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 Packham'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). 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). Their nearest relatives are still largely unknown with studies using either morphological or molecular data consistently producing different results.

Tooth morphology is central to the study of rodent systematics because rodents generally have conservative cranial and skeletal morphology (Tate 1951). Molars are largely flat with numerous cusps which act as the dominant occlusal surfaces for the grinding of food (Misonne 1969). The position and presence/absence of these cusps is key to the morphological identification of species and is particularly important for the identification of fossil species. The most comprehensive study of rodent molar morphology was conducted by Misonne in 1969. More recently, molecular techniques have been employed on extant species to determine relationships between groups, with Rowe *et al.* (2008) producing the most comprehensive molecular phylogeny to date. Tooth morphology, however, remains the backbone of rodent systematics because it continues to provide the physical da[illegible] test hypotheses based on molecular datasets and modelling, and to determine the relationships of fossil species to other fossil and modern taxa (Wiens 2004).

There have only been three species of fossil murines described from Australia: *Pseudomys vandycki* Godthelp, 1988, from the Pliocene-aged Chinchilla locality in southeastern Queensland, *Zyzomys rackhami* Godthelp, 1997, from the Pliocene Rackham's Roost Site in the Riversleigh World Heritage Area in northwestern Queensland, and *Conilurus capricornensis* Cramb and Hocknull, 2010, from late Pleistocene-Holocene cave deposits in eastern Queensland. There are a number of other fossil specimens awaiting description (Aplin 2006).

The first species to be described in the present study comes from the Riversleigh World Heritage Area in northwestern Queensland, which preserves a rich diversity of fossil vertebrates in limestone rocks from the late Oligocene to the late Pleistocene and Holocene (Archer *et al.* 1989; Archer *et al.* 2006; Travouillon *et al.* 2006). The Rackham's Roost Site at Riversleigh is a breccia deposit in the floor of a fossil cave situated in Cambrian limestone cliffs overlooking the Gregory River. This cave was inhabited by a population of the Ghost Bat *Macroderma gigas* during the Pliocene (Hand 1996). Fossils found at this site include small mammals believed to be the prey of the Ghost Bat colony, and occasionally larger animals which are believed to have fallen into the cave and been unable to escape (Archer, Hand & Godthelp 1991). Rodent fossils found in this deposit represent at least 12 taxa, namely from the genera *Pseudomys, Zyzomys* and *Leggadina* (Godthelp 2001), however only one species (*Zyzomys rackhami*) has so far been described (Godthelp 1997).

Site 5C at Floraville Station in northwestern Queensland is quite different from Riversleigh's Rackham's Roost Site. It contains a lower diversity of animals but a much greater cross-section of body sizes. This deposit consists of sandy riverine sediments suggestive of a billabong or waterhole (Rich *et al.* 1991). Rodent remains are thought to have been accumulated through natural mortality and marsupial carnivores (H. Godthelp, pers. comm. 2013). The site is Plio-Pleistocene in age (Rich *et al.* 1991), a period that was characterised by great climatic fluctuations and subsequent unpredictability of resources (Archer *et al.* 1998; Martin 2006). Site 5C contains specimens of the murine genera *Rattus*, *Pseudomys* and *Leggadina*, with *Rattus* being by far the most dominant taxon (H. Godthelp, pers. comm. 2013). No fossil rodent taxa have previously been described from Floraville.

The description of these two new species almost doubles the number of described fossil Australian murines and will assist in developing a better understanding on the evolution of the murines in Australia, including their initial migration.

Methods

Fossil Australian murid specimens were recovered from the Rackham's Roost Site in the Riversleigh World Heritage Area, northwestern Queensland, and Site 5C at Floraville Station, northwestern Queensland. Rackham's Roost fossils were recovered by dissolving limestone breccia in 5% acetic acid. Material from Site 5C was washed through fine screens to concentrate fossils which were later extracted under a microscope. A number of fossils recovered at each site were identified as potentially belonging to the genus *Leggadina*. Twenty-eight fossil specimens from Rackham's Roost and seventeen fossil specimens from Floraville were analysed and are denoted by the prefix QM F (Queensland Museum Fossil). These ranged from single upper molars to whole upper cheektooth rows.

Specimens from Rackham's Roost Site and Site 5C were first observed to confirm their status as potential new species of the genus *Leggadina*. Univariate and bivariate analyses were conducted using the statistical software program PAST (PAlaeontological STatistics; Hammer, Harper & Ryan 2001) to confirm that the two proposed fossil *Leggadina* species differ from others of the genus *Leggadina*. Univariate analyses were conducted to determine the amount of variance within measurements on both fossil and modern taxa using the Coefficient of Variation (CV). CV has been widely used to measure the degree of variation within a sample. Simpson, Roe & Lewontin (1960) proposed that an adequate sample has a variation between 4 and 10, with a score of less than 4 indicating an inadequate sample and more than 10 suggesting more than one species. However, caution must be taken when using this method because there are a number of external variables that can affect CV scores including small sample size, geographic variation and sexual dimorphism (Plavcan & Cope 2001).

Bivariate plots compared molar crown length and width data of *Leggadina* specimens (two fossil *Leggadina* specimens, *L. forresti* and *L. lakedownensis*) with closely related species from the 'Australian genera' as based on node W of Rowe *et al.*'s (2008) molecular phylogeny (*Zyzomys* *argurus, Pseudomys australis and Notomys fuscus*). *Mastacomys fuscus* was removed from the bivariate analysis because its molar morphology diverges so dramatically in both size and cusp arrangement that the fossil specimens collected from the two Queensland sites clearly do not belong to this genus. Maximum crown length and width of molars was used as molar cusp position in rodent species is highly variable, particularly with wear (Misonne 1969). Measurements were made at the University of New South Wales on a Wild 5MA stereomicroscope with Wild MMS235 Digital Length Measuring Set (accurate to 0.01mm) and at the Australian Museum on a Leica MZ95 stereomicroscope with graticule (accurate to 0.05mm). Measurements were cross-checked to ensure comparability by measuring a subset of specimens on both microscopes. Since M^3 or a molar row has yet to be discovered for the Floraville *Leggadina*, bivariate plots for M^1 and M^2 were used to assess separation of these murine species. *Leggadina lakedownensis* could not be included in the M^2 analysis as specimens could not be obtained.

Once it was confirmed that the fossil specimens were definitely *Leggadina* and were distinct from *L. forresti* and *L. lakedownensis*, they were described. Dental nomenclature used follows Musser and Newcomb (1983) as outlined in their study on Malaysian murids (Fig. 1). This particular format has been followed because it uses a simplified serial nomenclature that avoids potential issues of conflicting homologies in the upper molars for muroid rodents (Musser and Newcomb 1983). A Wild M3B stereomicroscope was used during the description. The description included only upper molar specimens as they display greater interspecific variation than the lower molars and are therefore more useful when identifying fossil species (Misonne 1969). Specimens were photographed using a Scanning Electron Microscope (Quanta 200) at the University of New South Wales Analytical Centre.

Results

Univariate analyses

Coefficients of Variation for all measurements of the fossil taxa suggest that only one species is present in each fossil sample, with values ranging from 3.23 to 7.80 in the *Leggadina* specimens from Rackham's Roost and 5.50 to 6.06 for the two measurements available for *Leggadina* specimens from Site 5C (Supplementary Material).

Bivariate analyses

In the bivariate plots, both length and width of M^1 and M^2 were effective in separating species (Fig. 2 and 3). The M^1 plot shows the Rackham's Roost *Leggadina* overlapping with both modern *Leggadina* species, whereas in the M^2 plot, the Rackham's Roost *Leggadina* groups predominately with the Floraville specimen. The Floraville *Leggadina* species distinctly separates from other species based on its greater M^1 length. *Pseudomys* and *Notomys* group together in both plots, but separate more in the M^2 plot based on length data. In both plots there is a close association between the fossil specimens and *Zyzomys*. More detailed morphological evidence effectively separates *Zyzomys* and the fossil specimens.

