The remarkable Australian rove beetle genus Myotyphlus: its cryptic diversity and significance for exploring mutualism among insects and mammals (Coleoptera: Staphylinidae)

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4　Running title: *Myotyphlus* and mutualism with mammals in rove beetles

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23 **The remarkable Australian rove beetle genus *Myotyphlus*: its cryptic diversity and significance**

24 **for exploring mutualism among insects and mammals (Coleoptera: Staphylinidae)**

25

26 'C'est un des types les plus curieux de l'immense famille des Staphylinides.' [it is one of the

27 most curious types of the vast family of rove beetles]. (Fauvel 1883)

28 '*Myotyphlus* remains the most enigmatic genus.' (Ashe & Timm 1988).

29

30 **Abstract**

31 *Myotyphlus jansoni* (Matthews, 1878), a rare and the only rove beetle species from the

32 subtribe Amblyopinina in Australia that occurs in the fur of small mammals, is revised. Male

33 genitalia have been examined for this species and, as a result, it is divided into three species:

34 *M. jansoni* restricted to Tasmania; as well as *M. newtoni* **sp. nov.** and *M. wurra* **sp. nov.**

35 described as new from mainland south-western Australia. Distribution, bionomics and host

36 associations are summarized for all three species with a conclusion that at least *M. newtoni* sp.

37 nov. and *M. wurra* sp. nov., in addition to the mammal-associated records, also occur in bat

38 guano in caves, or on the ground. Neither of three *Myotyphlus* species is specific for a

39 particular mammal species, and the genus as a whole occurs on several species of *Rattus*, on

40 *Pseudomys higginsi*, and on *Antechinus swainsonii*. Presumably *Myotyphlus* is not as strongly

41 associated with the host mammals as the more diverse American mammal-associated genera

42 of Amblyopinina. Ecology and putative sister-group relationships of *Myotyphlus* reviewed in

43 the broad context of mammal-rove beetle mutualism suggest an independent origin of this

44 mammal-associated lifestyle in the Neotropics and Australia from different free living

45 lineages of Amblyopinina.

46

47 **Key words**: systematics, Staphylinini, Amblyopinina, Australia, Neotropical, new species

48 **1. Introduction**

49 Insects and mammals are two very different, diverse, and evolutionarily successful animal

50 groups dominating all habitable landscapes on our planet. They are mutually dependent on

51 each other as valuable components of terrestrial ecosystems through indirect associations, for

52 example insects as pollinators of plants and grazing mammals as plant consumers, or dung

53 beetles as coprophages and mammals as dung producers. These balanced biotic interactions

54 between two animal classes are crucial for the biosphere and yield important benefits for

55 humans. At the same time direct interactions between insects and mammals mostly appear

56 antagonistic. For example, many mammals predate on insects, or some insects consume

57 mammal blood or otherwise utilize them as hosts during parasitism. In fact with about 6000

58 species of ectoparasitic insects (Marshall 1981), their parasitism on mammals is the main type

59 of direct relationships between these animal classes followed by mammal predation on

60 insects.

61   On the contrary, there seems to be hardly any examples of an insect-mammal

62 mutualism. This is quite remarkable since mutualisms, defined as interactions that benefit

63 both parties involved, are frequently encountered in the natural world (e.g. Boucher *et al.*

64 1982; Herre *et al.* 1999; Weiblen & Treiber 2015). One example of an insect-mammal direct

65 association interpreted as mutualism is the interaction between sloths and pyralid moths that,

66 however, also involve the third agent, the algae in Central America (Pauli *et al*. 2014). A

67 much more straightforward case of insects truly mutualistic to mammals has been discovered

68 earlier (Ashe & Timm 1987a) among Amblyopinina, a subtribe of rove beetles

69 (Staphylinidae) that are a mega-diverse, globally distributed beetle family. In fact, the

70 peculiar looking Amblyopinina rove beetles from the Neotropical region were known to

71 entomologists for more than a century who gradually described their 6 genera (*Amblyopinus*

72 Solsky, 1875, *Edrabius* Fauvel, 1900, *Amblyopinoides* Seevers, 1955, *Megamblyopinus*

73 Seevers, 1955 and *Chilamblyopinus* Ashe & Timm, 1988 from South America, and

74 *Myotyphlus* Fauvel, 1883 from Australia), altogether comprising 65 species (Herman 2001).

75 But due to these strange looking beetles (Fig. 1) repeatedly being collected in the fur of live

76 small mammals, mostly rodents, and reminiscent of fleas, they were always presumed to be

77 ectoparasites on their mammal hosts. Seevers (1955), however, had noted that the hosts were

78 'insensible' to the beetles on their bodies, even if the beetles were crossing the hosts' eyes.

79 Later, Ashe and Timm (1987a) extended Seevers' (1955) observation into an interesting

80 experiment. They took live specimens of *Amblyopinus tiptoni* Barrera, 1966 and placed them

81 on the mouse *Scotinomys teguine* (Alston, 1877) that is not a host of the beetle but one that is

82 similar in fur type and body size to its natural hosts. The mice reacted by actively grooming

83 the beetles out and exterminating them, such behavior suggesting a significant degree of

84 coadaptation among beetles and their natural hosts required in case of mutualism.

85 Additionally, they observed the beetles feeding on the 'real' ectoparasites of their hosts, such

86   as fleas or mites. Ashe and Timm (1987a) argued that as predatory rove beetles Amblyopinina

87   became adapted to hunt true mammal ectoparasitess directly from the fur of their hosts. In

88   return, the hosts evolved high tolerance to the beetles on their bodies. Therefore, these rove

89   beetles and their mammal host display a highly specialized case of mutualism.

90   In spite of the recent papers by Ashe and Timm (1987a, b) which gave a good summary

91   and a novel look at the amblyopinine biology, this rare and perhaps the only known example

92   of an insect-mammal mutualism, was not placed in the spotlight of the broader evolutionary

93   research. One reason for that is lack of a sound phylogenetic study of Amblyopinina resulting

94   in confusing definition of these rove beetles and their putative sister relationships. Secondly,

95   poor outreach of the specialized sections of systematic entomology to other biological

96   disciplines acted as an impediment for making these beetles accessible for studies outside that

97   field. Recently a series of phylogenetic studies of Staphylinini (Solodovnikov 2006;

98   Solodovnikov & Schomann 2009; Chatzimanolis *et al.* 2010; Brunke *et al.* 2015) finally

99   defined a broader monophyletic group that gave rise to these mammal mutualistic

100   amblyopinines. These studies, however, did not address one of the core evolutionary

101   questions about this mutualism: whether all mammal associated Amblyopinina stem from a

102   single free living ancestor, or whether they are in fact polyphyletic. In other words, it remains

103   open if this very unique case of mutualism among insects and mammals has a single origin or

104   arose multiple times from closely related free living ancestors within the rove beetle subtribe

105   Amblyopinina. *Myotyphlus jansoni* (Matthews, 1878), the only Australian representative of

106   the otherwise South and Central American mutualistic amblyopinines is the key taxon for

107   seeking answers for this question. In addition to its geographic distribution as an outlier,

108   morphology of that species is not as derived as in species of the main (Neotropical) mammal-

109   associated stock of Amblyopinina. And the ecology of its association with mammals, as far as

110   known (Hamilton-Smith & Adams 1966) seems less strict than in the Neotropical species.

