Two new species of fossil Leggadina (Rodentia: Muridae) from Northwestern Queensland

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Only three species of fossil murine have been described to date in Australia even though they are often found in fossil deposits and can be highly useful in understanding environmental change over time. Until now the genus *Leggadina*, a group of short-tailed mice that is particularly well adapted to an arid environment, was only known from two extant species: *L. forresti* and *L. lakedownensis*. Here two new fossil species of the genus are described from sites in northwestern Queensland. *Leggadina gregoriensis* sp. nov comes from the Pliocene Rackham's Roost Site in the Riversleigh World Heritage Area and *Leggadina macrodonta* sp. nov is from the Plio-Pleistocene Site 5C at Floraville Station. The evolution of the genus *Leggadina* and the lineage's response to palaeoecological factors is considered. Taphonomy of the two fossil deposits is examined and shows marked differences in both faunal composition of the assemblages and preservation. Presence of *L. gregoriensis* in an early Pliocene deposit extends the known temporal range of the *Leggadina* lineage by over 4 million years. *L. macrodonta* displays an obvious increase in size of M^1 and M^2, possibly explained by either environmental variability during the Pleistocene or body size increase.

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Introduction

Rodents in Australia include over 70 living species specialised to fill a range of environmental niches from rainforest to arid areas and arboreal to fossorial habitats (Godthelp, 2001). All rodents in Australia are part of the subfamily Murinae. This subfamily is thought to have originated in South East Asia, migrating to Australia by rafting and island hopping, and taking advantage of sea level fluctuations (Archer et al. 1998; Godthelp, 2001).

The murid genus *Leggadina* Thomas, 1910 belongs to the Conilurini tribe of the subfamily Murinae. This tribe is endemic to Australia and is also regularly referred to as the *Mesembriomys* series (Misonne, 1969; Musser & Carleton, 2005). Older studies using superseded molecular techniques placed *Leggadina* outside the Conilurini group (Baverstock et al. 1981; Watts et al. 1992). However more recent studies using DNA sequencing include *Leggadina* within the Conilurini (Steppan et al. 2005; Rowe et al. 2008; Nilsson et al. 2010; Schenk et al. 2013) which is supported by morphological studies (Tate 1951; Missone 1969). Within this broad Conilurini grouping, the nearest relatives of *Leggadina* are still unable to be determined as studies using either morphological or molecular data produce different results. The genus *Leggadina* contains two living species: *Leggadina forresti* (Thomas, 1906) and *Leggadina lakedownensis* Watts, 1976. Species of this genus are characterised by their enlarged first upper molar and reduced third upper molar, an accessory cusp on the anterior of the first upper molar, forward pointing incisors, narrow but large posterior palatal foramina, and straight (or convex) anterior edge to the zygomatic plate (Watts & Aslin, 1981).

Tooth morphology is central to the study of rodent systematics because rodents generally have conservative cranial and skeletal morphology, and molecular data is unable ascertain relationships between fossil groups (Tate, 1951). Molars are largely flat with numerous cusps which act as the dominant occlusal surfaces for the grinding of food (Misonne, 1969). The

34   position and presence/absence of cusps is key to the morphological identification of species and

35   is particularly important for the identification of fossil species. The most comprehensive study of

36   molar morphology in African and Indo-Australian murids was conducted by Misonne (1969).

37   More recently, molecular techniques have been employed on extant species to determine

38   relationships between groups, with Rowe et al. (2008) producing the most comprehensive

39   molecular phylogeny to date on rodents from Australia and New Guinea. Tooth morphology,

40   however, provides the most useful data for fossil rodent systematics because it seems to be the

41   most informative when testing hypotheses based on molecular datasets, modelling, and in

42   determining species relationships (Wiens, 2004).

43

44   There have only been three species of fossil murines described from Australia: *Pseudomys*

45   *vandycki* Godthelp, 1988, from the Pliocene-aged Chinchilla locality in southeastern

46   Queensland, *Zyzomys rackhami* Godthelp, 1997, from the Pleistocene Rackham's Roost Site in

47   the Riversleigh World Heritage Area in northwestern Queensland, and *Conilurus capricornensis*

48   Cramb and Hocknull, 2010, from late Pleistocene-Holocene cave deposits in eastern Queensland.

49

50   The first species to be described in the present study comes from the Riversleigh World Heritage

51   Area in northwestern Queensland, which preserves a rich diversity of fossil vertebrates in

52   limestone rocks from the late Oligocene to the late Pleistocene and Holocene (Archer et al. 1989;

53   Archer et al. 2006; Travouillon et al. 2006). The Rackham's Roost Site at Riversleigh is a

54   breccia deposit in the floor of a fossil cave situated in Cambrian limestone cliffs overlooking the

55   Gregory River. This cave was inhabited by a population of the Ghost Bat *Macroderma gigas*

56   (Hand, 1996). Originally identified as a Pliocene-aged site based on biocorrelation (Archer et al.

57   1989), recent radiometric dating of speleothems associated with fossil remains has indicated the

58   site is more likely Early Pleistocene in age (Woodhead et al. 2014). Fossils found at this site

59   include small mammals believed to be the prey of the Ghost Bat colony, and occasionally larger

60   animals which are believed to have fallen into the cave (Archer, Hand & Godthelp 1991). Rodent

61   fossils found in this deposit represent at least 12 taxa, namely from the genera *Pseudomys,*

62   *Zyzomys* and *Leggadina* (Godthelp, 2001). Prior to this study, Godthelp (1997) described one

63   species (*Zyzomys rackhami*) from this site.

64

65 Site 5C at Floraville Station in northwestern Queensland is quite different from Riversleigh's

66 Rackham's Roost Site. It contains a lower diversity of animals but a much greater range of body

67 sizes. This deposit consists of sandy riverine sediments suggestive of a billabong or waterhole

68 (Rich et al. 1991). Rodent remains are thought to have been accumulated through natural

69 mortality and prey of marsupial carnivores (H. Godthelp, unpublished data). The site is Plio-

70 Pleistocene in age (Rich et al. 1991), a period that was characterised by great climatic

71 fluctuations and subsequent unpredictability of resources (Archer et al. 1998; Martin, 2006). Site

72 5C contains specimens of the murine genera *Rattus*, *Pseudomys* and *Leggadina*, with *Rattus*

73 being by far the most dominant taxon (H. Godthelp, unpublished data). No fossil rodent taxa

74 have previously been described from Floraville.

75

76 The description of new species herein almost doubles the number of described fossil Australian

77 murines and will assist in developing a better understanding on the evolution of the murines in

78 Australia, including their initial migration.

79

80

81 **Methods**

82 Fossil Australian murid specimens were recovered from northwestern Queensland at the

83 Rackham's Roost Site in the Riversleigh World Heritage Area and Site 5C at Floraville Station.

84 Rackham's Roost fossils were recovered by dissolving limestone breccia in 5% acetic acid. The

85 sandy sediment from Site 5C was washed through fine screens to concentrate fossils which were

86 later extracted under a stereomicroscope. A number of fossils recovered at each site were

87 identified as potentially belonging to the genus *Leggadina*. Twenty-eight upper tooth and

88 maxillae specimens from Rackham's Roost and seventeen upper tooth and maxillae specimens

89 from Floraville were analysed and are denoted by the prefix QM F (Queensland Museum Fossil).

90

91 Upper molar and upper maxillae specimens from Rackham's Roost Site and Site 5C were

92 observed, as well as lower molar specimens from Site 5C. The upper molar and maxillae

93 specimens from both sites were confirmed as potential new species of the genus *Leggadina*.

94 Observations of the lower molar specimens from Site 5C indicate they are likely attributable to

95   the genus *Leggadina* based on overall similarities to living species of the genus. However, it is

96   not possible to confidently assign them to the same species as the upper molars since none were

97   found in articulation. For this reason, the lower molar specimens from Site 5C have not been

98   described herein.

99

100   Univariate and bivariate analyses were conducted using the statistical software program PAST

101   (PAlaeontological STatistics; Hammer, Harper & Ryan, 2001) to confirm that the two proposed

102   fossil *Leggadina* species differ from known living and fossil species of the genus. Univariate

103   analyses were conducted to determine the amount of variance within measurements on both

104   fossil and modern taxa using the Coefficient of Variation (CV). The Coefficient of Variation has

105   been widely used to measure the degree of variation within a sample (Simpson, Roe & Lewontin,

106   1960). However, caution must be taken when using this method because there are a number of

107   external variables that can affect CV scores including small sample size, geographic variation

108   and sexual dimorphism (Plavcan & Cope 2001).

109

110   Bivariate plots compared upper molar crown length and width data of *Leggadina* specimens (two

111   fossil *Leggadina* specimens, *L. forresti* and *L. lakedownensis*) with closely related species of

112   'Australian genera' from node W of Rowe *et al.*'s (2008) molecular phylogeny which represents

113   conilurine species most closely related to *Leggadina forresti* (*Zyzomys argurus*, *Pseudomys*

114   *australis* and *Notomys fuscus*). *Mastacomys fuscus* was removed from the bivariate analysis

115   because its molar morphology diverges so dramatically in both size and cusp arrangement that

116   the fossil specimens collected from the two Queensland sites clearly do not belong to this genus.

117   The greatest length and width of upper molars were used to determine species identification

118   because molar cusp position is too variable, especially with occlusal wear (Misonne, 1969).

119

120   Measurements were made at the University of New South Wales on a Wild 5MA

121   stereomicroscope with Wild MMS235 Digital Length Measuring Set (accurate to 0.01mm) and

122   at the Australian Museum on a Leica MZ95 stereomicroscope with graticule (accurate to

123   0.05mm). Measurements were cross-checked to ensure comparability by measuring a subset of

124   specimens on both microscopes. No M^3 or a molar row has been discovered for the Floraville

125   *Leggadina*, so bivariate plots for M^1 and M^2 were used to assess separation of these murine

126 species. *Leggadina lakedownensis* could not be included in the M^2 analysis as access to

127 specimens was not possible.