Differential Diagnosis

The fossil species described below as referable to the genus *Leggadina* display characteristics typical of species of this genus. An accessory cusp on the first upper molar is present on all fossil specimens, all upper molars are inclined posteriorly, molar size is reduced along the row, with M^3 often half the size or smaller than M^1, and the anterior edge of the zygomatic plate is relatively straight (Watts & Aslin 1981). However, bivariate analyses determined that these specimens could also have been referred to the genus *Zyzomys.* Shared morphological features and differences between *Leggadina* and *Zyzomys* are mentioned here (Fig. 4). *Zyzomys* species often display an accessory cusp on the first upper molar, have a relatively straight anterior edge to the zygomatic plate, and are of similar size to *Leggadina* (Watts & Aslin 1981). A feature clearly distinguishing species of the two genera is a buccal row of cusps present in *Leggadina* species that is absent in *Zyzomys*. Although this buccal row of cusps is present in *Leggadina* species, they are often reduced on M^1 (Tate 1951). A distinctive aspect of *Leggadina* molar morphology, not shared by *Zyzomys*, is the posterior extension of the lingual series of cusps. (Tate 1951). For these reasons, the fossil species are referred to the genus *Leggadina* rather than *Zyzomys*.

Systematics

Superfamily MUROIDEA Miller and Gidley, 1918

Family MURIDAE Gray, 1821

Subfamily MURINAE Gray, 1821

Genus *LEGGADINA* Thomas, 1910

Type species

Leggadina forresti (Thomas, 1906)

Other species

Leggadina lakedownensis Watts, 1976

Leggadina gregoriensis sp. nov.

Holotype

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

Type locality and age

Rackham's Roost Site, Riversleigh World Heritage Area, northwestern Queensland; Pliocene.

Paratypes

QM F57244, partial right maxilla with M^1 (Fig. 6); QM F57258, partial left maxilla including zygomatic plate with $M^{1\text{-}2}$ (Fig. 7).

Etymology

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

Diagnosis

Leggadina gregoriensis differs from other species of the genus in the following combination of features: greatly anteroposteriorly elongated T6 on M^1; T1-2 and T4-5 complexes oriented buccolingually with T3 and T6 swept back at right-angles to lean proximally; accessory cusp small; M^1 narrow, M^2 and M^3 wider; furrows present between lingual and central series of cusps in M^1 and M^2. Furrows function as an additional occlusal surface for increased grinding precision during mastication (Herring 1993).

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. 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 minimal molar overlap.

M^1. Elongated and narrow. Anterior cingulum with a single elliptical accessory cusp sweeping backwards along lingual edge. Accessory cusp small in all specimens. 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 distinct but merges completely with T1-2 complex after extreme wear. T4 small, circular and merged with T5 at most stages of wear. It sweeps posteriorly from T5 so anterior edge of T4 is in line with the posterior edge of T5. T5 large, subtriangular in occlusal outline and leans posteriorly. Enamel rim connects T5 to both T4 and T6. T6 positioned posterior to T5, elongated anteroposteriorly and directed proximally, similar to T3. T6 merges with T4-5 complex after extreme wear. T6 also distinct from T9 at early stages of wear but merges quickly. Posterior edge of cusps T4-T6 arcs anteriorly to enclose T8. T7 barely discernible in holotype but is present in other specimens at early stages of wear before merging completely with T8. In these specimens it is small and directed posteriorly. T8 very large and circular, directed posteriorly. T9 incorporated at all stages of wear with T8. Enamel rim around cusps uniform throughout tooth but becomes slightly wider with extreme wear.

M^2. Tooth is mostly circular in holotype but shape variable, with other specimens more elongate. Elongation is affected by size of T3 and T8, with the anterior of M^2 developing a bulge with increase in T3, similarly, posterior developing a bulge with increase in T8. T1 and T2 absent. T3 distinct and elliptical, directed proximally. T3 and T5 are the highest cusps at early stages of wear but T3 wears faster than T5 to become uniform with the other cusps. T4 small, circular and leans posteriorly. It is incorporated into T5, but also sweeps posteriorly from T5, with anterior edge of T4 in line with posterior edge of T5. T5 subtriangular and directed posteriorly. T6 positioned posterior to T5, elongated anteroposteriorly and oriented proximally. At later stages of wear T6 merges with T4-5 complex. Posterior edge of T4-5 complex and posterior edge connecting T6 with T9 forms anterior arc to enclose T8, similar to M^1. T7 absent. T8 large, circular in occlusal outline and directed posteriorly. At extreme stages of wear T8 merges with elongated T6. T9 merges with T8 at all stages of wear, similar to M^1. Enamel rim surrounding the cusps of uniform width, becoming thicker with wear.

M^3. Tooth circular with a bulge on anterolingual edge for T3, cusp height uniform. T1 and T2 absent. T3 small, circular and distinct, directed proximally. Furrow between T3 and T4-6 complex ensures T3 distinct in all but very late stages of wear. T4 completely incorporated into T5. It sweeps posteriorly markedly from T5, directed posterobuccally. T5 subtriangular in occlusal outline, large and directed posteriorly. T6 small and subtriangular. It merges with T5, slightly sweeping posteriorly from T5 with enamel rim connecting to T8-9 complex. Posterior edge of T4-5 complex curves anterobuccally, with posterior edge of T6 curving anterolingually. T7 absent. T8 large, elliptical and orientated vertically. Anterior edge of T8 curves posteriorly. Anterior edge of T8 combined with posterior edge of T4-6 complex creates elliptical furrow. T9 entirely incorporated into T8. Enamel rim uniform in width and connecting all cusps except T3 in holotype which only connects at very late stages of wear.

M^1. With three roots, all of which directed somewhat anteriorly. Anterior root largest of the three, circular in shape and positioned under accessory cusp and T1-T3. Lingual root anteroposteriorly stretched, narrow and positioned under T6 and T9. Posterior root smallest of the three, circular and positioned under T8.

M^2. With three roots, all directed vertically. The anterobuccal and posterobuccal roots of equal size and circular. Anterobuccal root extends from underneath T4 and T5, while posterobuccal root positioned beneath T8. Lingual root large and elongated, extending from T3 to T6.

M^3. With three roots all directed vertically. Anterobuccal root small and circular, extending from beneath T5. Anterolingual root slightly larger and more elongated than anterobuccal root and positioned under T3 and T6. Posterior root largest of the three, supporting approximately half tooth length and extending from T8.

Attachment node for the origin of the superficial masseter is of moderate size and well defined in some specimens, positioned anterior to M^1. Posterior extent of anterior palatal foramen lies at anterior root of M^1. Zygomatic plate of QMF57258 wide with posterior edge convex (Fig. 7).

Leggadina macrodonta sp. nov.

Holotype

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

Type locality and age

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

Paratypes

QM F57273, partial left maxillary with M^2 (Fig. 9); QM F57268, left M^1 (Fig. 10); QM F57275, partial left maxillary with M^1 and alveoli of M^2 (Fig. 11).

Etymology

Named for the distinctivly large size of the first upper molar.

Diagnosis

Leggadina macrodonta differs from other species of the genus in the following combination of characters: M^1 enlarged, approximately 18% larger than in *Leggadina forresti* and *L. lakedownensis*; M^2 similarly enlarged, approximately 16% larger than in those species;.anterior cingulum enlarged with two accessory cuspules that wear to a greatly elongated accessory cusp; well-developed T1 and T4 posterolingually aligned; T1 sup present on some specimens; central series of cusps enlarged.