111   Although being a truly unique beetle in Australia critical for understanding the rare biological

112   phenomenon of insect-mammal mutualism, *M. jansoni* remains a very poorly known species

113   without a proper modern taxonomic treatment. Even its aedeagus, for example, has never

114   been dissected and studied, although illustrating this structure is now a standard in species

115   diagnostics of rove beetles, especially Staphylinini. To fill all abovementioned gaps, here we

116   target the systematic revision of *M. jansoni* and summarize all available data about its

117   distribution, bionomics and biology. We discuss these data in the phylogenetic context

118   elucidating the origin of the unique example of insect-mammal mutualism displayed by rove

119   beetles. Morphology of *M. jansoni* had to be revisited since none of the previous descriptions

120 accounted for systematically important characters that have been introduced in the latest

121 phylogenetic work on Staphylinini. Morphology is particularly important in this case as hosts

122 and/or symbionts frequently evolve novel characters or lose them (Herre *et al.* 1999). With

123 the closer examination of this amazing living species of the Australian continent, we have

124 discovered that in fact it consists of three species two of which are new to science and are

125 described here. Due to the paucity of the available material, our knowledge of the distribution

126 and biology of this species complex remains limited, while its species discrimination is

127 possible only with the examination of male genitalia. But we hope that this paper will

128 stimulate further study of this species complex, also by DNA-based methods and with

129 biological observations. By reviewing mammal-associated mutualism in beetles and insects in

130 general here, we also aim to bridge the gap between technical systematics of Amblyopinina

131 and broader evolutionary research of this group, potentially manifesting the multiple origin of

132 a remarkable and unique case of mutualism between insects and mammals.

133 **2. Materials and methods**

134 Beetles were examined using a Leica MZ APO dissection microscope. They were studied as

135 either dry pinned material or as wet specimens in petri dishes containing glycerin. Dissected

136 genitalia are stored in glycerin in vials or mounted in water soluble transparent Lompe

137 solution on see-through cards, those attached to an insect pin beneath respective specimens.

138 Measurements were taken using an ocular micrometer and are given in millimeters (mm).

139 Morphological characters are abbreviated as follows FL = Forebody Length (posterior margin

140 of elytra to anterior margin of labrum), HL = Head Length (from apex of labrum to neck

141 constriction), HW= Head Width at widest point, HL*HW= Head Length X Head Width.

142 Specimen label data is repeated verbatim, one forward slash (/) indicates separation of labels.

143 This paper is based on the study of specimens from the following collections:

144 BMNH – Natural History Museum, London (R. Booth, M. Barclay)

145 CSIRO - Australian National Insect Collection Canberra (C. Lemann)

146 FMNH - Field Museum of Natural History, Chicago (J. Boone, C. Maier)

147 SAM - South Australian Museum, Adelaide (P. Hudson)

148 ZMUC – Zoological Museum at the University of Copenhagen (part of the Natural History

149 Museum of Denmark (A. Solodovnikov, S. Selvantharan)

150   Habitus photographs were taken using either the Visionary Digital Imaging Systems with a

151   Canon EOS 7D (*Myotyphlus jansoni* habitus) or a Leica MZ 16 A dissection scope combined

152   with a Leica DFC450 C camera (habitus images in Fig. 1) and stacked using Zerene Stacker

153   software. A middle leg was taken from *M. jansoni*, mounted on aluminium stubs, coated with

154   platinum/palladium and studied in a JEOL JSM-6335F scanning electron microscope. The

155   distribution map was created using QGIS 2.12 Lyon and the Natural Earth Free vector and

156   raster map data (naturalearthdata.com). The schematic phylogeny (Fig. 1) was drawn in

157   Adobe Illustrator CS6. The graph (Fig. 2A) was made using R studio 3.2.3 using the package

158   'ggplot2'. Male genitalia were digitally inked from photos using Adobe Illustrator CS6.

159

3. Systematics of the genus *Myotyphlus*

3.1. Taxonomic history

162   Until present the genus *Myotyphlus* was known from a single species *Myotyphlus jansoni*

163   (Matthews, 1878). That species was described in the genus *Amblyopinus,* at that time

164   associated with the rove beetle subfamily Tachyporinae. Its original description (Matthews

165   1878) was based on two specimens collected in Tasmania. The description was very careful

166   and even contained illustrations of morphological details which was rare at that time. Fauvel

167   (1883), who studied this species shortly after, argued that it must be moved from

168   *Amblyopinus* to its own genus that he named *Myotyphlus.* Matthews (1884) agreed with the

169   separate generic status of this species, but he did not like Fauvel's name *Myotyphlus* and

170   proposed the genus name *Cryptommatus* instead. Contrary to Fauvel (1883) who erected

171   *Myotyphlus* without elaborate character assessment or even a genus description, Matthews'

172   (1884) description of *Cryptommatus* was very detailed. Also Matthews (1878, 1884) pointed

173   to the affinity of *Myotyphlus jansoni* with the genus *Philonthus,* i.e. towards the subfamily

174   Staphylininae where *Myotyphlus* currently belongs. Naturally, Matthews' genus

175   *Cryptommatus* was placed in synonymy with *Myotyphlus* in accordance with the rules of

176   zoological nomenclature. Apart from several catalogues and ecological faunistic records (Lea

177   1925; Hamilton-Smith & Adams 1966), *Myotyphlus jansoni* was redescribed, illustrated and

178   compared to the American members of the group only several decades later, in the

179   monograph of Seevers (1955). Later, the species was mentioned in Machado-Allison (1963),

180   Newton (1985), and Ashe & Timm (1988) who expressed opinions on its possible

181   phylogenetic affinities that we address in the discussion.

182 **3.2. Recognition of the genus**

183 Among all rove beetles of Australia *Myotyphlus* is easily recognized based on the following

184 features of its habitus (Fig. 2D): overall depigmented body; characteristically trapezoidal head

185 noticeably widened posteriorly and with very reduced eyes situated anteriad on the head;

186 reduced elytra that are slightly shorter than the pronotum; and a black comb on the first

187 mesotarsomere in both sexes (Fig. 3). Additional characters such as the quadrate pronotum;

188 apical segment of labial and maxillary palpi about half the length of the penultimate segment;

189 lack of post-coxal process on the strongly deflexed hypomera; and presence of sub-basal

190 carina connecting spiracles on abdominal tergites III to V are important to note for placing *M.*

191 *jansoni* in its proper lineage within Amblyopinina (for more details see below). Among

192 Australian Staphylinidae *Myotyphlus* may superficially appear similar to *Quedius*

193 *mediofuscus* Lea, 1910.

194

195 **3.3. *Myotyphlus jansoni*, revised concept**

196 **Type material examined: Australia: *Tasmania:*** syntypes: 2 males, 1 female, 'Tasmania A.

197 Simson // 3137' (SAM).

198 **Other material: Australia: *Tasmania:*** 2 females, '3137 *Cryptommatus jansoni* Matth

199 Tasmania (SAM); 1 female, 'From bush rat [something illegible] Tas. H.M. Nicholls/ J.

200 12506 *Cryptommatus janssoni* Matth. Tasmania base of rats tail cotype'; 2 females with same

201 geographic labels but without determination label; (SAM); 1 male, 1 female: 'Cradle Mt,

202 6.xii.1964, R.H Green/ *Pseudomys higginsi/ Myotyphlus* >3 spp. (2+ new) det. A. Newton

203 1981'. 2 males: 'Franklin River, below Gordons Peak, 15 Jan. 1983, E.B Britton'. 1 male, 1

204 female: 'Mt Kate, 16.x.1964, R.H Green/ *Rattus lutreolus'*. 1 female: 'Florentine Valley,

205 7.vii.1959, B.C Mollison/ *Rattus lutreolus valentinus'*. 1 female: 'Corinna, 8.ii.1965, R.H

206 Green/ *Antechinus swainsonii'*. 1 female: 'Tasmania/ *Myotyphlus jansoni* Matth./ 296 [in

207 red]/ M. Cameron Bequest B.M. 1955-147' (BMNH).