128

129 Dental nomenclature used herein follows Musser and Newcomb (1983) which uses a simplified

130 serial nomenclature that reduces potential issues of conflicting homologies in the upper molars

131 for muroid rodents (Fig. 1). A Wild M3B stereomicroscope was used during the description of

132 new species. Specimens were photographed using a scanning electron microscope (Quanta 200)

133 housed at the University of New South Wales Analytical Centre.

134

135 Abbreviations used in this study are defined as follows: M^1 = first upper molar, M^2 = second

136 upper molar, M^3 = third upper molar. All measurements are in millimeters (mm).

137

138

139 **Results**

140

141 **Univariate analyses**

142 Coefficients of Variation for all measurements of the fossil taxa suggest that only one species is

143 present in each fossil sample, with values ranging from 3.23 to 7.80 in the *Leggadina* specimens

144 from Rackham's Roost and 5.50 to 6.06 for the two measurements available for *Leggadina*

145 specimens from Site 5C (Supplementary Material).

146

147 **Bivariate analyses**

148 In the bivariate plots, both length and width of M^1 and M^2 were effective in separating species

149 (Fig. 2 and 3). The M^1 plot shows the Rackham's Roost *Leggadina* overlapping with both

150 modern *Leggadina* species (*L. forresti* and *L. lakedownensis*), whereas in the M^2 plot, the

151 Rackham's Roost *Leggadina* groups predominately with the Floraville specimens. The Floraville

152 *Leggadina* species distinctly separates from other species based on its greater M^1 length.

153 *Pseudomys* and *Notomys* group together in both plots, but separate more in the M^2 plot based on

154 length data. In both plots there is a close association between the fossil specimens and *Zyzomys*.

155 More detailed morphological evidence effectively separates *Zyzomys* and the fossil specimens, as

156 detailed in the differential diagnosis.

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158

159

160 **Systematics**

161

162 **Differential Diagnosis**

163 The fossil species described below refer to the genus *Leggadina* and display characteristics

164 typical of species of this genus. An accessory cusp on the first upper molar is present on all fossil

165 specimens, all upper molars are inclined posteriorly, molar size is reduced along the row, with

166 M^3 often half the size or smaller than M^1, and the anterior edge of the zygomatic plate is

167 relatively straight (Watts & Aslin, 1981). *Leggadina gregoriensis* differs from other species of

168 the genus in the following combination of features: a greatly anteroposteriorly elongated T6 on

169 M^1; T1-2 and T4-5 complexes are oriented buccolingually with T3 and T6 swept back at right-

170 angles to lean proximally; an accessory cusp is present but small; M^1 is narrow, with M^2 and M^3

171 being wider than M^1. *Leggadina macrodonta* differs from other species of the genus in the

172 following combination of characters: M^1 is enlarged, being approximately 18% larger than

173 *Leggadina forresti* and *L. lakedownensis*; M^2 is similarly enlarged, approximately 16% larger

174 than in those species; an anterior cingulum is present and is enlarged with two accessory

175 cuspules that wear to a greatly elongated accessory cusp; T1 and T4 are well-developed and

176 posterolingually aligned; a T1 sup is present on some specimens; the central series of cusps is

177 also enlarged. Both fossil species also differentiate themselves from the two modern *Leggadina*

178 species through the presence of furrows between the lingual and central series of cusps in M^1 and

179 M^2. Bivariate analyses determined that *L. gregoriensis* and *L. macrodonta* could have been

180 referred to the genus *Zyzomys*. Shared morphological features and differences between

181 *Leggadina* and *Zyzomys* are mentioned here (Fig. 4). *Zyzomys* species often display an accessory

182 cusp on the first upper molar, have a relatively straight anterior edge to the zygomatic plate, and

183 are of similar size to *Leggadina* (Watts & Aslin, 1981). A feature clearly distinguishing species

184 of the two genera is a buccal row of cusps present in *Leggadina* species that is absent in

185 *Zyzomys*. A distinctive aspect of *Leggadina* molar morphology, not shared by *Zyzomys*, is the

186 posterior extension of the lingual series of cusps. (Tate, 1951). For these reasons, the fossil

187 species are referred to the genus *Leggadina* rather than *Zyzomys*. Character states are unable to

188 be discussed here as relationships between the genus *Leggadina* and other murines are uncertain

189 and can change depending on methods used. This situation is not helped by the lack of fossil

190 evidence on murines in Australia.

191

192

193 Superfamily MUROIDEA Miller and Gidley, 1918

194 Family MURIDAE Gray, 1821

195 Subfamily MURINAE Gray, 1821

196 Genus *LEGGADINA* Thomas, 1910

197

198 **Type species**

199 *Leggadina forresti* (Thomas, 1906)

200

201 **Other species**

202 *Leggadina lakedownensis* Watts, 1976

203

204 *Leggadina gregoriensis* sp. nov.

205 **Holotype**

206 QM F57259, partial right maxilla with M^{1-3} (Fig. 5).

207

208 **Type locality and age**

209 Rackham's Roost Site, Riversleigh World Heritage Area, northwestern Queensland; Pleistocene

210 (Woodhead et al. 2014).

211

212 **Paratypes**

213 QM F57244, partial right maxilla with M^1 and alveoli of M^2 and M^3 (Fig. 6); QM F57258, partial

214 left maxilla including zygomatic plate with M^1 and M^2 (Fig. 7).

215

216 **Etymology**

217 Named for the Gregory River which flows next to the Rackham's Roost Site.

218

Diagnosis

Leggadina gregoriensis is characterised by a small accessory cusp, greatly anteroposteriorly
elongated T6 on M^1; T3 and T6 swept back at right-angles to lean proximally; M^1 narrow, M^2
and M^3 wider.

Referred specimens

QM F57240, right M^1; QM F57241, left M^1 in partial maxilla; QM F57242, right M^1; QM
F57243, right M^1; QM F57245, left M^1; QM F57246, right upper molar row in partial maxilla;
QM F57247, left M^2 in partial maxilla; QM F57248, right M^1 and M^2 in partial maxilla; QM
F57249, right M^1 and M^2 in partial maxilla; QM F57250, right M^1 and M^2; QM F57251, right M^1
and M^2; QM F57252, left M^1 and M^2; QM F57253, right M^{1-3} in partial maxilla; QM F57254, left
M^1; QM F57255, left M^1 in partial maxilla; QM F57256, right M^1 and M^2 in partial maxilla; QM
F57257, left M^1 and M^2 in partial maxilla; QM F57260, right M^{1-3}; QM F57261, right M^1; QM
F57262, right M^{1-3}; QM F57263, right M^1 and M^2; QM F57264, left M^1 in partial maxilla; QM
F57265, right M^1 in partial maxilla; QM F57283, left upper molar row; QM F39958, left M^{1-3}
(Table 1).

Description

M^1 large and elongated. M^2 approximately two-thirds the size of M^1. M^3 smaller again,
approximately half the size of M^2 (Table 1). Tooth row exhibits spiral torsion, M^1 straight with
M^2 and M^3 twisted slightly to the buccal edge. Furrow present between lingual series of cusps
and central series of cusps in M^1 and M^2. Buccal series of cusps reduced along tooth row, central
series of cusps enlarged. All cusps inclined posteriorly with tooth crown overlap.

M^1. Elongated and narrow. Anterior cingulum with a single and small elliptical accessory
cusp sweeping backwards along lingual edge. Accessory cusp small in all specimens, almost
indistinguishable in QM F57244. T1 very small and circular, connected to T2 at early stages of
wear. T2 posteriorly inclined, large and elliptical. It is the highest cusp at early stages of wear but
becomes uniform with the other M^1 cusps after wear. T1-2 complex buccolingually aligned.T3
positioned to posterior of T1-2 complex, at mid-point of tooth. T3 elliptical, directed proximally
and connected to T2 by an enamel rim in the holotype. At early stages of wear it is entirely

250   distinct but merges completely with T1-2 complex after extreme wear. T4 small, circular and

251   merged with T5 at most stages of wear. It sweeps posteriorly from T5 so anterior edge of T4 is in

252   line with the posterior edge of T5. T5 large, subtriangular in occlusal outline and leans

253   posteriorly. Enamel rim connects T5 to both T4 and T6. T6 positioned posterior to T5, elongated

254   anteroposteriorly and directed proximally, similar to T3. T6 merges with T4-5 complex after

255   extreme wear. T6 also distinct from T9 at early stages of wear but merges quickly. Posterior edge

256   of cusps T4-T6 arcs anteriorly to enclose T8. T7 barely discernible in holotype but is present in

257   other specimens at early stages of wear before merging completely with T8. In these specimens it

258   is small and directed posteriorly. T8 very large and circular, directed posteriorly. T9 incorporated

259   at all stages of wear with T8. Enamel rim around cusps uniform throughout tooth but becomes

260   slightly wider with extreme wear.Has three roots, all of which directed somewhat anteriorly.

261   Anterior root largest of the three, circular in shape and positioned under accessory cusp and

262   T1-T3. Lingual root anteroposteriorly stretched, narrow and positioned under T6 and T9.

263   Posterior root smallest of the three, circular and positioned under T8.

264   **M^2.** Tooth is mostly circular in holotype but shape variable, with other specimens more

265   elongate. Elongation is affected by size of T3 and T8, with the anterior of M^2 developing a bulge

266   with increase in T3, similarly, posterior developing a bulge with increase in T8. T1 and T2

267   absent. T3 distinct and elliptical, directed proximally. T3 and T5 are the highest cusps at early

268   stages of wear but T3 wears faster than T5 to become uniform with the other cusps. T4 small,

269   circular and leans posteriorly. It is incorporated into T5, but also sweeps posteriorly from T5,

270   with anterior edge of T4 in line with posterior edge of T5. T5 subtriangular and directed

271   posteriorly. T6 positioned posterior to T5, elongated anteroposteriorly and oriented proximally.