Referred specimens

QM F57266, right M^1; QM F57267, left M^1; QM F57269, left M^1; QM F57270, right M^1; QM F57271, left M^1; QM F57272, right M^1; QM F57274, left M^1; QM F57277, left M^1; QM F57278, right M^1; QM F57279, right M^1; QM F57280, right M^1; QM F57281, right M^1; QM F57282, left M^1 (Table 2).

Description

Complete tooth row not known. M^1 and M^2 are isolated specimens, no specimen of M^3 found to date. M^1 large, M^2 approximately half length of M^1. Furrow between lingual series and central series of cusps in M^1 and M^2. Buccal series of cusps reduced in M^1, all cusps inclined posteriorly.

M^1: Tooth elliptical with thin and uniform enamel rim around all cusps. Two small accessory cusplets present on anterior cingulum in holotype. With wear they become one very large accessory cusp, elongated posterolingually, sweeping back along lingual edge. T1 large and elongated, becoming more elongated with wear. Anterior edge of T1 sits posterior to T2, at half-way point of tooth. T1 orientated posteriorly with axis of cusp stretching posterolingually, parallel to single accessory cusp in specimens other than holotype. It merges with T2 at late stages of wear. T1 sup present on some specimens, situated on posterolingual edge of T1. It is 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.

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. All cusps of equal height and incline posteriorly at varying degrees, with T5 and T8 leaning posteriorly more than T1 and T4.

M^3: No specimen known.

M^1: 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 but more circular and stretches vertically from T8 and T9.

M^2: Roots not visible on only available specimen of M^2. Description has been gathered from alveoli in a specimen also preserving M^1 (QM F57275). M^2 has three roots. Lingual root very large and elongated, directed vertically. Anterobuccal root smaller than lingual root and circular, stretching to anterior. Posterobuccal root smallest of the three, elongated and extends vertically.

M^3: No specimen known.

Information on dental arcade is limited. Large posterior palatal foramen extends distally from posterior of M^1. Zygomatic plate wide with posterior edge appearing almost straight but is slightly convex.

Discussion

Taphonomy

Even though Riversleigh's Rackham's Roost Site and Floraville's Site 5C represent vast differences in both mode of death and environment of preservation, similar skeletal elements have been preserved. Rackham's Roost Site is interpreted to have been a Ghost Bat (*Macroderma gigas*) roost during the Pliocene (Hand 1996) and specimens of *Leggadina* found there are thought to be the result of bat predation (Godthelp 1997). Floraville's Site 5C specimens are more likely to have come from marsupial predators, fossils of which have also been found at the site (Rich *et al.* 1991). Both sites preserve individual teeth, with the Rackham's Roost site preserving molar rows and some of the surrounding dental arcade and zygomatic plate. There have been no complete skulls found at either site. The fractured cranial and post cranial elements found cannot be attributed to individual murine taxa due to overlaps in size and a lack of features known to separate them (H. Godthelp, pers. comm. 2013).

Within the broad similarity of the two sites, the individual teeth found are different. The Rackham's Roost assemblage includes a large number of upper molars (upper = 28, lower = 0), including whole molar rows, whereas Site 5C specimens are dominated by lower molars but lack any molar rows (upper = 17, lower = 20). The increased preservation of upper molars over lower molars is expected since the lower molars, attached to the mandible, have a greater chance of early disarticulation before preservation, whereas the upper molars are more likely to be retained in situ with the skull and post cranial bones for a longer period of time (Behrensmeyer 1984). Nevertheless, it is important to note that the mandible tends to be stronger than the cranium, suggesting the large number of lower molars at Site 5C is the result of the lowers surviving the preservation process more readily than the uppers (Behrensmeyer 1984). It is possible that sampling could have played a part in these results. The question then is whether further sampling at numerous places on Site 5C would increase the number of upper molars found. The only way to test this is through continued sampling. The Rackham's Roost specimens on the other hand would have suffered little disturbance during the process of fossilisation as specimens would have been protected inside the cave until it eroded. This is the likely reason more complete molar rows have been found at this site, however this does not explain why so few lower molars have been found. Again this could be due to sampling (Lundelius 2006).

The occlusal surface of molars from specimens found at Rackham's Roost Site provides additional information on the age of individual animals through the degree of wear present on molars. The specimens collected from Rackham's Roost are dominated by largely unworn occlusal features, indicating a large number of the specimens were juveniles. *Macroderma gigas* moves to different feeding roosts to take advantage of seasonal resources, and it is likely they followed the breeding cycles of its prey, explaining the dominance of juveniles in the sample (Tidemann *et al.* 1985).

Environmental Impact

The early and middle Miocene in Australia was characterised by high levels of rainfall and the dominance of rainforest communities (Martin 2006). As Australia moved from 'greenhouse' to 'icehouse' conditions in the later Miocene (10-5mya) the environment became increasingly arid and the biota needed to adapt (Dawson & Dawson 2006). Rackham's Roost at this time represents the result of a community changing from rainforest to mosaics of grassland and open woodland (Archer, Hand & Godthelp 1991). The changing distribution and diversity of mammals in the Riversleigh World Heritage Area fossil deposits is evidence of these changes (Archer *et al.* 1989; Travouillon *et al.* 2009). It is likely that as this change occurred it produced arid-type responses in much of its fauna (Archer *et al.* 1998), as seen in the Alcoota assemblage in the Northern Territory which shows a marked change in biota present in the late Miocene and early Pliocene (Black *et al.* 2012). The Pleistocene period was characterised by great climatic fluctuations caused by over 20 cycles of glacial and interglacial periods (Martin 2006). This would have resulted in great unpredictability of resources, forcing animals of all types to adapt their diet and behaviour where possible in order to survive these widespread changes (Archer *et al.* 1998).

Continent-wide climatic shifts during the Pliocene and Pleistocene were very fast in terms of evolutionary response time, requiring taxa to either adapt quickly, be resilient enough to survive, or to be lost entirely (Archer *et al.* 1998). One of the factors that characterises the success of rodents in Australia is their rapid speciation (Bush *et al.* 1977). Modern *Leggadina* species inhabit arid-environments in northeastern Queensland (*L. lakedownensis*) and a variety of areas through inland Australia (*L. forresti*) (Watts & Aslin 1981). However, climatic fluctuations mean that these arid-adapted rodents evolved from an ancestor which was not arid-adapted. The environment of Southeast Asia during the Miocene, thought to be the originating point of Australian murids, was characterised by tropical rainforest which were slowly beginning to contract (Heaney 1991).

Species of *Leggadina* have reasonably complex molars in comparison to closely related taxa, for example, both *Leggadina gregoriensis* and *L. macrodonta* have an additional occlusal structure (furrows) that allows for increased precision during mastication, indicating the evolution and specialisation of their teeth for a predominantly granivorous diet (Herring 1993; Evans *et al.* 2007). Similarly, the width of the zygomatic plate is a useful indicator of the kinds of food eaten by rodents, because width of the zygomatic plate increases with an increase in the size of the anterior deep masseter muscle used for pulverising food (Watts & Aslin 1981; Satoh 1997). The zygomatic plate in both fossil species is quite wide suggesting further specialisation for a predominately granivorous diet. Whether these fossil *Leggadina* species evolved these adaptations within Australia or before they migrated cannot be determined at the moment due to the lack of knowledge on both the timing and method of their dispersal to and within Australia, as well as appropriate morphological evidence for other Australian fossil species.

An especially distinguishing feature of *Leggadina macrodonta* is the size of its teeth, particularly M^1 which is up to 18% larger than the M^1 of *L. gregoriensis* or the two modern forms. The increase in size of the teeth and occlusal structures could be due to a number of different factors. Larger teeth would be a useful adaptation for taking advantage of a wider variety of resources necessary for survival in the changeable Pleistocene climate; however it could also represent specialisation for a more selective diet also resulting from a changing environment. Broader ecological evidence would need to be presented on changes in tooth structure in other species during the Pleistocene and associated reasons to make a more informed determination on the effect of a changing climate on tooth changes in *L. macrodonta*. It is also possible the increase in size of the molars was due to an increase in overall body mass, with this particular species growing larger in order to compete against larger animals for resources, as well as becoming able to process low nutrient foods more easily and reduce water loss (Archer *et al.* 1998; Dawson & Dawson 2006). Unfortunately it is not possible to calculate body mass of this species currently due to the absence of adequate lower molar data and a lack of long bones in the fossil assemblage relatable to this species (Hopkins 2008).