208 ***Redescription***

209 Measurements: FL (2.6-2.8), HL (0.7-0.8), HW (0.95-1.1), HL*HW (0.665-0.88).

210 Overall pale brown, not strongly pigmented beetles with highly reduced eyes, a distinctive

211 trapezoid shaped head and black combs on the first mesotarsomere in both sexes (best viewed

212   from a lateral angle, Fig. 3). Habitus as in Fig. 2D.

213   Head trapezoidal, posteriorly widened, with fully developed neck constriction. Nuchal

214   ridge developed laterally, absent dorsally. Eyes consisting of few ommatidia and therefore

215   extremely small, positioned anteriorly very close to base of mandibles. Gular sutures slightly

216   diverging anteriorly. Postmandibular ridge present. Postgenal ridge weakly developed,

217   sinuate, projecting anteriad and connecting the gular suture and infraorbital ridge. Infraorbital

218   ridge short, extending just past the post-genal ridge. Anterior area of gula with pair of setae.

219   Apical segment of labial and maxillary palpi aciculate, about half the length of penultimate

220   segments. Labrum short and bilobed with translucent membrane bearing setae. Mandibles

221   with long and distinct dorsal groove. Dorsal and ventral sides of head with distinct transversal

222   microsculpture. Temples with scattered setae in addition to macro setae. Antennae rather

223   short; first antennomere about as long as antennomeres 2 and 3 combined. Antennomeres 1–3

224   only with setae; antennomeres 4-11 with tomentose pubescence and setae. Pronotum quadrate

225   (sometimes slightly transverse) with one pair of shallow punctures in each dorsal row and

226   sparse micropunctures covering pronotum (visible under adequate light and magnification).

227   Pronotal hypomera strongly deflexed and thus not visible in lateral view. Pronotum without

228   translucent postcoxal process. Basisternum with pair of macro setae. Elytra shorter than

229   pronotum, with even but sparse punctation. Scutellum only with one (anterior) scutellar ridge.

230   Humeral angles of elytra with several spines. Hind wings absent entirely. Mesosternal process

231   obtuse, rounded. Metasternal process notched. Legs concolorous with body. Tarsal formula 5-

232   5-5. Both sexes with protarsi moderately dilated with white adhesive setation ventrally. Both

233   sexes with the first tarsomere of the mesotarsus bearing a black comb (Fig. 3). Fifth tarsal

234   segment with a pair of empodial setae. Mesocoxae larger than metacoxae. Metacoxae with

235   transverse carina. Abdomen moderately dorsoventrally flattened. Tergites III to V with sub-

236   basal carinae connecting spiracles. Male sternite VIII with apical median incision. Protergal

237   glands (hidden under elytra) positioned anteriorly, manifested as an oval impression bordered

238   by small setae.

239   Male. Aedeagus with paramere closely attached to median lobe, apex of paramere in

240   dorsal or ventral view very blunt (Fig. 2B).

241   ***Distribution***

242   Based on new data from specimens examined here and earlier records (Hamilton-Smith &

243   Adams 1966), *M. jansoni* has been recorded from several isolated localities in Tasmania (Fig.

244   2C, Table 1). Earlier records of *M. jansoni* for Victoria and New South Wales (Hamilton-

245   Smith & Adams 1966) in fact probably belong to the new species described below, but study

246   of those specimens and male genitalia is required to clarify their identity.

Bionomics

248   According to the specimen label data available to us, *M. jansoni* has been recorded from the

249   following mammals in Tasmania: from *Rattus lutreolus, R. velutinus*, *Pseudomys higginsi* and

250   *Antechinis swainsonii* (Table 1). The only available information about the two specimens of

251   *M. jansoni* studied by Matthews (1878) is that they were received by Mr. Janson in 1877 from

252   Mr. Simson among other Coleoptera collected in Gould's Country, Tasmania. Bionomic

253   records associated with both specimens indicated that they were collected 'in the fur of a

254   living rat'. Fauvel (1883) mentioned that he had studied *M. jansoni* based on the same

255   Tasmanian material from Mr. Simson and an additional specimen found in Brussels museum.

256   He did not mention any biological information about the species other than published in

257   Matthews (1878). The second contribution to the study of this species by Matthews (1884)

258   was based on the same material as its original description. In the summary on parasitic

259   beetles, Kolbe (1911) similarly to South American amblyopinines, listed *M. jansoni* as a

260   mammal ectoparasite, solely based on the information earlier published about that species in

261   Matthews (1878, 1884). Lea (1925) listed nine specimens of *M. jansoni* (as *Cryptommatus*

262   *jansoni*) that 'were all taken clinging to the anal hairs of bush rats [modern perception of

263   'bush rats' seems to refer to *Rattus fuscipes*], in Tasmania, by Messrs. Aug. Simson and H.M.

264   Nichols, and in Victoria by Mr. E. Jarvis'. With new species concepts based on male

265   genitalia, Lea's (1925) records from Victoria correspond not to *M. jansoni* but to either *M.*

266   *newtoni* or *M. wurra*. As far as the Tasmanian material of real *M. jansoni* is concerned,

267   clearly the specimens mentioned by Lea (1925) were additional to the type material,

268   confirming both its rat-associated biology. In his revision of Amblyopinina, Seevers (1955)

269   based his treatment of *Myotyphlus* on the previously published data, and he assumed that the

270   host of *M. jansoni* must be 'the house rat as there are no native Tasmanian rodents'.

Comparison

272   *Myotyphlus jansoni* differs from its two newly described congeners (see below) only in the

273   shape of the aedeagus: its paramere apex is distinctly more blunt than either *M. newtoni* or *M.*

274   *wurra*, and therefore looking somewhat truncate (Fig. 2B). Based on the available males that

275   can be assigned to species, *M. jansoni* is larger than the largest specimens of *M. newtoni*. On

276   Tasmania *Myotyphlus jansoni* is the only species of the genus.

277 **3.4 *Myotyphlus newtoni* sp. nov.**

278 ***Holotype*: Australia: *Victoria:* 1 male, 'Victoria, French Island, 29.viii.1967, R.M.**

279 **Warneke'/'*Rattus fuscipes assimilis*'. (CSIRO)**

280 ***Paratypes*: Australia: *Victoria*: 2 males: 'Olson's Bridge, 11.ix.1959, R.M Warneke/ *Rattus***

281 *assimilis'* (CSIRO). 1 female: 'French Island, 29.viii.1967, R.M Warneke/ *Rattus fuscipes*

282 *assimilis'* (CSIRO). 1 male: 'Loch Valley, in fur of *Rattus assimilis*, 27.vii.63, R.M Warneke/

283 *Myotyphlus jansoni* det. Seevers' (CSIRO). 1 male, 1 female: 'Bat's Ridge, 20.i.1968, J.H

284 Seebeck/ *Rattus fuscipes grayii*' (CSIRO). ***New South Wales***: 1 male: 'Deua NP NSW, Deua

285 Cave, 5 Apr. 1986, E. Holm, ex. Bat guano/ *Myotyphlus* sp. Det. J.F. Lawrence' (CSIRO).

286 ***Description***

287 Measurements: FL (1.5-2.4), HL (0.6-0.9), HW (0.6-0.9), HL*HW (0.36-0.81)

288 Externally the new species is the same as *M. jansoni*, but on average smaller. The smallest

289 specimens of *M. newtoni* are significantly smaller than *M. jansoni* (Fig. 2A). *Myotyphlus*

290 *newtoni* has very characteristic acute apex of the paramere (Fig. 2B), that easily distinguishes

291 this species from either *M. jansoni* or *M. wurra*.