272   At later stages of wear T6 merges with T4-5 complex. Posterior edge of T4-5 complex and

273   posterior edge connecting T6 with T9 forms anterior arc to enclose T8, similar to M^1. T7 absent.

274   T8 large, circular in occlusal outline and directed posteriorly. At extreme stages of wear T8

275   merges with elongated T6. T9 merges with T8 at all stages of wear, similar to M^1. Enamel rim

276   surrounding the cusps of uniform width, becoming thicker with wear.

277   With three roots, all directed vertically. The anterobuccal and posterobuccal roots of equal

278   size and circular. Anterobuccal root extends from underneath T4 and T5, while posterobuccal

279   root positioned beneath T8. Lingual root large and elongated, extending from T3 to T6.

280   **M³.** Tooth circular with a bulge on anterolingual edge for T3, cusp height uniform. T1 and

281   T2 absent. T3 small, circular and distinct, directed proximally. Furrow between T3 and T4-6

282   complex ensures T3 distinct in all but very late stages of wear. T4 completely incorporated into

283   T5. It sweeps posteriorly markedly from T5, directed posterobuccally. T5 subtriangular in

284   occlusal outline, large and directed posteriorly. T6 small and subtriangular. It merges with T5,

285   slightly sweeping posteriorly from T5 with enamel rim connecting to T8-9 complex. Posterior

286   edge of T4-5 complex curves anterobuccally, with posterior edge of T6 curving anterolingually.

287   T7 absent. T8 large, elliptical and orientated vertically. Anterior edge of T8 curves posteriorly.

288   Anterior edge of T8 combined with posterior edge of T4-6 complex creates elliptical furrow. T9

289   entirely incorporated into T8. Enamel rim uniform in width and connecting all cusps except T3

290   in holotype which only connects at very late stages of wear.

291   With three roots all directed vertically. Anterobuccal root small and circular, extending

292   from beneath T5. Anterolingual root slightly larger and more elongated than anterobuccal root

293   and positioned under T3 and T6. Posterior root largest of the three, supporting approximately

294   half tooth length and extending from T8.

295

296   Attachment node for the origin of the superficial masseter is of moderate size and well defined in

297   some specimens, positioned anterior to M^1. Posterior extent of anterior palatal foramen lies at

298   anterior root of M^1. Zygomatic plate of QMF57258 wide with posterior edge convex (Fig. 7).

299

300

301   *Leggadina macrodonta* sp. nov.

302

303   **Holotype**

304   QM F57276, partial left maxillary including zygomatic plate with M^1 (Fig. 8).

305

306   **Type locality and age**

307   Site 5C, Floraville Station, northwestern Queensland; Plio-Pleistocene (Rich et al. 1991).

308

309   **Paratypes**

310   QM F57273, partial left maxillary with M^2 (Fig. 9); QM F57268, left M^1 (Fig. 10); QM F57275,

311   partial left maxillary with M^1 and alveoli of M^2 (Fig. 11).

312

313   **Etymology**

314   Named for the distinctively large size of the first upper molar.

315

316   **Diagnosis**

317   *Leggadina macrodonta* is characterised by a greatly enlarged M^1 and M^2; enlarged anterior

318   cingulum with two accessory cuspules that wear to a greatly elongated accessory cusp; well-

319   developed T1 and T4 posterolingually aligned; enlarged central series of cusps.

320

321   **Referred specimens**

322   QM F57266, right M^1; QM F57267, left M^1; QM F57269, left M^1; QM F57270, right M^1; QM

323   F57271, left M^1; QM F57272, right M^1; QM F57274, left M^1; QM F57277, left M^1; QM F57278,

324   right M^1; QM F57279, right M^1; QM F57280, right M^1; QM F57281, right M^1; QM F57282, left

325   M^1 (Table 2).

326

327   **Description**

328   Complete tooth row not known. M^1 and M^2 are isolated specimens, no specimen of M^3 found to

329   date. M^1 large, M^2 approximately half length of M^1 (Table 2). Furrow between lingual series and

330   central series of cusps in M^1 and M^2. Buccal series of cusps reduced in M^1, all cusps inclined

331   posteriorly.

332

333   **M^1:** Tooth elliptical with thin and uniform enamel rim around all cusps. Two small

334   accessory cusplets present on anterior cingulum in holotype. With wear they become one very

335   large accessory cusp, elongated posterolingually, sweeping back along lingual edge. T1 large and

336   elongated, becoming more elongated with wear. Anterior edge of T1 sits posterior to T2, at half-

337   way point of tooth. T1 orientated posteriorly with axis of cusp stretching posterolingually,

338   parallel to single accessory cusp in specimens other than holotype. It merges with T2 at late

339   stages of wear. T1 sup present on some specimens, situated on posterolingual edge of T1. It is

340   small and circular, merging into T1 with wear. T2 of moderate size and subtriangular in occlusal

outline. T3 very small and circular, sweeping slightly posteriorly from T2 in some specimens. T3 often connected to T2 by enamel rim, later merging with wear. T4 large and tear-shaped, increasing in size posteriorly with wear but never merging with T7 or T8. It only barely merges with T5, even at late stages of wear. Large size of T4 together with similarly sized T1 creates a bulge on lingual edge of tooth, enlarging width of otherwise slender tooth. Anterior edge of T4 sits posterior to the posterior edge of T5. T4 higher at posterior edge than anterior edge. Cusp posteriorly inclined, with axis running almost parallel to main axis of tooth. T5 large and subtriangular, orientated posteriorly. T6 circular, elongating anteroposteriorly with wear and merged with T5 at most stages of wear. Posterior edge of T6 sweeps posteriorly slightly from T5 in most specimens. Posterior edge of T4-6 complex mostly arcuate anteriorly, enclosing T7-9 complex, especially on lingual side. T7 indistinguishable from T8 in the holotype but very small and completely incorporated into T8 in other specimens. T8 large and circular, orientated posteriorly. It is the highest cusp with all others roughly uniform in height. T9 small and elliptical. Lower half of T9 connects to T8 at early stages of wear, becoming fully incorporated with further wear.

With three roots. Anterior root the largest of the three. It is circular and directed anteriorly from the accessory cusp and T2. Posterolingual root narrow and plunges vertically from T1 and T4. Posterior root of equal size with posterolingual root, is more circular and is elongate vertically from T8 and T9.

M^2: Triangular in shape with broadest point along anterior edge. T1 circular and distinct, cusp directed posteriorly with occlusal surface inclined proximally. Deep furrows on buccal and posterior side of T1 separate it from other cusps and retains identity through wear. T2 and T3 absent. T4 large, elongated and tear-shaped, stretching posterolingually. Anterior edge of T4 sits posterior to posterior edge of T5. T4 posteriorly inclined, with occlusal surface facing proximally, similar to T1. T5 only slightly larger than T4 and subtriangular, connecting to T4 by its enamel rim and directed posteriorly. T6 absent. Posterior edge of T4-5 complex arcuate anteriorly, enclosing T8. T7 almost indistinguishable from T8 but indicated by a small bulge on the lingual edge of T8. T8 large and circular, directed posteriorly. Posterior edge arcuate posteriorly and delineates the most posterior edge of the tooth. No obvious indication of presence of T9. Remnant of furrow that marked its position present, indicating it has been wholly incorporated into T8. Enamel rim of cusps is variable, with T5 and T8 thicker than other cusps.

372   All cusps of equal height and incline posteriorly at varying degrees, with T5 and T8 leaning

373   posteriorly more than T1 and T4.

374   Roots not visible on only available specimen of M^2. Description has been gathered from

375   alveoli in a specimen also preserving M^1 (QM F57275). M^2 has three roots. Lingual root very

376   large and elongated, directed vertically. Anterobuccal root is circular, extends anteriorly, and is

377   smaller than the lingual root. Posterobuccal root smallest of the three, elongated and extends

378   vertically.

379   **M^3:** No specimen known.

380

381   Information on dental arcade is limited. Large posterior palatal foramen extends distally from

382   posterior of M^1. Zygomatic plate wide with posterior edge appearing almost straight but is

383   slightly convex.

384

385

386   **Discussion**

387   *Taphonomy*

388   Even though Riversleigh's Rackham's Roost Site and Floraville's Site 5C represent vast

389   differences in both mode of death and environment of preservation, similar skeletal elements

390   have been preserved. Rackham's Roost Site is interpreted to have been a Ghost Bat

391   (*Macroderma gigas*) roost during the Early Pleistocene (Hand, 1996; Woodhead et al. 2014) and

392   specimens of *Leggadina* found there are thought to be the result of bat predation (Godthelp,

393   1997). Floraville's Site 5C specimens are more likely to have come from marsupial predators,

394   fossils of which have also been found at the site (Rich et al. 1991). There have been no complete

395   skulls found at either site. The fractured cranial and post cranial elements found cannot be

396   attributed to individual murine taxa due to overlaps in size and a lack of features known to

397   separate them (H. Godthelp, unpublished data).

398

399   The Rackham's Roost assemblage contains only upper molars (upper = 28, lower = 0) which are

400   all identifiable as belonging to the same species of *Leggadina*. They include complete molar

401   rows, dental arcades and zygomatic plates. Site 5C specimens are dominated by lower molars but

402   lack any molar rows (upper = 17, lower = 20). Upper molars all belong to the same species of

403 *Leggadina*. Lower molars are observed to belong to the genus *Leggadina* but since they are not

404 associated at all with the upper molars found, it is not possible to confidently identify them as

405 belonging to the same species. Dental arcade and zygomatic plate information is fragmentary.