There are no current estimates on the timing of evolutionary divergence of *Leggadina* from related taxa. The most recent and comprehensive study on divergence times of murids (Nilsson *et al.* 2010) suggests divergence of the Conilurini from a *Mus* ancestor between 11 and 7.3 million years ago, with the Conilurini dispersing from New Guinea to Australia between 7.19 and 6.48 million years ago. This is congruent with available evidence from the fossil record and provides sufficient time for the colonisation of Australia and the establishment of native Australian species before their first appearance in the fossil record at around 5 million years, as seen in the appearance of *Leggadina gregoriensis* at this time (Nilsson *et al.* 2010). Unfortunately, with the paucity of investigated fossil evidence from Australia, even with the description of two new species here, it is not possible to develop divergence dates for individual Australian genera as more fossils are necessary for use as calibration points for molecular clocks.

Future Work

Molar morphology has been an important tool for understanding the evolution of the Murinae and other rodent groups for over 100 years. At this point in time it is still essential for the description of new species of Australian murids. However, to date there has been no comprehensive phylogenetic analysis based on morphology including both fossil and modern species. The leading analysis on morphological relationships relied almost solely on molar morphology and was conducted over 40 years ago (Misonne 1969). On the other hand, advances in molecular assessment of murid relationships have proliferated over the past 30 years (Baverstock *et al.* 1981; Pascale, Valle & Furano 1990; Catzeflis, Aguilar & Jaeger 1992; Watts *et al.* 1992; Jansa and Weksler 2004; Steppan *et al.* 2005; Rowe *et al.* 2008; Nilsson *et al.* 2010; Schenk, Rowe & Steppan 2013). An updated morphological phylogeny combined with molecular phylogenies would give a much more cohesive picture of Australian murid evolutionary history than using either alone (Wiens 2004; Aplin 2006).

Conclusion

Murid rodents are the most speciose mammalian family in Australia, but their evolutionary relationships and origins have been shrouded in mystery due in large part to the paucity of fossil evidence available. This project has gone some way to rectifying that by describing two new species of the genus *Leggadina*: *Leggadina gregoriensis* from the Pliocene Rackham's Roost Site in the Riversleigh World Heritage Area and *Leggadina macrodonta* from the Plio-Pleistocene Site 5C at Floraville Station, both in northwestern Queensland. *Leggadina gregoriensis* extends the temporal range of the genus *Leggadina* to 5 million years. Both fossil species display an increased complexity in the molars and larger attachment sites on the zygomatic plate, likely due to the development of a predominately granivorous diet. *L. macrodonta* also displays an increase in size of M^1 and M^2 which may be the result of a number of factors including adaptation to the unpredictability of, and increased competition for, resources during the Pleistocene or an increase in body size. Further research is essential to further develop understanding on the relationships and evolution of the genus *Leggadina* as well as the broader Murinae group.

Acknowledgements

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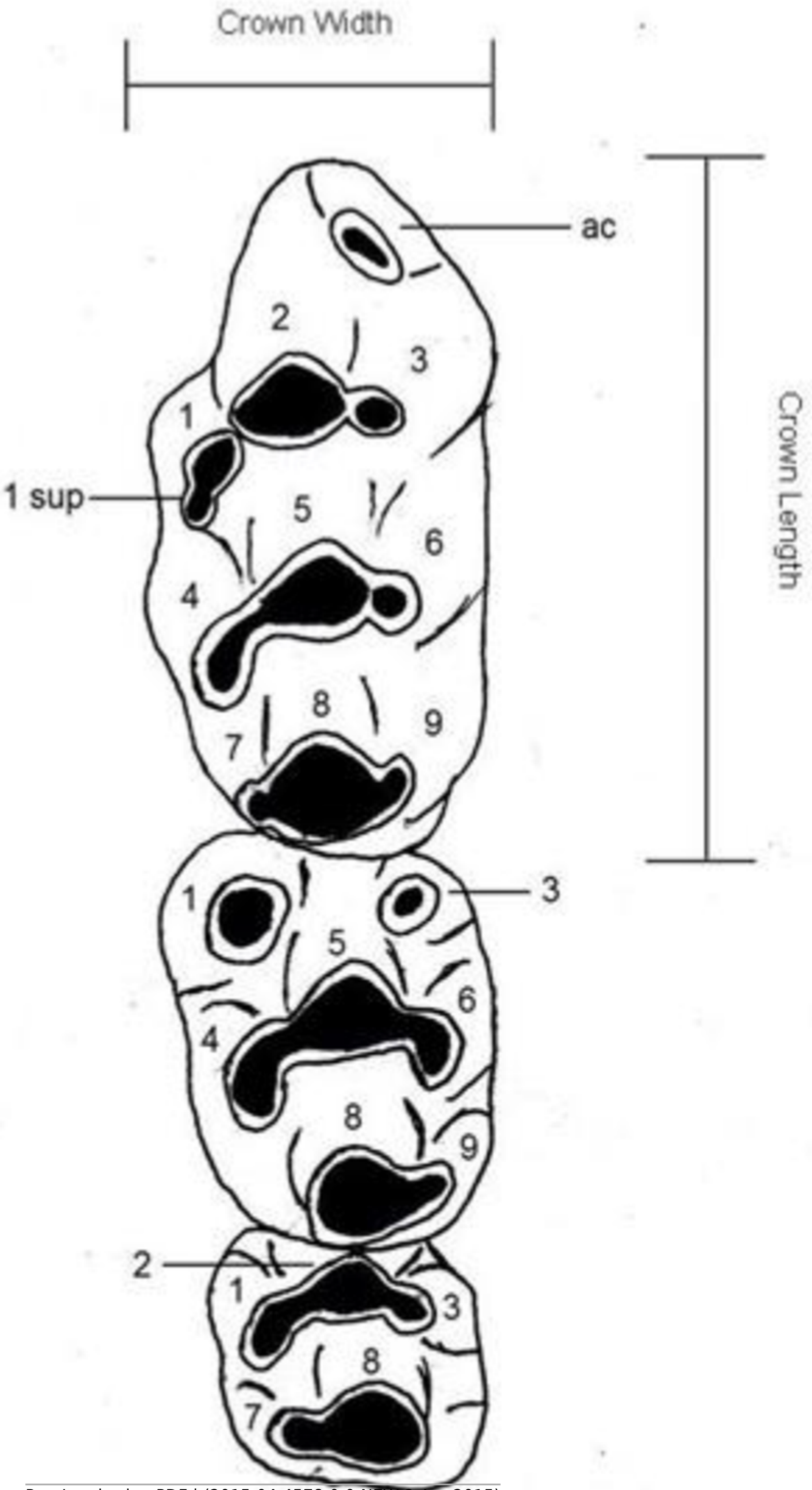
1

Dental nomenclature used for descriptions.