292 ***Etymology***

293 We are pleased to dedicate the new species to Alfred Newton, who invested significant time

294 and effort in the study of Australian Staphylinidae. In particular, he has examined some of the

295 material we used in this paper, and based on his notes we could see that he also thought that

296 *'M. jansoni'* maybe a complex of several species.

297 ***Distribution***

298 Presumably *M. newtoni* is broadly distributed in South-Eastern Australia. Reliable male-

299 associated records stretch from Bat's Ridge in the west to Deua Cave in the east (Fig. 2C,

300 Table 1).

301 ***Bionomics***

302 According to the specimen label data available to us, *M. newtoni* has been collected in the

303 usual ground surface habitats of various localities, and in Deua Cave in New South Wales. In

304 the ground surface habitats, it was recorded from *Rattus fuscipes*, *R. assimilis*, and *R. grayii*.

305   In the Deua Cave a single male was collected not from rats but in the layer of bat guano.

306   Significant material reported as *'M. jansoni'* in Hamilton-Smith and Adams (1966) from

307   *Miniopterus schreibergsi* (Kuhl) bat guano in Lake Gillear Guano Cave near Warnambool,

308   Victoria, and in a cave within the Southern Limestone at Jenolan, New South Wales

309   apparently can be attributed to *M. newtoni* based on the distribution. Interestingly, that

310   Hamilton-Smith and Adams (1966) also reported a personal communication of R.M.

311   Warnecke of the Victorian Fisheries and Wildlife Department who had found '*M. jansoni'*

312   (presumably *M. newtoni*) on only three of the 2000 examined *Rattus assimilis.* Among beetles

313   found on these three rats, some were found on scrotum of one rat, and all other were confined

314   to the area immediately surrounding the anus of the host animal. All beetles were attached to

315   rats by the feet only without any signs of skin disorders on host rats. Hamilton-Smith and

316   Adams (1966) stressed that larva of '*M. jansoni'* has never been found anywhere. Based on

317   new findings, they overall concluded that this species is not an obligate parasite of mammals

318   as in Neotropical amblyopinines, but maybe the case of an initial evolutionary step from a

319   free-living lifestyle to ectoparasitism. Although we have examined a number of specimens

320   collected by R.M. Warnecke, it is not clear if any of them are related to the personal

321   communication between R.M. Warnecke and Hamilton-Smith and Adams (1966).

322

323   **3.5 *Myotyphlus wurra* sp. nov.**

324   ***Holotype*: Australia: *Victoria:* 1 male, 'Olson's Bridge, 11-9-59 (Sept), R.M. Warneke,**

325   ***Rattus assimilis'* [specimen mounted from alcohol, label handwritten by JJS]. (CSIRO).**

326   ***Paratypes*: Australia: *Victoria:* 4 males: details as for holotype. (CSIRO).**

327   ***Description***

328   Measurements: FL (2.2-2.7), HL (0.8-1), HW (0.8-1), HL*HW (0.64-1).

329   Externally the new species is the same as *M. jansoni* or *M. newtoni*, but differs from both of

330   them in a characteristically rounded apex of the paramere (Fig. 2B). In body size *M. wurra*

331   greatly overlaps with *M. jansoni* and some larger specimens of *M. newtoni*.

332   ***Etymology***

333 The species epithet refers to the aboriginal word for 'rat' or 'common rat', from which all

334 known specimens of *M. wurra* were collected. The species name 'wurra' is a noun in

335 apposition.

336 ***Distribution***

337 So far *Myotyphlus wurra* is known only from the type locality, Olson's Bridge in Victoria

338 (Fig. 2C), where it occurs sympatrically with *M. newtoni*.

339 ***Bionomics***

340 The new species was collected on *Rattus assimilis* and is only known from the type locality.

341

342 ***3.6 Myotyphlus sp.***

343 The following specimens refer to females which were collected from Olson's Bridge, Victoria

344 where *M. newtoni* and *M. wurra* occur sympatrically and therefore female cannot be assigned

345 to species. The specimen from New South Wales refers to a female collected without

346 association with males. Female only specimen records from Tasmania are presumed to be *M.*

347 *jansoni* since that is the only known species from Tasmania.

348 **Material examined: Australia: *Victoria:*** 3 females, 'Olson's Bridge, 11.ix.1959, R.M

349 Warneke/ *Rattus assimilis'* (CSIRO). ***New South Wales:*** 1 female, 'South Ramshead, 1850m

350 Kosciusko Nat. Pk. NSW, May 1981, Ken Green, pitfalls/ A.N.I.C Coleoptera, Voucher No.

351 83-0058'. (CSIRO).

352

353 **4. Discussion**

354 **4.1 *Myotyphlus jansoni: how many species?***

355 Observed variation in the shape of the aedeagus suggested that '*M. jansoni*' is a complex of at

356 least three species where, based on the identity of the type material, true *M. jansoni* is

357 confined to Tasmania only. Strong geographic isolation of Tasmania, combined with the

358 noticeable difference in the shape of aedeagus between *M. jansoni* and two new species from

359 the mainland Australia, speaks for the lacking gene flow between the Tasmanian and the

360 mainland populations. Sympatric occurrence of *M. wurra* and *M. newtoni* and lacking

361   transitional states between their respective aedeagi shapes suggest their genetic isolation from

362   each other and thus separate species status even though we did not find difference between

363   these species in external characters. Additional material from throughout the genus range

364   would help resolve its taxonomy more rigorously using morphology and DNA based markers.

365   Combined with its unique biology and occurrence in caves, there may be complex

366   microevolutionary processes that take place in this species complex, with a possibility that

367   new material may reveal more new species.

368

4.2 *Sister group relationships and biogeography of* Myotyphlus

370   Seevers (1955) expressed an idea that *Myotyphlus* was the basal Amblyopinini connecting

371   them to related tribe Quediini. He proposed the affinity of *Myotyphlus* with the South

372   American *Edrabius* based on a single character – the highly reduced eyes located close behind

373   the antennal insertions. As Quediini were known mostly as a Northern Hemisphere group,

374   Seevers (1955) proposed a complex hypothesis of the northern origin of Amblyopinini from

375   Quediini ancestors and their dispersal from North to South America together with mammals

376   during great faunal exchange between both continents. Therefore, basal nature of the

377   Australian *Myotyphlus* and its affiliation with *Edrabius* was a perplexing fact for Seevers'

378   hypothesis, which he could not explain. Machado-Allison (1963) also argued that *Myotyphlus*

379   could be closely related to the South American genus *Edrabius*, but, contrary to Seevers

380   (1955), he suggested a southern origin of Amblyopinini. Bringing new biological

381   observations for *M. jansoni*, Hamilton-Smith and Adams (1966) also mentioned that it was

382   apparently closely allied to the Neotropical amblyopinine genus *Edrabius*. Largely based on

383   their finding that *Myotyphlus* was not as strictly associated with rats as it was thought before,

384   they suggested that it may have to be moved from Amblyopinini to Quediini. Newton (1985)

385   was the first who raised the possibility that *Myotyphlus* may be derived from the free-living

386   'quediines' of Australia, independently of the genera found in the Neotropical region which

387   would result in a polyphyletic origin of this mammal-associated group. Ashe and Timm

388   (1988) recognized a few lineages among mammal-associated amblyopinines: Chilean

389   *Chilamblyopinus* as a very basal lineage; South-Central American genera *Amblyopinodes,*

390   *Amblyopinus* and *Megamblyopinus* as a more derived lineage; and *Edrabius* and *Myotyphlus*

391   as two isolated lineages of unclear sister-group relationships, not necessarily related to each

392   other (Fig.1). They emphasized the more ecologically generalized *Myotyphlus* as a very

important taxon for testing the monophyly of the mammal-associated amblyopinines. Based on the presence of tarsal combs in *Myotyphlus* and some Australian Quediini (unique feature among Staphylinini), Ashe and Timm (1988) agreed with Newton (1985) that the former may be more closely related to the latter than to other (Neotropical) Amblyopinini.

