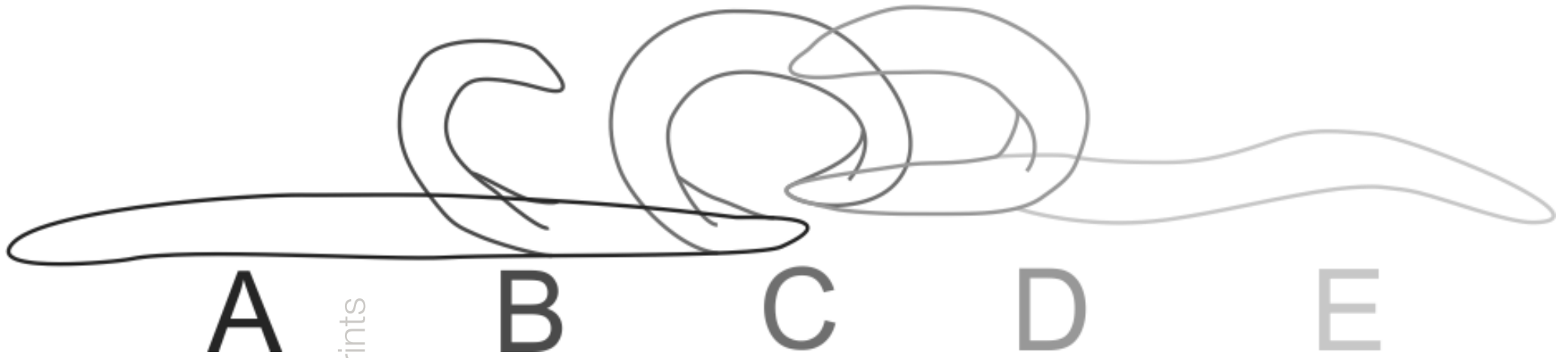
10 mm

D

Figure 3(on next page)

Figure 3 Tumbling behavior of *Endeavouria septemlineata*.

Figure 3 Tumbling behavior of *Endeavouria septemlineata* : (A) initial position; (B) posterior end lifted and bent forward; (C) posterior end touching the substrate ahead of the anterior end; (D) anterior end lifted; (E) final position. Arrows show head in initial and final positions.



PeerJ PrePrints