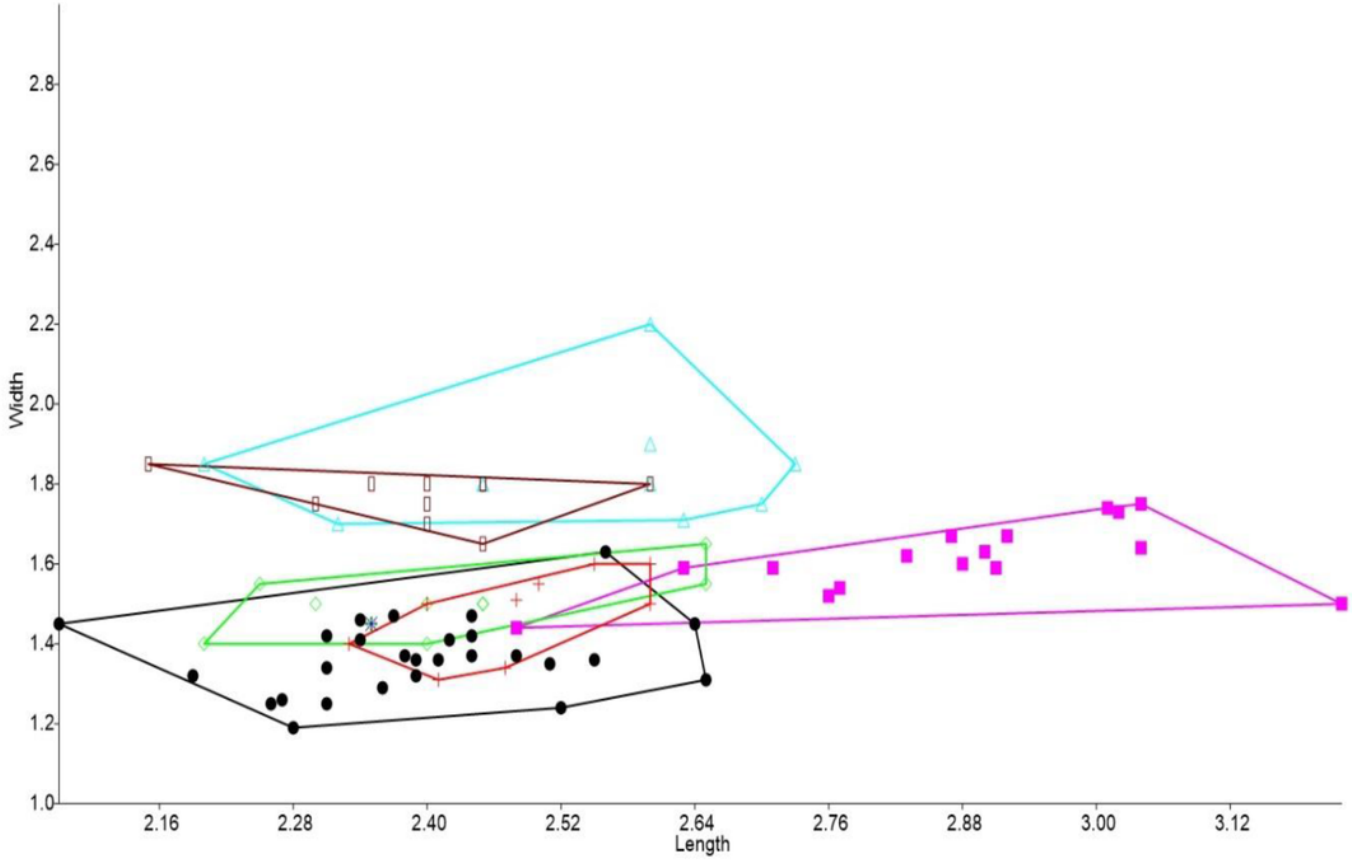
Dental nomenclature used in the description of fossil *Leggadina*. Adapted from Musser and Newcomb (1983) but modified to better represent features of fossil *Leggadina* specimens. Left upper molar row, cusps (1-9) referred to in text with the prefix ‘T’, ac = accessory cusp, sup = supplementary. Measurements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


Crown Width
ac
2
3
1
1 sup
5
6
4
8
9
7
Crown Length
1
3
5
6
4
8
9
2
1
3
8
7

2

Bivariate plot comparing M^1 between murine species.

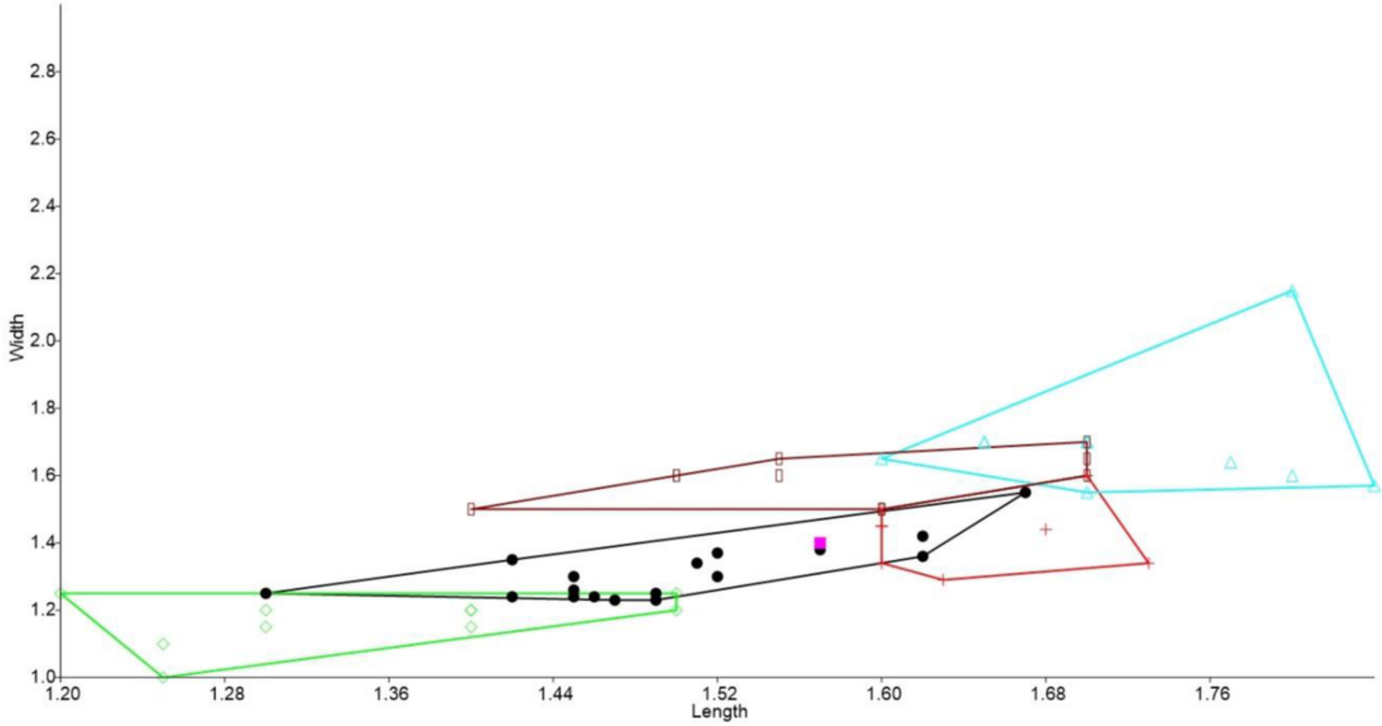
Bivariate plot of maximum crown length and width of M^1 (mm). *Leggadina forresti* = green diamond; *Leggadina lakedownensis* = blue star; *Leggadina gregoriensis* = black circle; *Leggadina macrodonta* = pink square; *Zyzomys argurus* = red cross; *Pseudomys australis* = blue triangle; *Notomys fuscus*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



3

Bivariate plot comparing M^2 between murine species.