406 The increased preservation of upper molars over lower molars is expected since the lower

407 molars, attached to the mandible, have a greater chance of early disarticulation before

408 preservation, whereas the upper molars are more likely to be retained in situ with the skull and

409 post cranial bones for a longer period of time (Behrensmeyer, 1984). Nevertheless, it is

410 important to note that the mandible tends to be stronger than the cranium, suggesting the large

411 number of lower molars at Site 5C is the result of the lowers surviving the preservation process

412 more readily than the uppers (Behrensmeyer, 1984). It is possible that sampling could have

413 played a part in these results. The question then is whether further sampling at numerous places

414 at Site 5C would increase the number of upper molars found. The only way to test this is through

415 continued sampling. The Rackham's Roost specimens on the other hand would have suffered

416 little disturbance during the process of fossilisation as specimens would have been protected

417 inside the cave until it eroded. This is the likely reason more complete molar rows have been

418 found at this site, however this does not explain why so few lower molars have been found.

419 Again this could be due to sampling (Lundelius, 2006).

420

421 The occlusal surface of molars from specimens found at Rackham's Roost Site provides

422 additional information on the age of individual animals through the degree of wear present on

423 molars. The specimens collected from Rackham's Roost are dominated by largely unworn

424 occlusal features, indicating a large number of the specimens were juveniles. *Macroderma gigas*

425 moves to different feeding roosts to take advantage of seasonal resources, and it is likely they

426 followed the breeding cycles of its prey, explaining the dominance of juveniles in the sample

427 (Tidemann et al. 1985).

428

429 *Environmental Impact*

430 The early and middle Miocene in Australia was characterised by high levels of rainfall and the

431 dominance of rainforest communities (Martin, 2006). As Australia moved from 'greenhouse' to

432 'icehouse' conditions in the later Miocene (10-5mya) the environment became increasingly arid

433 and the biota needed to adapt (Dawson & Dawson, 2006). Environmental communities also

434 changed during the Pliocene from rainforest dominated areas to mosaics of grassland and open

435 woodland (Archer, Hand & Godthelp, 1991). The changing distribution and diversity of

436 mammals in the Riversleigh World Heritage Area fossil deposits is evidence of these changes

437 (Archer et al. 1989; Travouillon et al. 2009). It is likely that as these changes occurred, arid-type

438 responses were produced in much of its fauna (Archer *et al.* 1998), as seen in the Alcoota

439 assemblage in the Northern Territory which shows a marked change in biota present in the late

440 Miocene and early Pliocene (Black et al. 2012). By the end of the Pleistocene period animals of

441 all types were forced to adapt their diet and behaviour where possible in order to survive because

442 great climatic fluctuations caused by over 20 cycles of glacial and interglacial periods resulted in

443 unpredictability of resources (Archer et al. 1998; Martin, 2006).

444

445 Continent-wide climatic shifts during the Pliocene and Pleistocene were very fast in terms of

446 evolutionary response time, requiring taxa to either adapt quickly, be resilient enough to survive,

447 or to be lost entirely (Archer et al. 1998). One of the factors that characterises the success of

448 rodents in Australia is their rapid speciation (Bush et al. 1977). Modern *Leggadina* species

449 inhabit arid-environments in northeastern Queensland (*L. lakedownensis*) and a variety of areas

450 through inland Australia (*L. forresti*) (Watts & Aslin, 1981). However, the environment of

451 Southeast Asia during the Miocene, thought to be the originating point of Australian murids, was

452 characterised by tropical rainforests which were slowly beginning to contract (Heaney, 1991). It

453 is therefore likely that the genus *Leggadina* evolved from an ancestor which was not arid-

454 adapted.

455

456 Species of *Leggadina* have reasonably complex upper molars in comparison to closely related

457 taxa, for example, both *Leggadina gregoriensis* and *L. macrodonta* have an additional occlusal

458 structure (furrows) that allows for increased precision during mastication, indicating the

459 evolution and specialisation of their teeth for a predominantly granivorous diet (Herring, 1993;

460 Evans et al. 2007). Similarly, the width of the zygomatic plate is a useful indicator of the kinds

461 of food eaten by rodents, because width of the zygomatic plate increases with an increase in the

462 size of the anterior deep masseter muscle used for pulverising food (Watts & Aslin, 1981; Satoh,

463 1997). The zygomatic plate in both fossil species is quite wide suggesting further specialisation

464 for a predominately granivorous diet. When the fossil *Leggadina* species evolved these

465 adaptations cannot be determined at the moment due to the lack of knowledge on both the timing

466 and method of their dispersal to and within Australia, as well as appropriate morphological

467 evidence for other Australian fossil species.

468

469 One particularly interesting feature distinguishing *Leggadina macrodonta* is the size of its teeth,

470 particularly M^1 which is up to 18% larger than the M^1 of *L. gregoriensis* or the two modern

471 forms. The increase in size of the teeth and occlusal structures could be due to a number of

472 different factors. Larger teeth would be a useful adaptation for taking advantage of a wider

473 variety of resources necessary for survival in a changeable climate. Alternatively, increased tooth

474 size could represent specialisation for a more selective diet, again resulting from a changing

475 environment. It is also possible the increase in size of the molars of *L. macrodonta* was due to an

476 increase in overall body mass, with this particular species growing larger in order to compete

477 against larger animals for resources, as well as becoming able to process low nutrient foods more

478 easily and reduce water loss (Archer et al. 1998; Dawson & Dawson, 2006). Unfortunately it is

479 not possible to calculate body mass of this species currently due to the absence of adequate lower

480 molar data and a lack of long bones in the fossil assemblage relatable to this species (Hopkins

481 2008). However, the question that remains is why did *L. macrodonta* develop exceptionally

482 large molars, while molar size in *L. gregoriensis* remained more closely aligned with its modern

483 relatives. Broader ecological evidence needs to be presented on changes in tooth structure in

484 other species during the Plio-Pleistocene to make a more informed determination on tooth

485 variation between *L. macrodonta* and *L. gregoriensis*.

486

487 *Future Work*

488 Molar morphology has been an important tool for understanding the evolution of the Murinae

489 and other rodent groups for over 100 years. At this point in time it is still essential for the

490 description of new fossil species of Australian murids. However, to date there has been no

491 comprehensive phylogenetic analysis based on morphology including both fossil and modern

492 species. The leading analysis on morphological relationships using molar morphology was

493 conducted over 40 years ago (Misonne, 1969). On the other hand, advances in molecular

494 assessment of murid relationships have proliferated over the past 30 years (Baverstock et al.

495 1981; Pascale, Valle & Furano, 1990; Catzeflis, Aguilar & Jaeger, 1992; Watts et al. 1992; Jansa

496 and Weksler, 2004; Steppan et al. 2005; Rowe et al. 2008; Nilsson et al. 2010; Schenk, Rowe &

497 Steppan, 2013). An updated morphological phylogeny combined with molecular phylogenies

498 would give a much more cohesive picture of Australian murid evolutionary history than using

499 either alone (Wiens, 2004; Aplin, 2006).

500

501

502 **Conclusion**

503 Murid rodents are speciose in Australia, but their evolutionary relationships and origins have

504 been shrouded in mystery due in large part to the paucity of fossil evidence available. Two new

505 species of the genus *Leggadina*: *Leggadina gregoriensis* from the Pleistocene Rackham's Roost

506 Site in the Riversleigh World Heritage Area and *Leggadina macrodonta* from the Plio-

507 Pleistocene Site 5C at Floraville Station, both in northwestern Queensland, have been described

508 here. Their description extends the temporal range of the genus *Leggadina* to around 2.5 million

509 years. Both fossil species display increased complexity in the upper molars and larger attachment

510 sites on the zygomatic plate, likely due to the development of a predominately granivorous diet.

511 *L. macrodonta* also displays an increase in size of M^1 and M^2 which may be the result of a

512 number of factors including adaptation to the unpredictability of, and increased competition for,

513 resources in a changing climate or an increase in body size. Further research is essential to

514 further develop understanding on the relationships and evolution of the genus *Leggadina* as well

515 as the broader Murinae group.