Much uncertainty and controversy about sister-group relationships for *Myotyphlus* and other amblyopinines came from the very poor state of knowledge of the 'Southern Hemisphere quediines' and the fact that Seevers (1955), Machado-Allison (1963), Ashe and Timm (1988) or others thought that their putative sister group had to be sought within the bipolar global subtribe Quediina. Since then systematics of Staphylinini has changed significantly. In particular, it was shown that 'north temperate' and 'south temperate' 'Quediina' are non-related lineages (Solodovnikov 2006; Solodovnikov & Schomann 2009; Chatzimanolis *et al.* 2010; Brunke *et al.* 2015). The former became a subtribe Quediina in a restricted sense, while the latter became a subtribe of its own that received the name Amblyopinina since it included the name bearing genus *Amblyopinus* Solsky, 1875 and other mammal associated genera (*Amblyopinoides* Seevers, 1955, *Chilamblyopinus* Ashe & Timm, 1988, *Edrabius* Fauvel, 1900, *Megamblyopinus* Seevers, 1955 from South America and *Myotyphlus* Fauvel, 1883 from Australia). Internal phylogeny of Amblyopinina in that new sense, however, remains unknown and currently impossible to reconstruct because of the very poor state of the alpha-taxonomic knowledge of the numerous free living members of this subtribe. Our work in progress suggests that free living amblyopinines comprise the following major lineages: *Loncovilius*-lineage for species with enlarged middle and hind tarsi; *NatalignathusAtanygnathus*-lineage with elongated mouthparts; *Heterothops*-lineage with fully fused paramere and median lobe of the aedeagus; *Cheilocolpus-Rolla-Philonthellus*-lineage with species characterized by short 'infraorbital ridges', absent translucent post coxal process, wide anterior tarsi, often narrow or aciculate apical segment of maxillary palps and two basal carinae on abdominal segments III-V; a lineage consisting of one-two new genera to be described with fully developed 'infraorbital ridges', narrow anterior tarsi, absent translucent post coxal process and two basal carinae on abdominal segments III-V; *Quediopsis*-lineage with securiform last segment of maxillary palps; and *Sphingoquedius-Quediomimus-Mimosticus-Ctenandropus*- lineage with species bearing black iridescent combs. Such combs are unique among Staphylinini (and Staphylinidae) and, in different species or genera, they can be located on the first mesotarsomere, mesotrochanter, mesofemora, or metacoxae, respectively. Often these combs are present only in males, but those on mesotarsomeres may be developed in both sexes. Except the strictly South American

427 *Loncovilius*-lineage, South African (*Natalignathus*) and wide-spread (*Atanygnathus*) lineage

428 and wide-spread *Heterothops*-lineage, all other lineages have disjunct distributions across

429 several Gondwana-derived landmasses (mainly South America, Australia, New Zealand, New

430 Caledonia and New Guinea) where they form major to notable share of the entire Staphylinini

431 fauna. Amblyopinina are notably absent or very poorly represented in India, Madagascar and

432 Africa, i.e. the Gondwana-derived landmasses that got separated earlier. Such distribution

433 pattern hints that Amblyopinina is a relatively old lineage of Staphylinini whose major

434 lineages evolved during Cretaceous - Early Tertiary when at least South America, Australia

435 and New Zealand were connected via Antractica. Except the *Loncovilius*-lineage, all other

436 amblyopinine lineages occur in Australia. Based on the presence of combs and characters of

437 *Myotyphlus,* it can be assigned to *Sphingoquedius-Quediomimus-Mimosticus-Ctenandropus*

438 lineage where the majority of the Australian Amblyopinina belong (e.g., '*Quedius*' *bellus*

439 Lea, 1925, '*Quedius*' *cordatus* Lea, 1925, *Quedius lateroflavus* Lea, 1925, *Quedius*

440 *metallicus* Fauvel, 1878 and many other species still formally remaining in the genus

441 *Quedius*). Noteworthy that the black combs are absent in all genera of the truly mammal-

442 mutualistic genera of the Neotropical region even though there are free living comb-bearing

443 species Amblyopinina there. All these observations suggest that *Myotyphlus* stems from a

444 lineage different from the one(s) that gave rise to South American mammal mutualistic

445 mammals.

446

447 **4.3 Myotyphlus** *association with Australian mammals, historical perspective*

448 According to the available data, all species of *Myotyphlus* are known only as adults that have

449 been recorded. *Myotyphlus jansoni* was found on rodents (*Rattus spp.* and *Pseudomys*

450 *higginsi*) and on *Antechinus swainsonii*, a species of carnivorous dasyurid marsupial

451 *Myotyphlus newtoni* and *M. wurra* were found only on *Rattus* spp., and, at least on two

452 occasions they were collected not from mammals but in caves from under the surface of bat

453 guano. Finally, one female specimen identified as *M. newtoni* based on the distribution was

454 collected in a pitfall trap in the usual above ground microhabitat at high elevation of Mt.

455 Kostiusko. Therefore, it seems that none of *Myotyphlus* species has strict association with any

456 particular host mammal species. Probably, beetles do not even stay on the mammal body all

457 the time, or even some populations, for example those found in bat guano, do not occur on

458 mammals at all. Presumably, larvae of the species develop outside the mammal host body.

The strength of the association between *Myotyphlus* and caves, is also unknown. Presumably, the mammals which the *Myotyphlus* specimens were taken from, have been trapped in the usual above ground habitats. But it may well be that mammals with beetles also occur in caves, at least episodically. It is also unclear whether a specialized depigmented and small-eyed habitus of *Myotyphlus* was a primary adaptation for subterranean biology where beetles and mammals could come in contact, or the association with mammals came first, followed by adaptations to cave microhabitats. In any case, specialized biology and associated morphological adaptations of *Myotyphlus* seem to be a relatively young phenomenon in the evolutionary history of Australian Amblyopinina given the time estimates derived from the study of the evolutionary history of their hosts in Australia.

Since amblyopinines must have been present in Australia for tens of millions of years, it is quite noteworthy that in spite of rich ancient indigenous and diverse fauna of marsupials in Australia, the only marsupial that *Myotyphlus* has been recorded from, is the carnivorous marsupial genus *Antechinus* (Dasyuridae). It is comprised of 12 species distributed in Australia and New Guinea (Flannery 1995; Strahan 1995; Armstrong *et al.* 1998) with the genera from those two regions forming two monophyletic lineages (Armstrong *et al.* 1998). In that study, Armstrong *et al.* (1998) made no biogeographic inference from their phylogeny, however like rodents dasyurids also appear to be a recent group in Australia (Crowther & Blacket 2003), with the oldest fossil that can be placed in an extant genus dated at around 4.5 mya (early Pliocene). More recently it has been suggested that extant Dasyuridae have earlier origins in Australia with *Antechinus* originating around 11.9 (9.5–14.5) mya (Woolley *et al.* 2015).