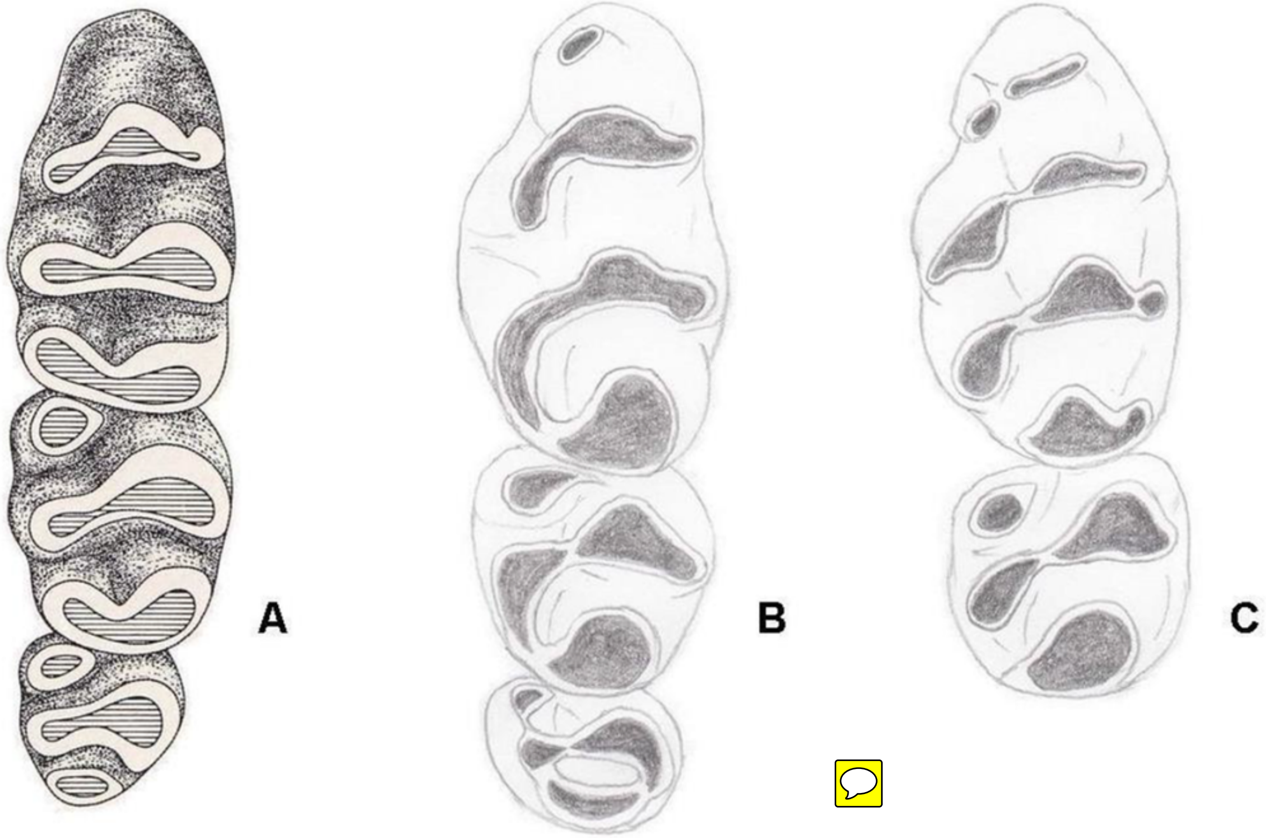
Bivariate plot of maximum crown length and width of M^2 (mm). *Leggadina forresti* = green diamond; *Leggadina gregoriensis* = black circle; *Leggadina macrodonta* = pink square; *Zyzomys argurus* = red cross; *Pseudomys australis* = blue triangle; *Notomys fuscus* = brown rectangle (*L. lakedownensis*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



4

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

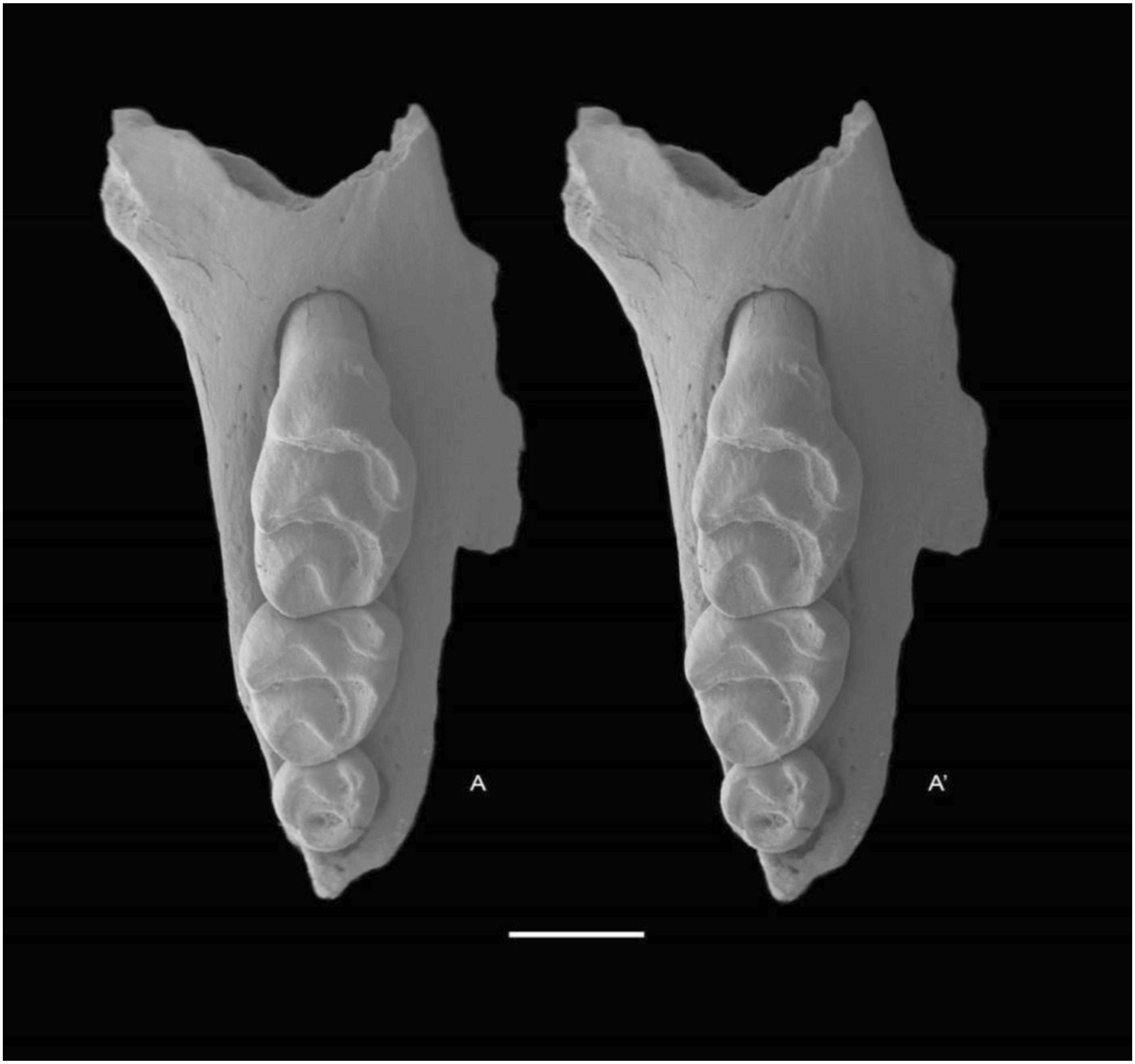
A = left upper molar row of *Zyzomys argurus* (Misonne 1969); B = right upper molar row of holotype (QM F 57259) of *Leggadina gregoriensis*, image has been reversed to represent left upper molar row for comparative purposes; C = left M^1 and M^2 of *Leggadina macrodonta*, composite of holotype (QM F57276)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



5

Leggadina gregoriensis sp. nov. Holotype. QM F57259.