516

517

518 **Acknowledgements**

524

525

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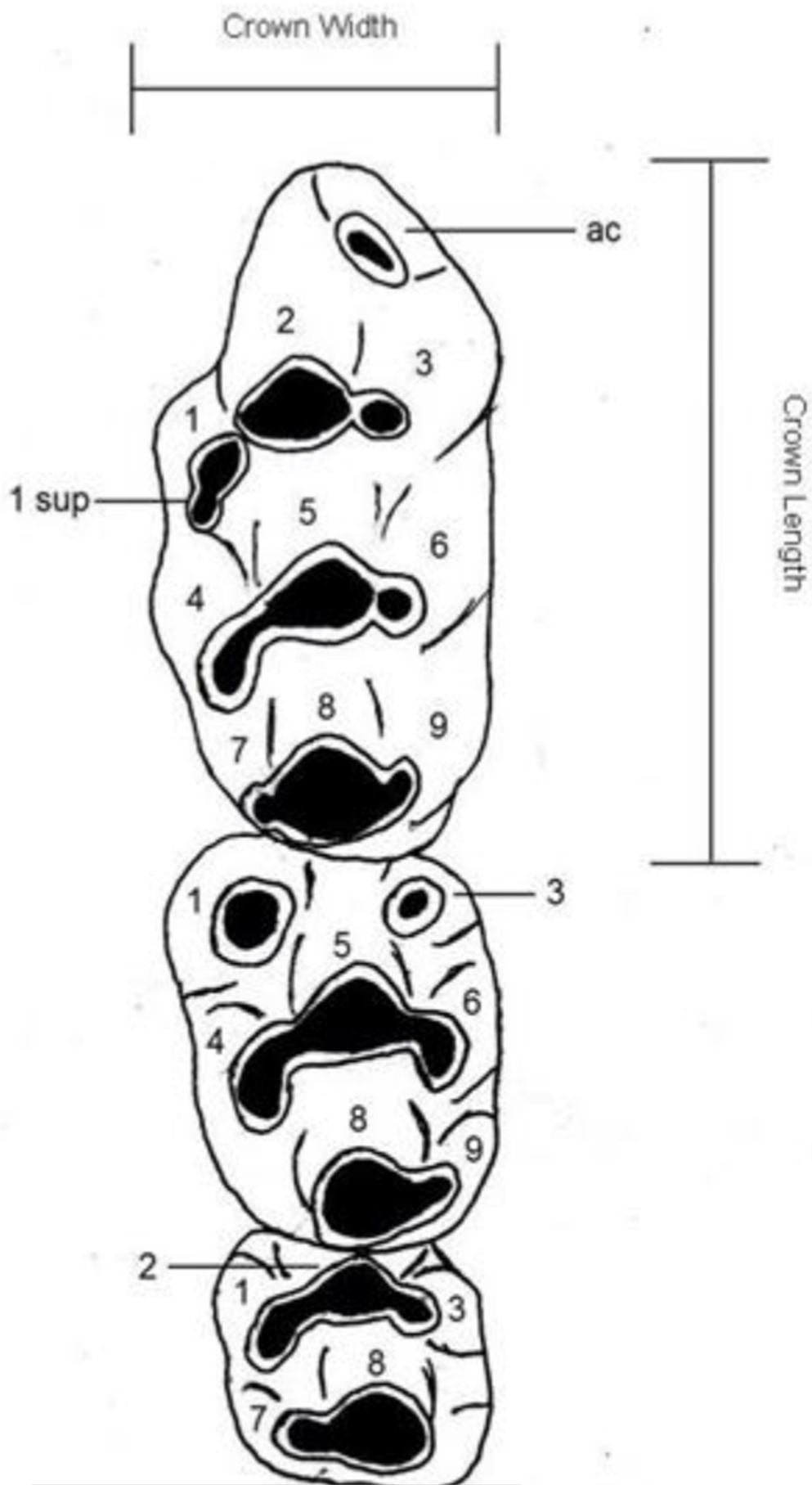687 *Biology* **53**: 653-661.

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690 **K.H., Godthelp, H., Creaser, P., Price, E. 2014.** Developing a radiometrically-dated

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1

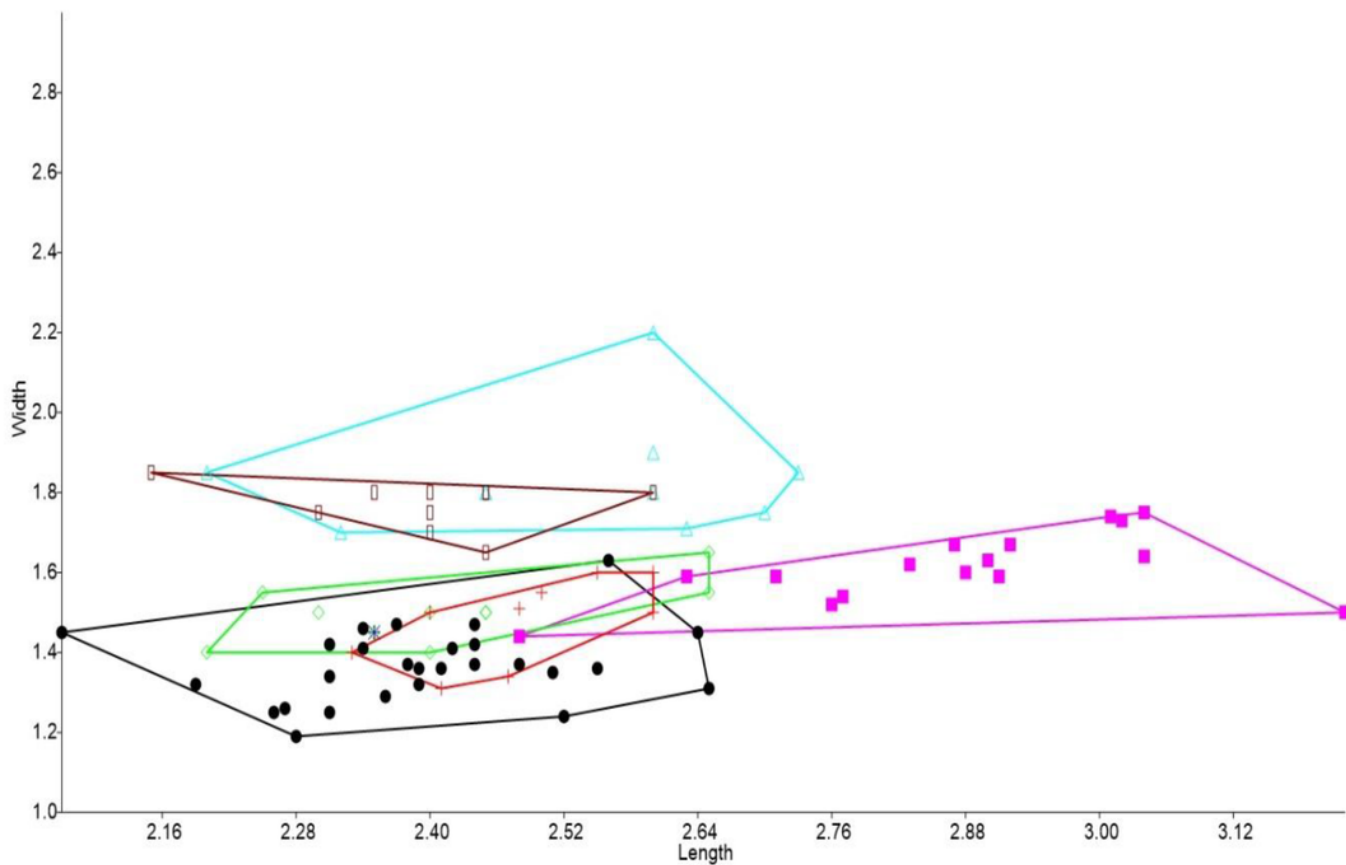Dental nomenclature used for descriptions.

Dental nomenclature used in the description of fossil *Leggadina*. Adapted from Musser and Newcomb (1983) but modified to better represent features of fossil *Leggadina* specimens. Left upper molar row, cusps (1-9) referred to in text with the prefix 'T', ac = accessory cusp, sup = supplementary. Measurements were taken on maximum crown length and width.

Crown Width

Crown Length

ac

2

3

1

1 sup

5

6

4

8

7

9

1

3

5

6

4

8

9

2

1

3

8

7

2

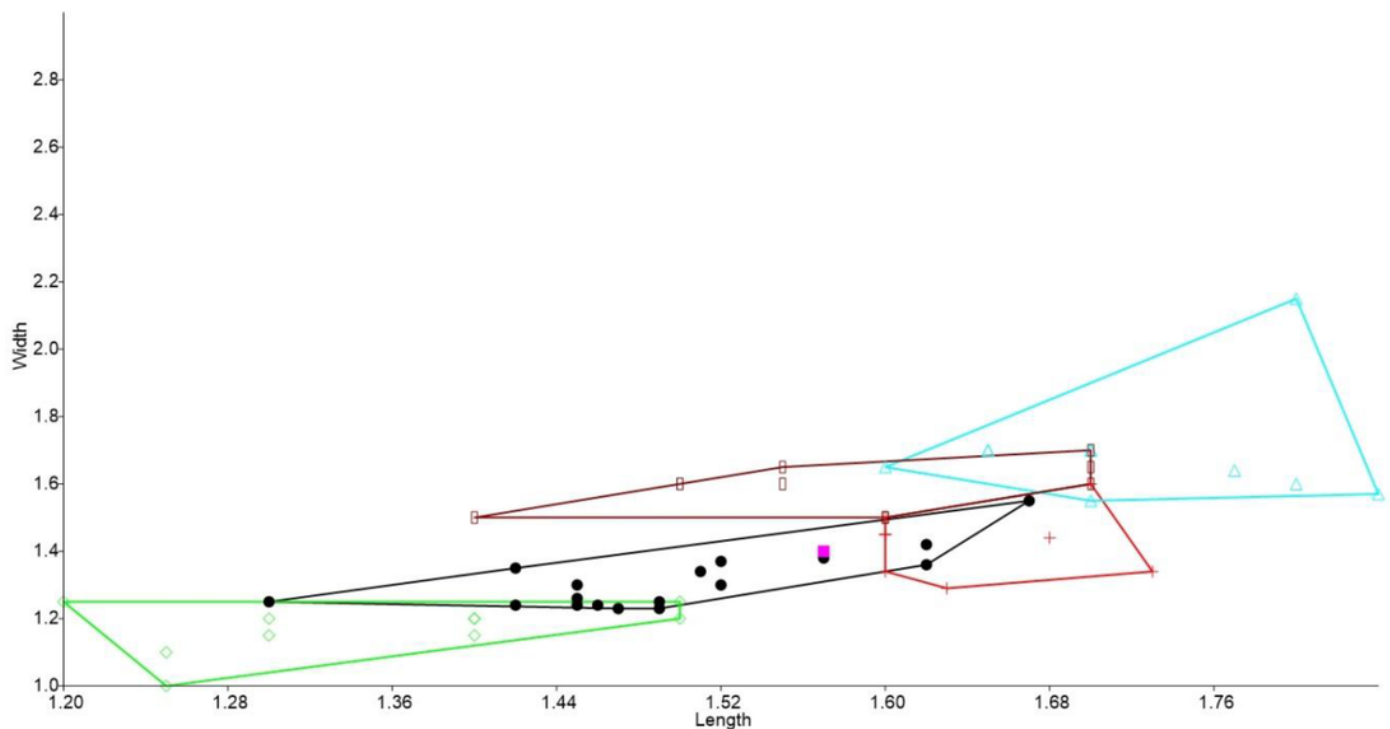Bivariate plot comparing M^1 between murine species.