The first group of rodents that reached Australia from Asia most likely via New Guinea were the *Pseudomys*-group of rodents (Muridae), with one genus and species recorded as a host of *M. jansoni* (*Pseudomys higginsi*) (Simpson 1961). This pattern of colonization of Australia from Asia via New Guinea has been found in a number of studies on different organisms and can be explained by the close geographic affinity of Australia and New Guinea and frequent land connections between those during the Pliocene. The diversity of native *Rattus* (Muridae) species is the highest in New Guinea and followed by Australia, mainland south-east Asia and Sulawesi (Aplin *et al.* 2003). Molecular phylogenetic dating and the earliest of Australian murine fossils suggest that diversification of the native Australian rodents began between 5.1 and 5.5 mya (Rowe *et al.* 2008). Based on mitochondrial genome data, Robins *et al.* (2011) proposed that *Rattus fuscipes* and *R. lutreolus* (recorded as *Myotyphlus* hosts) are among the oldest lineages of Australian rats and not part of the

493   colonization from New Guinea, but rather share a common ancestor with *Rattus* that

494   colonized Australia out of New Guinea. In that paper they also suggested recent interchanges

495   between the Australian and New Guinean *Rattus* fauna during the Pleistocene, supporting

496   previous morphology-based analysis (Taylor *et al.* 1983). Finally, it is interesting to note that

497   *Rattus rattus* and *Rattus norvegicus* were introduced to Australia by Europeans and there are

498   no records of *Myotyphlus* from those species.

499   For comparison, hosts of the more diverse American symbiotic amblyopinines

500   represented by many more different mammal species, almost equally split between marsupials

501   and rodents (Seevers 1944, 1955). The earliest fossil marsupials in South America are dated

502   to 61-65mya. The marsupial genera *Didelphis*, *Metachirus* and *Monodelphis* from which

503   American symbiotic amblyopinines have been recorded, are part of a clade that originated

504   during the early Eocene (ca.51 mya), based on semi-parametric divergence dating methods

505   which relax the molecular clock (Nilsson *et al.* 2004). Those amblyopinines are also recorded

506   from *Rhyncholestes*, a genus sister to *Caenolestes* (Meredith *et al.* 2008) and Palma &

507   Spotorno 1999). Nilsson *et al.* (2004) suggested a divergence time between those two sister

508   genera of around 30 mya, during the Oligocene.

509   Hystricomorpha, a suborder of rodents and recorded host of South American

510   Amblyopinina have been suggested to have Oligocene (23-34mya) origins in South America,

511   although the exact source of their South American fauna seems to still be controversial

512   (Huchon & Douzery 2001; Upham & Patterson 2012). According to Smith and Patton (1999),

513   the ancestor of the rodent subfamily Sigmodontinae from which many mammal-mutualistic

514   Amblyopinina have been collected, dispersed to South America from North America across

515   the water barrier, probably during the Miocene. The earliest recognized fossils of the

516   Sigmodontinae from Argentina dated at about 4-5 mya (early Pliocene) are consistent with

517   that hypothesis (Pardiñas & Tonni 1998). There are variations on each of the two hypotheses

518   mentioned above, but it is not within the scope of this paper to discuss them in detail, but

519   rather we aim to draw attention to the controversy and potential temporal variation in the

520   colonization and radiation of Amblyopinina hosts in South America. It is apparent that

521   American symbiotic Amblyopinina are adapted to mammals that had much earlier origins

522   (particularly the marsupials), but also more recent rodent lineages.

523   Lower degree of morphological specialization, frequency of records outside mammal bodies,

524   and relatively short period of time available for possible co-evolution with their hosts, suggest

525 that *Myotyphlus* may not be as strong case of mutualism with mammals as manifested by

526 South American genera.

527 **4.4 *Myotyphlus as an early stage of insect-mammal mutualism and other other examples of***

528 ***mammal-insect***

529

530 The case of *Myotyphlus*, that possibly displays an early stage of the evolution towards more

531 refined mutualism, reveals a certain gradient within such insect-mammal interactions, and it

532 draws our attention to other rare cases of similarly looking relationships. When Popham

533 (1962) reported the presumably ectoparasitic earwig *Arixenia esau* Jordon, 1909

534 (Dermaptera) feeding on the skin of *Cheiromeles,* he noted that another species of the same

535 genus, *A. jacobsoni* Burr, 1912 with less specialized mouthparts, feeds on insects found in bat

536 guano. Later, Marshall (1972) suggested the interaction between *Arixenia* earwigs and

537 *Cheiromeles* bats to be a mutualism where earwig feeding mode keep the bat body clean.

538 Waage (1979) further discussed the relationship between *Arixenia* and its bat hosts and

539 described it as a commensalism with the potential of actually being a mutualism if a sanitary

540 benefit to the bat can be attributed to the feeding strategy of *Arixenia*. Noteworthy is that even

541 though rove beetles and earwigs are members of phylogenetically remote insect orders,

542 convergently they represent very similar adaptive types, with flexible elongate body and short

543 elytra.

544   Another example is phylogenetically close to rove beetles since it concerns a derived

545 staphylinoid beetle *Platypsyllus castoris* Ritsema, 1869 from the family Leiodidae.

546 *Platypsyllus castoris* is believed to be an ectoparastic beetle specialized on Old and New

547 world beavers (Peck 2006) based on observations of its larvae consuming the epidermal tissue

548 of beavers as well as skin secretions and wood exudates (Wood 1965). In view of the

549 Amblyopinina and earwig examples, it would therefore appear that this relationship also has

550 the potential to be a mutualism, if evidence can be attained of any sanitary (or other) benefit

551 to the beaver.

552   Finally, the last example of insect-mammal mutualism involves Lepidoptera. Initially it

553 was described as phoresis between *Cryptoses* moths and a species of three-toed sloth (Waage

554 & Montgomery 1976) where moths require the relationship but they pose no consequence

555 (positive or negative) on the sloth. Adult female moths that occur in the fur of sloths

556 disembark their host during its descent to the forest floor for defecation. Female moths

557 oviposit on the fresh dung of their host sloth where development of the moth next generation

558 takes place until newly hatched moth adults disperse into the forest canopy and find sloths

559 again. The relationship between moths and sloths started to be seen as mutualism only

560 recently after Pauli *et al*. (2014) added a third organismal type (algae *Trichophilus sp*.) in the

561 system. They found that sloths with algae-infested fur consume their algae via self-grooming

562 and apparently benefit from adding algae in their diet, while moths, presumably, facilitate the

563 increase of algal biomass in the sloth's fur. In turn, by descending for defecation to the

564 ground, the sloths facilitate moth's life cycle. However, the exact mechanism driving the

565 positive relationship between moth density and algal biomass remains speculative, and

566 therefore this entire complex case of presumed mutualism is not fully understood yet.

567

568 **5. Conclusions**

569 The Staphylinini subtribe Amblyopinina under its most recent concept (Chatzimanolis *et al.*

570 2010; Brunke *et al.* 2015) comprises a diverse and species-rich monophylum forming a

571 predominant type of rove beetles in the mesophilic habitats of the highly disjunct south

572 temperate areas of the globe. Based on a rather basal position of the Amblyopinina in the

573 phylogenetic tree of Staphylinini, fossil-inferred age of this tribe, and the distribution pattern

574 of tentative amblyopinine monophyletic lineages, early diversification of this group is

575 associated with the Gondwana-derived South America-Antarctica-Australia-New Zealand

576 landmass before its fragmentation. Mammal-associated, morphologically highly derived

577 species constitute a minority within Amblyopinina and they are mainly confined to South and

578 Central America. Existing evidence suggests that American mammal-associated

579 amblyopinines form a fine tuned mutualistic relationship with the mammal hosts by feeding

580 on their ectoparasites.

581   *Myotyphlus*, endemic to Australia, is the only mammal-associated amblyopinine

582 outside America. The genus comprises at least three species diagnosable by the shape of the

583 aedeagus two of which, *M. newtoni* sp. nov. and *M. wurra* sp. nov*.,* occur sympatrically in the

584 south-western Australia, and one, *M. jansoni*, is confined to Tasmania. Most specimens of

585 *Myotyphlus* were collected from the bodies of small mammals, rodents and one marsupial,

586 while some – in bat guano in the caves. There seems to be no strict association with one

587 particular mammal species in any of three *Myotyphlus* species. Larvae of *Myotyphlus* are

588 unknown and it is unclear how long and when any of its species occur on mammal hosts

589 during their life cycle.