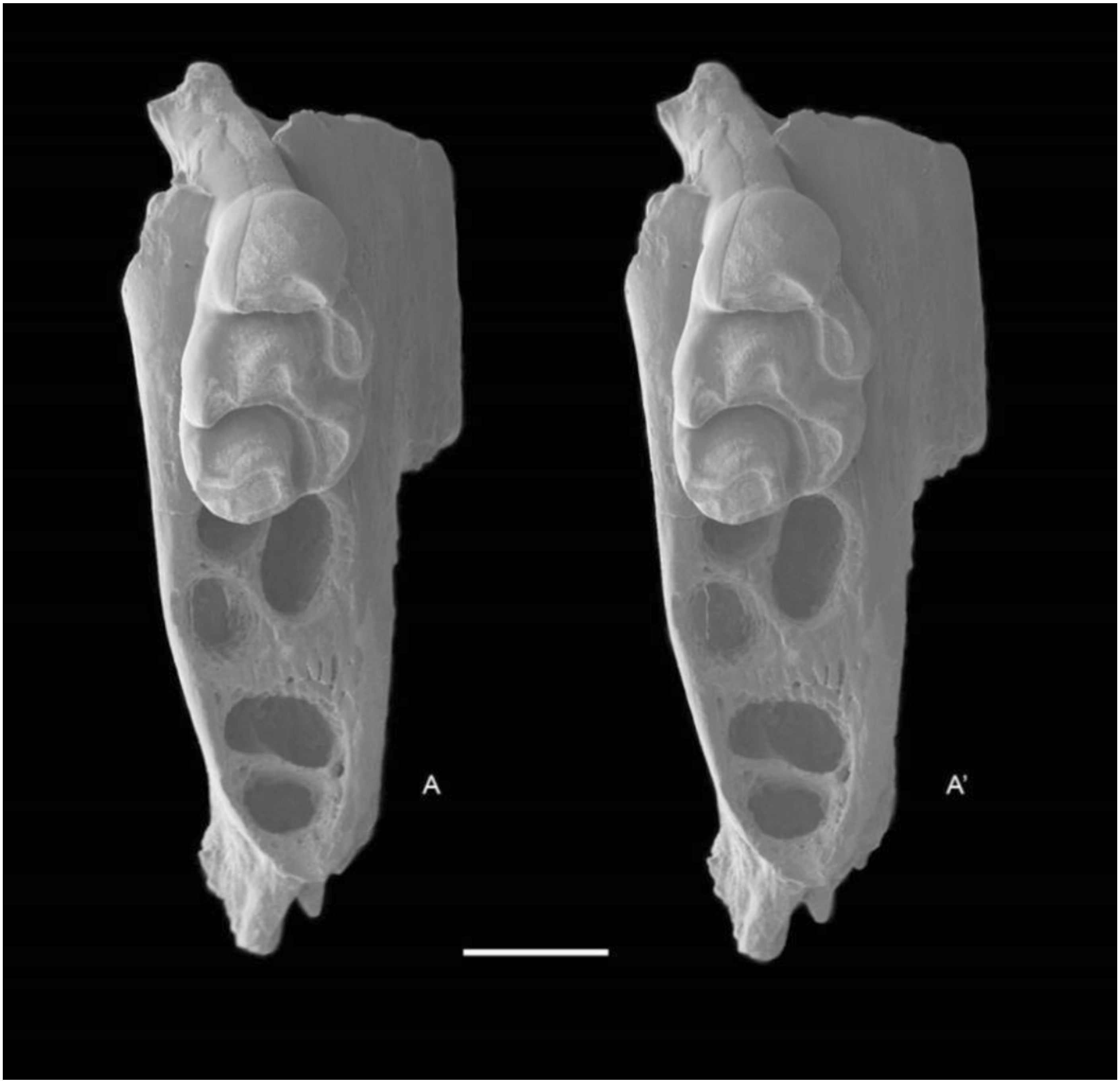
Partial right maxillary with M^{1-3}. Occlusal view. AA' = stereopair. Scale = 1 mm.



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 $M^{1\text{-}2}$. Occlusal view. A-A’ = stereopair. Scale = 1 mm.

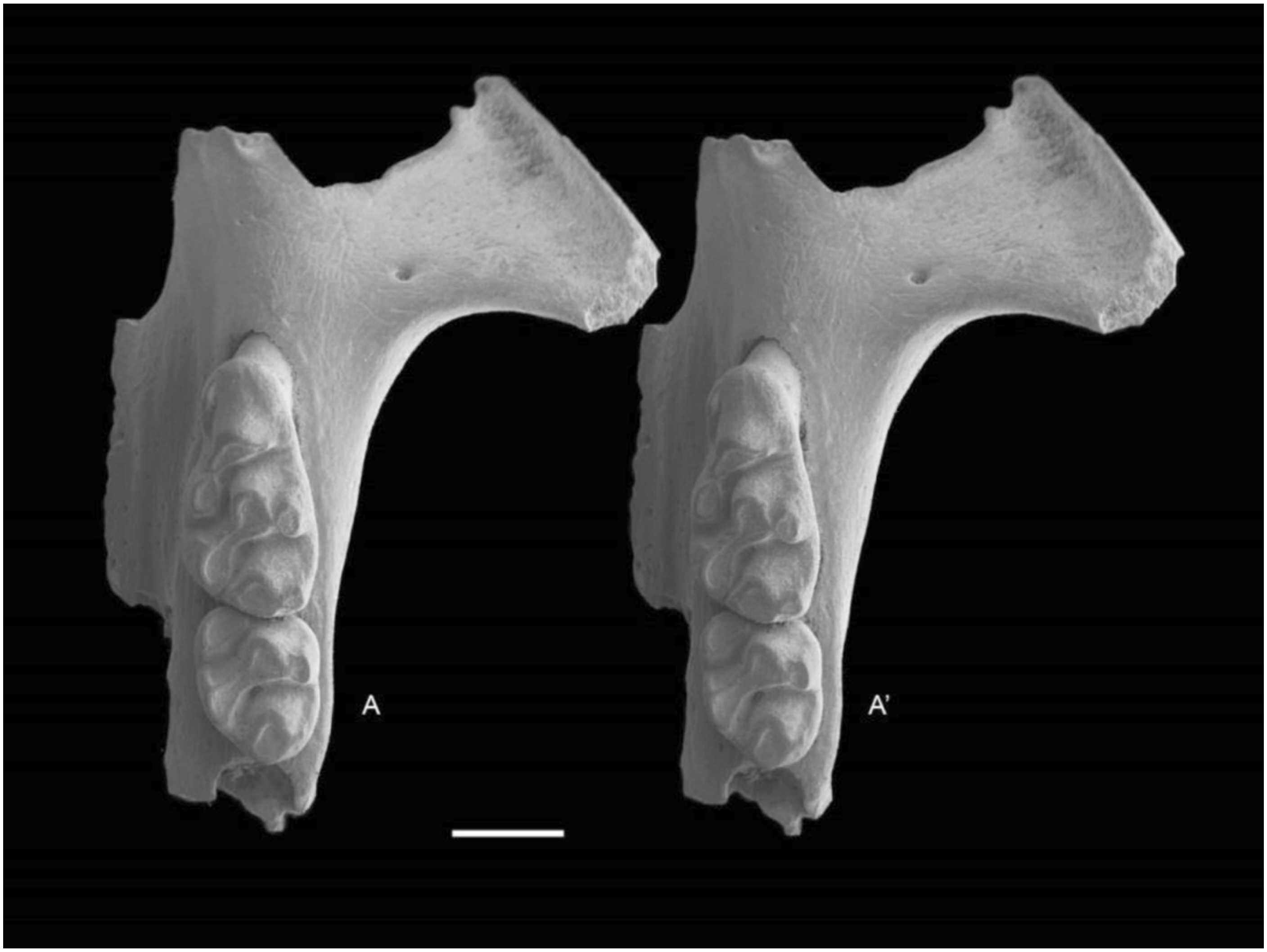


Table 1(on next page)

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

L = maximum length, W = maximum width.