Bivariate plot of maximum crown length and width of M^1 (mm). *Leggadina forresti* = green diamond; *Leggadina lakedownensis* = blue star; *Leggadina gregoriensis* = black circle; *Leggadina macrodonta* = pink square; *Zyzomys argurus* = red cross; *Pseudomys australis* = blue triangle; *Notomys fuscus* = brown rectangle.

3

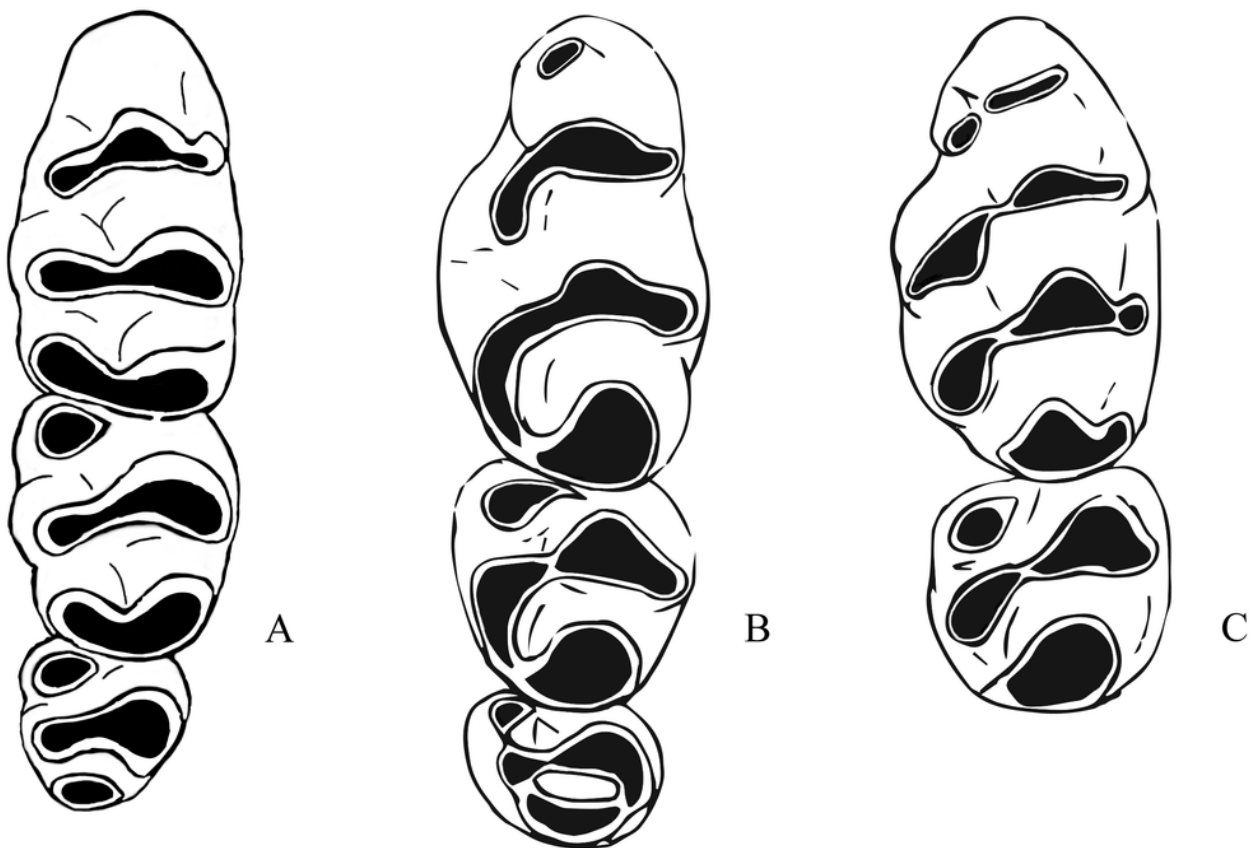Bivariate plot comparing M^2 between murine species.

Bivariate plot of maximum crown length and width of M^2 (mm). *Leggadina forresti* = green diamond; *Leggadina gregoriensis* = black circle; *Leggadina macrodonta* = pink square; *Zyzomys argurus* = red cross; *Pseudomys australis* = blue triangle; *Notomys fuscus* = brown rectangle (*L. lakedownensis* not included).

4

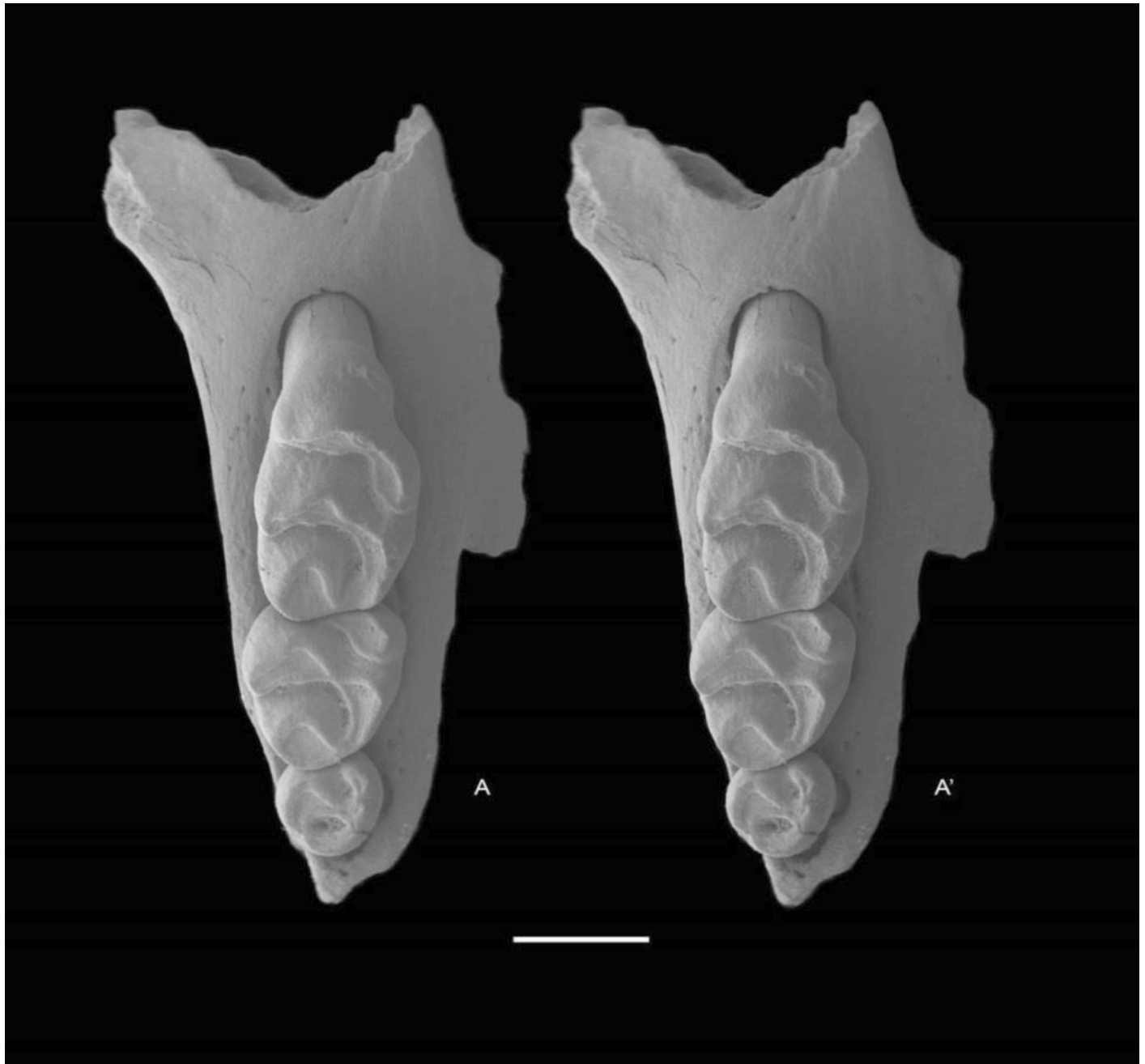Morphological differences between fossil *Leggadina* species and *Zyzomys*.

A = left upper molar row of *Zyzomys argurus* (Misonne 1969); B = right upper molar row of holotype (QM F 57259) of *Leggadina gregoriensis*, image has been reversed to represent left upper molar row for comparative purposes; C = left M^1 and M^2 of *Leggadina macrodonta*, composite of holotype (QM F57276) and paratype (QM F57273). Not to scale.