590 Current state of knowledge suggests that mammal mutualistic *Myotyphlus* has an independent

591 origin from the Neotropical mammal mutualists, and even within the latter different genera

592 could have originated from independent free living lineages. Presumably *M. jansoni* has

593 originated from a species of free living Australian Amblyopinine. Highly reduced eyes in

594 *Myotyphlus* and South American *Edrabius*, a feature contributing to their similarity and

595 causing earlier views about phylogenetic affinity of both genera, seems as a convergent

596 adaptation to caves in the case of *Myotyphlus* and nocturnal, mammal and/or mammal-burrow

597 associated behavior in the case of *Edrabius*.

598   Although sister group relationship of *Myotyphlus* remain to be rigorously explored, it

599 is logical to assume that its association with mammals in Australia evolved a relatively short

600 time ago, after the colonization of the Australian continent by rodents and dasyurine

601 carnivorous marsupials. The distinctly less specialized morphology of *Myotyphlus* compared

602 to the mammal-associated species from the Neotropical region, is consistent with relatively

603 shorter time of existence there of its mammal hosts providing therefore shorter evolutionary

604 time for *Myotyphlus* to develop its co-adaptations with mammals. It is not clear if the rodent-

605 associated lifestyle was primary with subsequent shifts to guano dwelling in caves via their

606 rodent hosts visiting caves. Or the adaptation to guano-associated biology in caves was the

607 original state for *Mytotyphlus*, serving as a precondition for the next evolutionary step

608 towards an association with rats, frequently seeking shelter in caves and thus getting into

609 proximity with guano-dwelling beetles there.

610   An ongoing generic revision of free-living Amblyopinina and a molecular phylogeny

611 of the subtribe will hopefully provide a baseline to further investigate the sister-group

612 relationships of *Myotyphlus*. In addition, phylogenetic reconstruction of the Neotropical

613 mutualistic Amblyopinina and their hosts has the potential to reveal the level of congruence

614 between both sides of a mutualistic relationship and provide an insight into the origin(s) of the

615 unique relationship.

616   Insect-mammal cases of mutualism are very rare and, apart from Amblyopinina rove

617 beetles, is known for *Cryptoses* moths and sloths in South America. Other staphylinoid beetle,

618 Holarctic *Platypsyllus castoris* (Leiodidae), that is thought to be parasitic on beavers, may in

619 fact be mutualistic similarly to Amblyopinina. The example of *Myotyphlus* has some

620 similarity with a rare case of *Arixenia* earwig and *Cheiromeles* bat interaction that perhaps is

621 also a case of mutualism.

622

Acknowledgements

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763 **Figures**
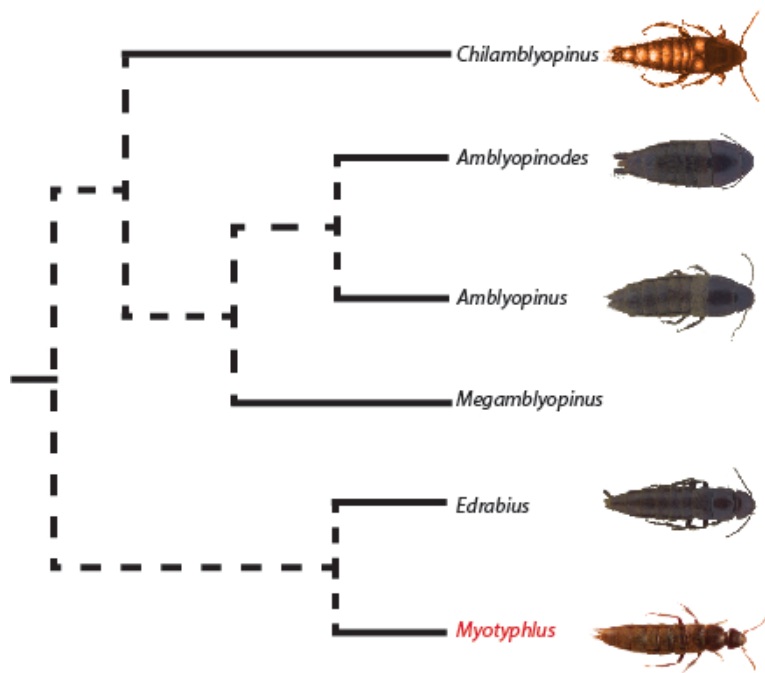
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765 **Fig. 1.** Schematic phylogeny of the tribe Amblyopinini expressing the ideas of Ashe and

766 Timm (1988). Illustrated are: *Chilamblyopinus piceus*, adapted from the illustration of Ashe

767 and Timm (1988), *Amblyopinodes* sp. from Brazil, *Amblyopinus jelskii* Solsky, 1875,