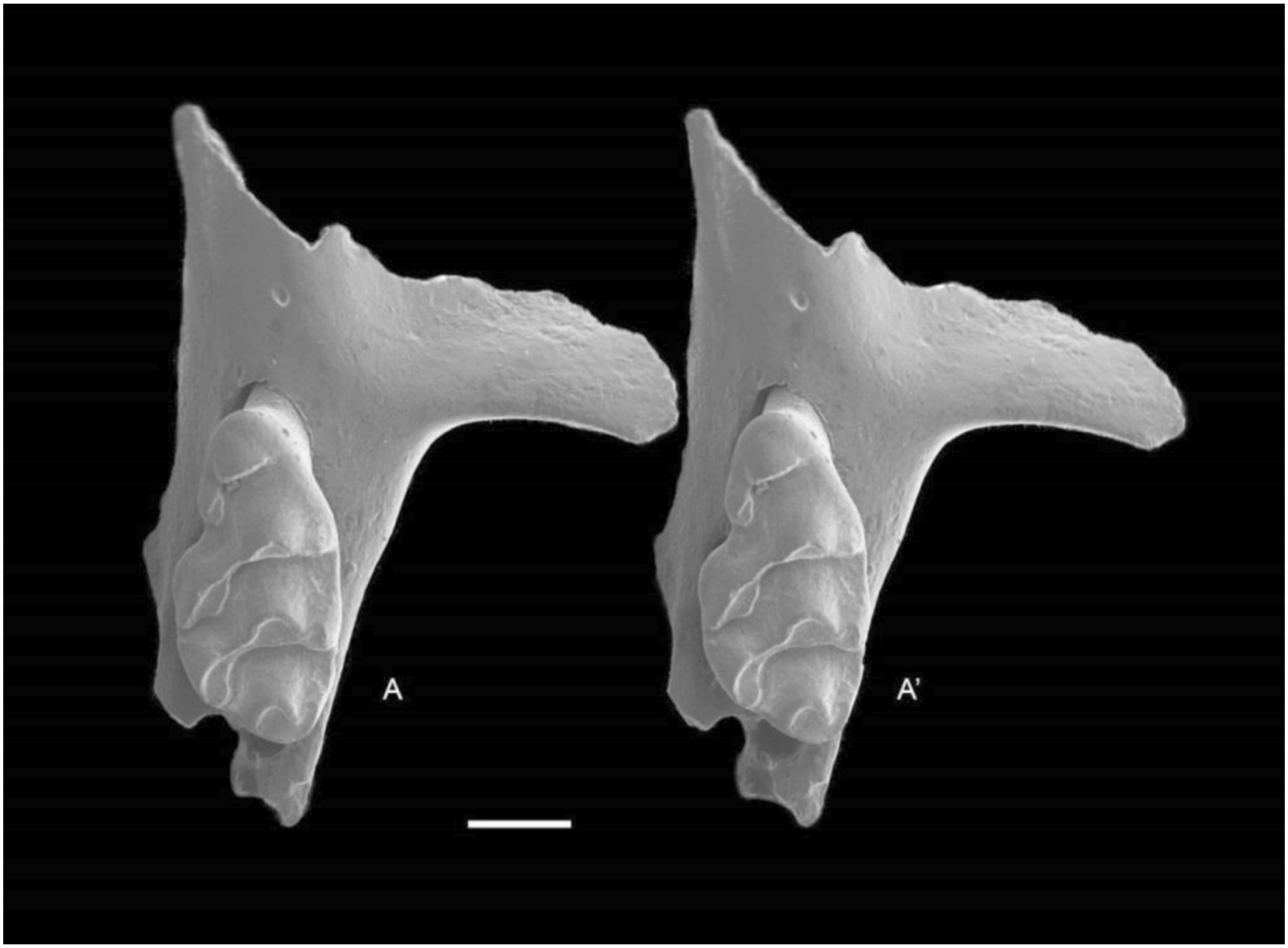
Table 1: **Measurements (mm) of *Leggadina gregoriensis* sp. nov.** L = maximum length, W = maximum width.

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

8

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 M^1. 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.

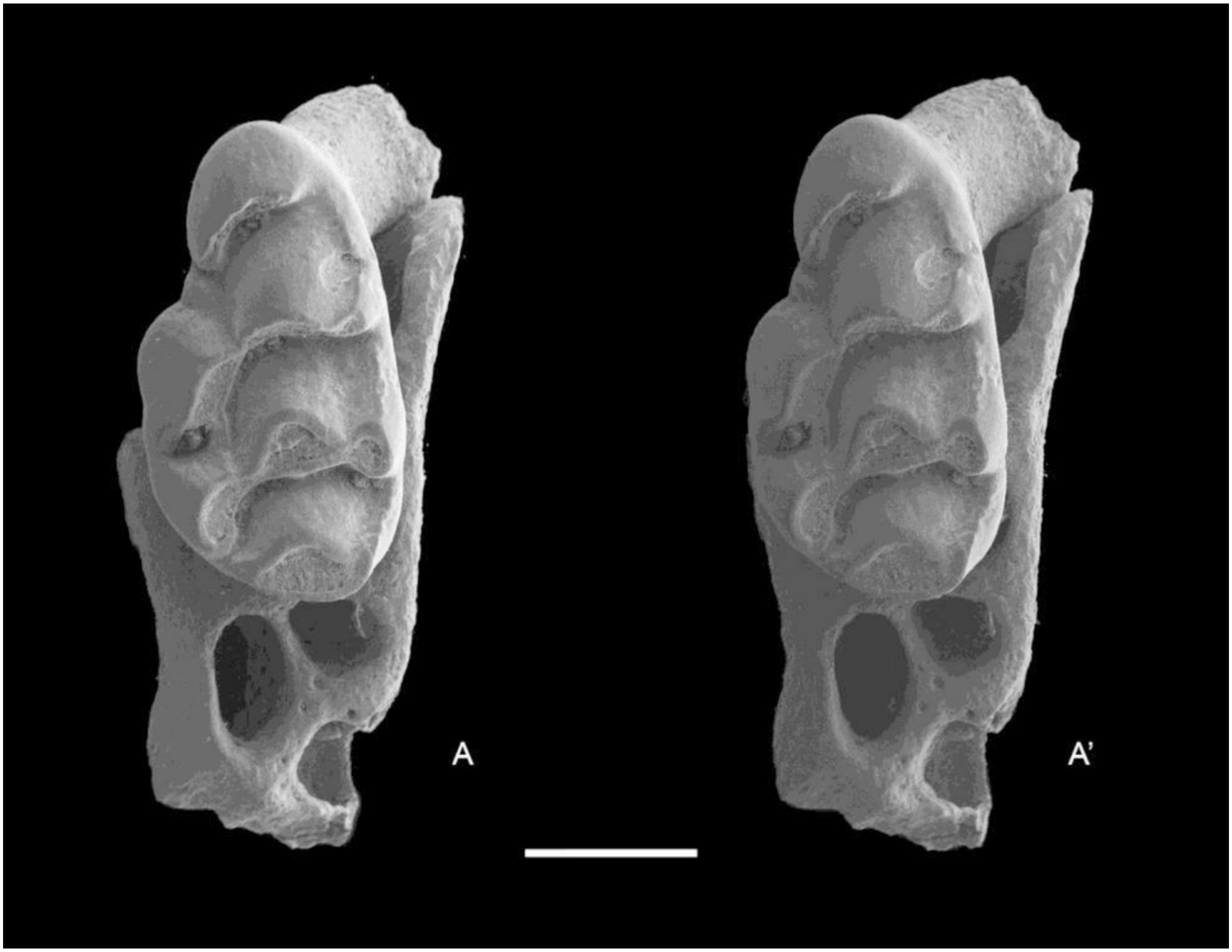


Table 2(on next page)

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

L = maximum length, W = maximum width.

Table 2: **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	-	-