5

Leggadina gregoriensis sp. nov. Holotype. QM F57259.
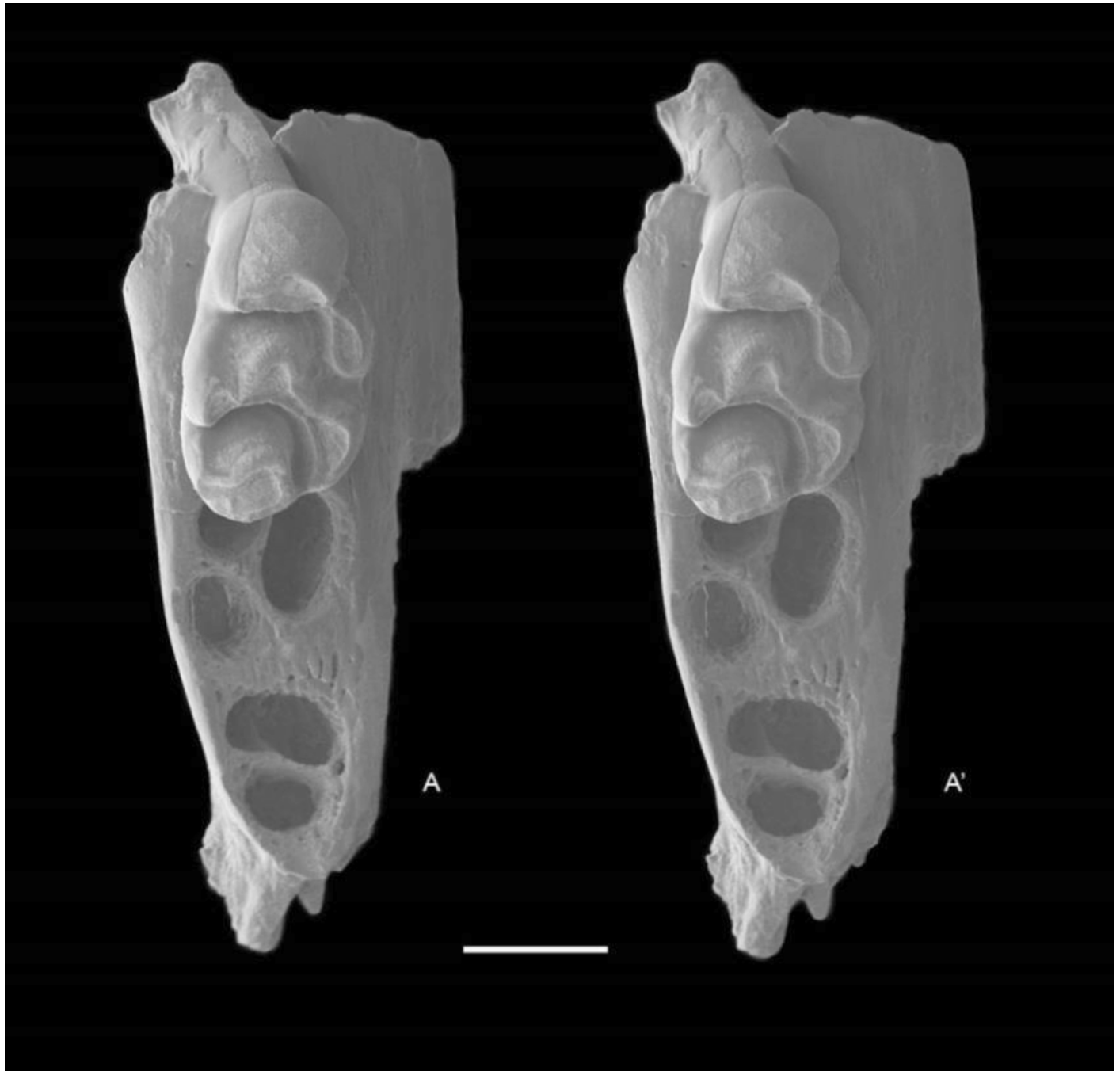
Partial right maxillary with M^{1-3}. Occlusal view. AA' = stereopair. Scale = 1 mm.

6

Leggadina gregoriensis sp. nov. Paratype. QM F57244.

Partial right maxillary with M^1. Occlusal view. A-A' = stereopair. Scale = 1 mm.

7

Leggadina gregoriensis sp. nov. Paratype. QM F57258.

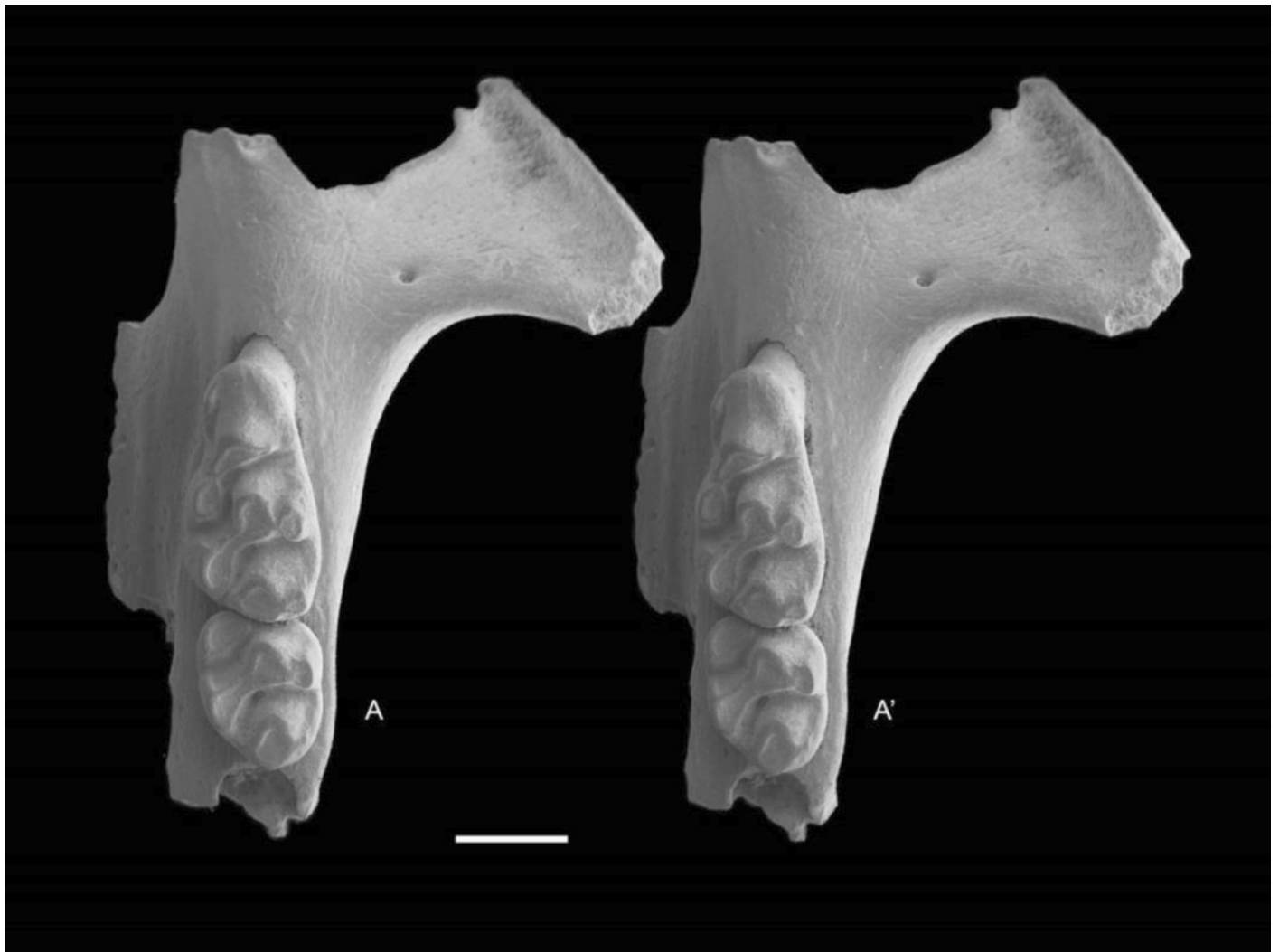Partial left maxillary including zygomatic plate with M^{1-2}. Occlusal view. A-A' = stereopair.

Scale = 1 mm.

Table 1(on next page)

Measurements (mm) of *Leggadina gregoriensis* sp. nov.

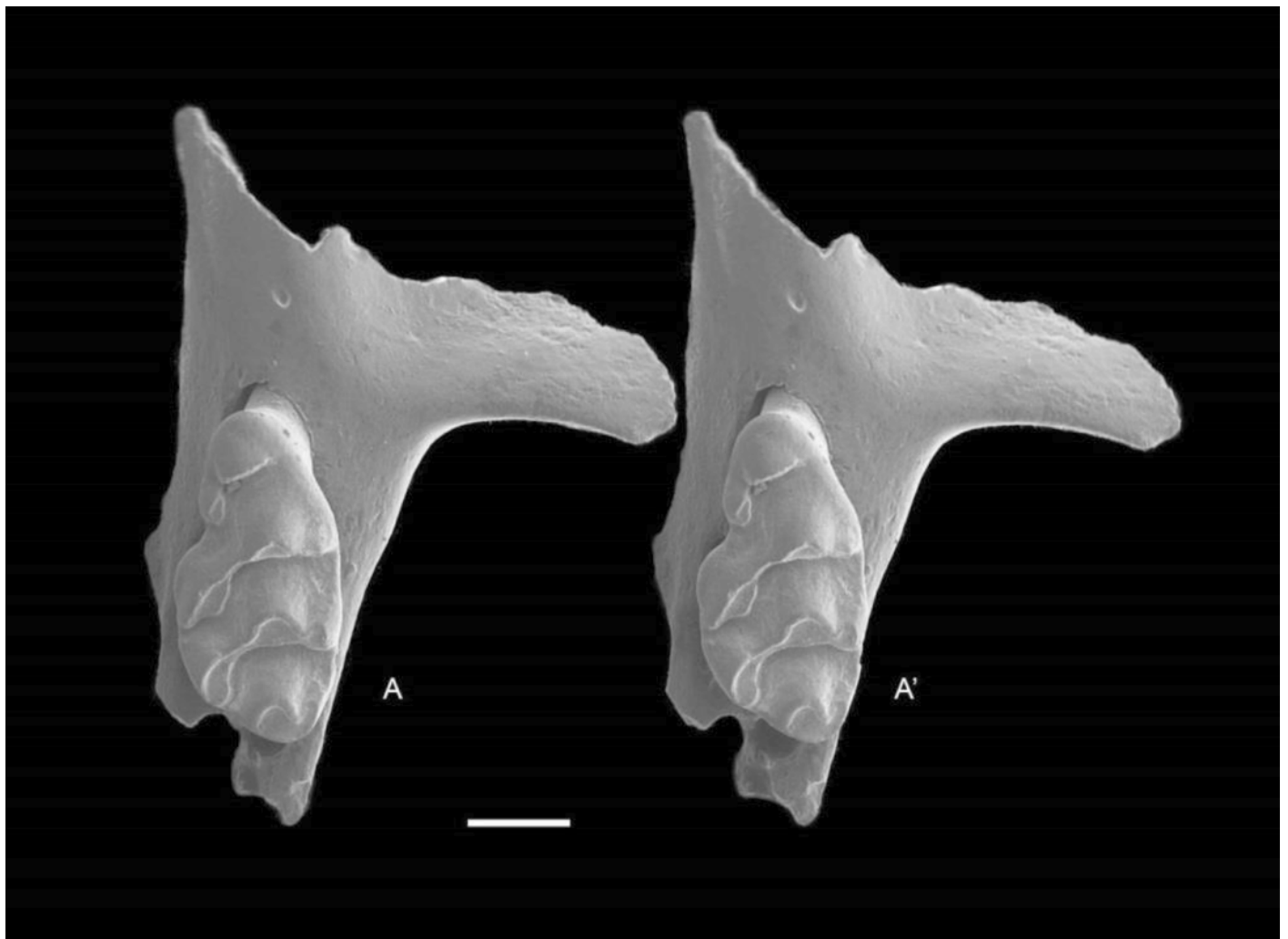L = maximum length, W = maximum width.