768 *Edrabius kuscheli* Scheerpeltz, 1957 from Chile and *Myotyphlus* sp. (female) from Australia.
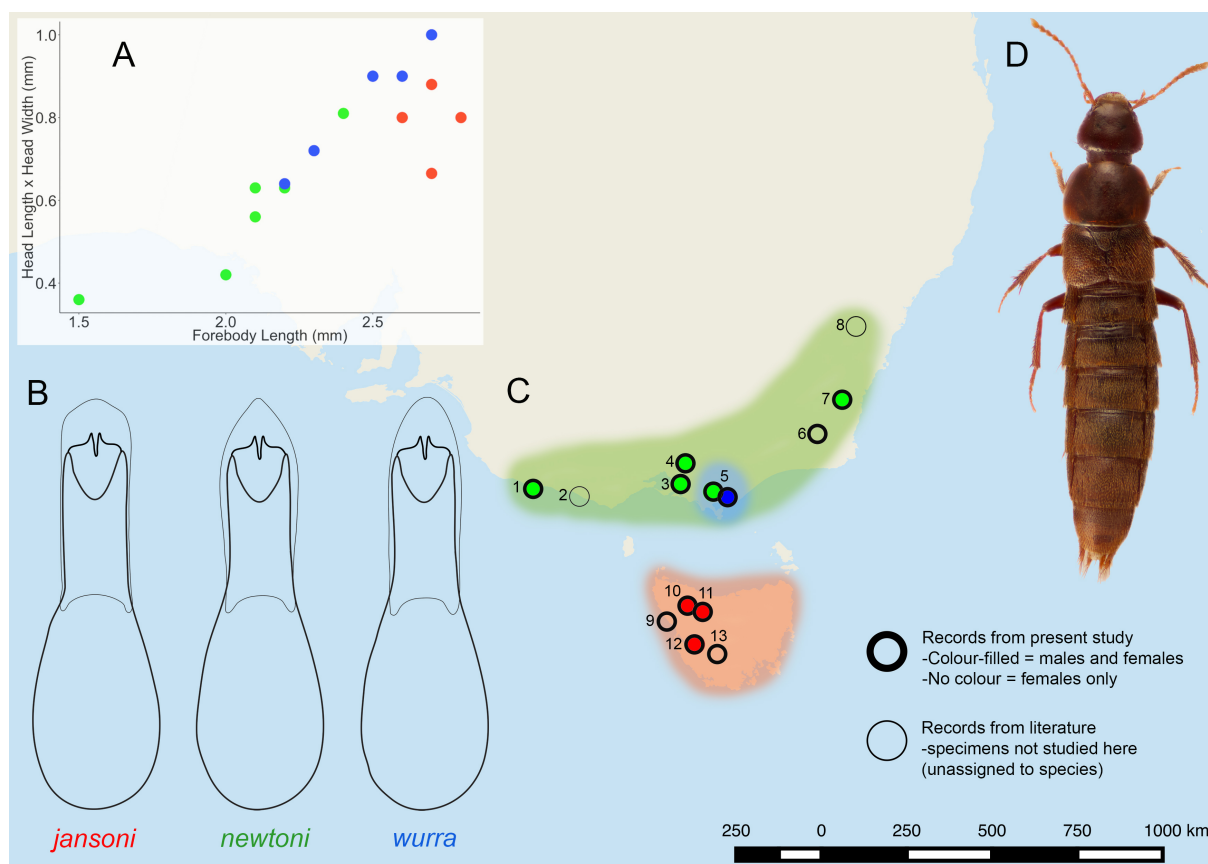
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Fig. 2. A - The relationship between Forebody Length (mm) and Head Length x Head Width (mm) for three species of *Myotyphlus: M. jansoni* (red), *M. newtoni* **sp. nov.** (green) and *M. wurra* **sp. nov.** (blue). **B** – Aedeagi of *Myotyphlus jansoni*, *M. newtoni* and *M. wurra*. **C** – distribution of specimens and species studied in this paper (thick circles) and records from literature (thin circles). Colours in circles correspond to those used in 2A and B. Corresponding shaded areas indicate hypothesized distribution of respective species based on locality data so far available. **D** – habitus of female *Myotyphlus* sp. from Olson's Bridge, Victoria.
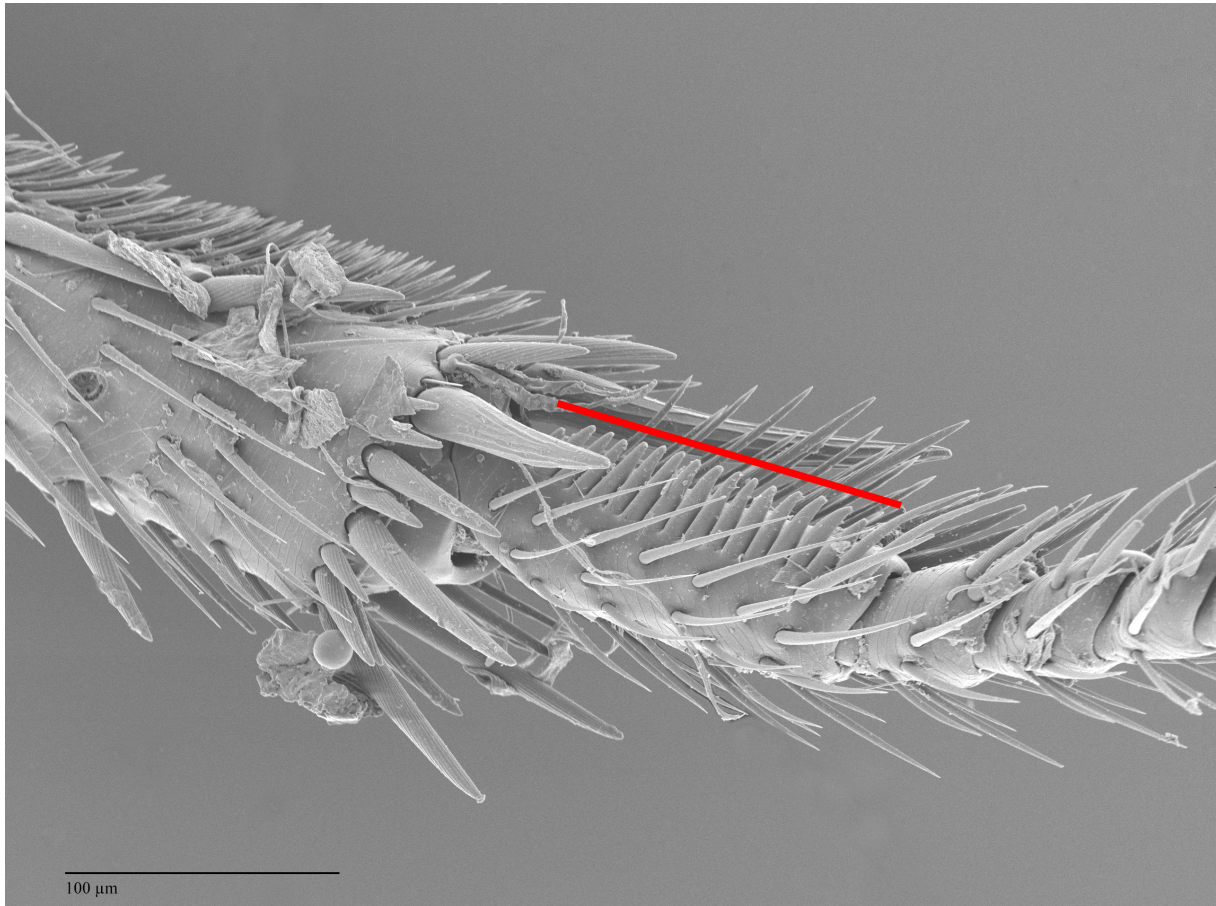
Fig. 3. Mesotarsus of *Myotyphlus jansoni* (female) from Tasmania showing the comb on the first tarsomere (red line). Scale bar = 100 micro metres (μm).

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98   **Table. 1.** Synthesis of *Myotyphlus* species and associated data used in this study. [a] = records

799   from Hamilton-Smith and Adams (1966) and personal communication therein. Locality, Date,

800   Host and Collector data are repeated verbatime from data labels beneath specimens or from

801   literature.

Species	Locality	State	Date	Males	Putative Females	Host	Collector	Locality (number on map)
M. jansoni	Cradle Mt	Tasmania	6.xiii.1964	1	1	*Pseudomys higginsi*	R.H. Green	10
M. jansoni	Franklin River, below Gordons Peak	Tasmania	15 Jan. 1983	2	-	-	E.B. Britton	12
M. jansoni	Mt Kate	Tasmania	16.x.1964	1	1	*Rattus lutreolus*	R.H. Green	11
M. jansoni	Florentine Valley	Tasmania	7.vii.1959	-	1	*Rattus lutreolus velutinus*	B.C. Mollison	13
M. jansoni	Corinna	Tasmania	8.ii.1965	-	1	*Antechinus swainsonii*	R.H. Green	9
M. newtoni	Olson's Bridge	Victoria	11-9-59 (Sept)	2	-	*Rattus assimilis*	R.M Warneke	5
M. newtoni	Loch Valley	Victoria	27.vii.63	1	-	In fur of *Rattus assimilis*	R.M Warneke	4
M. newtoni	Deua NP, Deua Cave	New South Wales	5 Apr. 1986	1	-	Bat guano	E. Holm	7
M. newtoni	French Island	Victoria	29.viii.1967	1	1	*Rattus fuscipes assimilis*	R.M Warneke	3
M. newtoni	Bat's Ridge	Victoria	20.i.1968	1	1	*Rattus assimilis grayii*	J.H. Seebeck	1

M. wurra	Olson's Bridge	Victoria	7.vii.1959	5	-	*Rattus assimilis*	R.M Warneke	5
Myotyphlus sp.	South Ramshead, 1850m, Kosciuskco Nat. Pk.	New South Wales	May 1981	-	1	-	Ken Green	6
Myotyphlus sp.	Olson's Bridge	Victoria	7.vii.1959	-	3	*Rattus assimilis*	R.M. Warneke	5
'M. newtoni' [a]	Lake Gillear Guano Cave near Warrnambool	Victoria	May 13, 1962 May 19, 1973 Jan 12, 1964	-	-	Bat guano of *Miniopterus schreibersi* (Kuhl)	-	2
'M. newtoni' [a]	Southern Limestone (cave), Jenolan	New South Wales	July 25 1964	-	-	Bat guano of *Miniopterus schreibersi* (Kuhl)	B. Dew	8

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