2

Specimen no.	M^1		M^2		M^3		M^{1-3}		M^{1-2}	
	L	W	L	W	L	W	L	W	L	W
QM F57240	2.44	1.42	-	-	-	-	-	-	-	-
QM F57241	2.65	1.31	-	-	-	-	-	-	-	-
QM F57242	2.07	1.45	-	-	-	-	-	-	-	-
QM F57243	2.31	1.42	-	-	-	-	-	-	-	-
QM F57244	2.37	1.47	-	-	-	-	-	-	-	-
QM F57245	2.34	1.46	-	-	-	-	-	-	-	-
QM F57246	2.55	1.36	1.52	1.30	1.07	1.02	4.84	1.47	3.90	1.47
QM F57247	-	-	1.62	1.42	-	-	-	-	-	-
QM F57248	2.44	1.37	1.62	1.36	-	-	-	-	3.82	1.39
QM F57249	2.48	1.37	1.51	1.34	-	-	-	-	3.90	1.42
QM F57250	2.34	1.41	1.45	1.30	-	-	-	-	3.79	1.45
QM F57251	2.56	1.63	1.67	1.55	-	-	-	-	4.02	1.64
QM F57252	2.28	1.19	1.49	1.23	-	-	-	-	3.70	1.24
QM F57253	2.19	1.32	1.42	1.35	1.05	0.92	4.54	1.46	3.60	1.46
QM F57254	2.38	1.37	-	-	-	-	-	-	-	-
QM F57255	2.52	1.24	-	-	-	-	-	-	-	-
QM F57256	2.39	1.32	1.47	1.23	-	-	-	-	3.78	1.32
QM F57257	2.31	1.25	1.46	1.24	-	-	-	-	3.59	1.34
QM F57258	2.41	1.36	1.49	1.25	-	-	-	-	3.81	1.36
QM F57259	2.26	1.25	1.30	1.25	0.85	0.85	4.29	1.37	3.51	1.37
QM F57260	2.27	1.26	1.45	1.24	1.00	0.95	4.45	1.39	3.65	1.39
QM F57261	2.44	1.47	-	-	-	-	-	-	-	-
QM F57262	2.36	1.29	1.42	1.24	0.96	0.90	4.56	1.35	3.10	1.35
QM F57263	2.39	1.36	1.45	1.26	-	-	-	-	3.70	1.39
QM F57264	2.31	1.34	-	-	-	-	-	-	-	-
QM F57265	2.64	1.45	-	-	-	-	-	-	-	-
QM F57283	2.51	1.35	1.52	1.37	1.04	1.00	4.68	1.35	3.79	1.35
QM F39958	2.42	1.41	1.57	1.38	0.94	0.90	4.57	1.42	3.84	1.42

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Leggadina macrodonta sp. nov. Holotype. QM F57276.

Partial left maxillary including zygomatic plate with M^1. Occlusal view. A-A' = stereopair.

Scale = 1 mm.

9

Leggadina macrodonta sp. nov. Paratype. QM F57273.

Partial left maxillary with M^2. Occlusal view. A-A' = stereopair. Scale = 1 mm.

10

Leggadina macrodonta sp. nov. Paratype. QM F57268.

Left M¹. Occlusal view. A-A' = stereopair. Scale = 1 mm.

11

Leggadina macrodonta sp. nov. Paratype. QM F57275.

Partial left maxillary with M^1 and alveoli of M^2. Occlusal view. A-A' = stereopair. Scale = 1 mm.
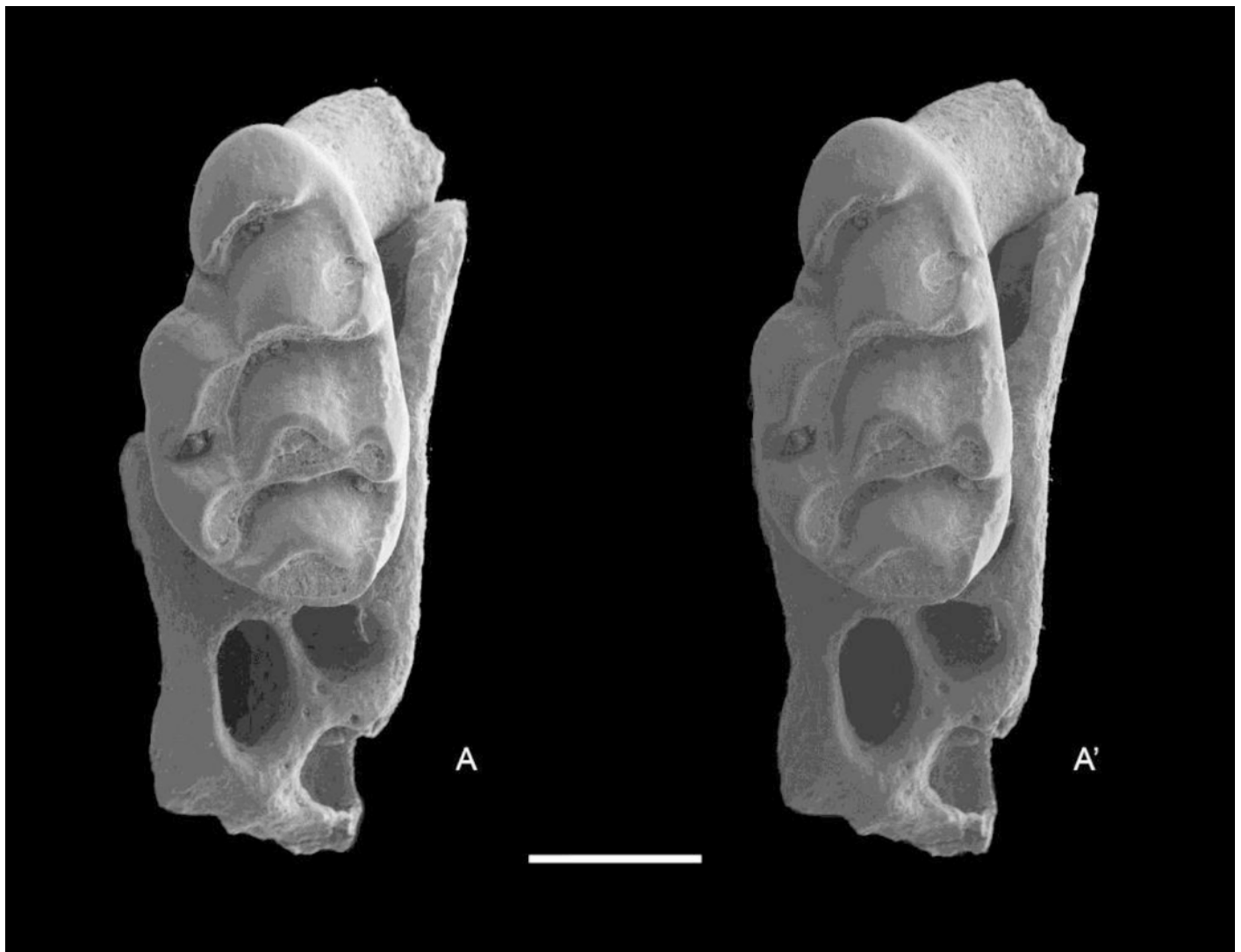
Table 2(on next page)

Measurements (mm) of *Leggadina macrodonta* sp. nov.

L = maximum length, W = maximum width.

Specimen no.	M^1		M^2	
	L	W	L	W
QM F57266	2.48	1.44	-	-
QM F57267	3.04	1.75	-	-
QM F57268	3.04	1.64	-	-
QM F57269	2.77	1.54	-	-
QM F57270	2.91	1.59	-	-
QM F57271	2.92	1.67	-	-
QM F57272	2.71	1.59	-	-
QM F57273	-	-	1.57	1.40
QM F57274	2.83	1.62	-	-
QM F57275	2.88	1.60	-	-
QM F57276	3.22	1.50	-	-
QM F57277	3.02	1.73	-	-
QM F57278	3.01	1.74	-	-
QM F57279	2.90	1.63	-	-
QM F57280	2.87	1.67	-	-
QM F57281	2.63	1.59	-	-
QM F57282	2.76	1.52	-	-