“Evolución, paleobiología y sistemática de la familia Dinomyidae (Mammalia, Rodentia)”

Recostrucción de *Josephoartigasia monesi*, aparecida en la revista National Geographic (diciembre, 2015) a propósito de uno de los trabajos de esta tesis.

TESIS DE DOCTORADO
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ÍNDICE

Y cuando yo vi estos huesos acabé de persuadirme que en esta tierra hubo gigantes

Diego de Ocaña, 1607

Resumen

La presente tesis trata sobre el estudio de restos fósiles de roedores caviomorfos pertenecientes a la familia Dinomyidae (subfamilias Eumegamyinae y Tetrastylinae). Los materiales aquí estudiados provienen de la costa del Departamento de San José (Uruguay) y de la Argentina, abarcando un lapso temporal que va desde el Mioceno tardío al Plioceno. Si bien los primeros fósiles conocidos para la mencionada familia datan de finales del siglo XIX, recién en los últimos años se han venido realizando estudios pormenorizados sobre este grupo de roedores ampliamente distribuidos en Sudamérica. Además de ser una "puesta a punto" sobre el estado actual del conocimiento del grupo, en esta tesis presentamos nuestros resultados como una serie de 5 artículos publicados. También, y debido al alto impacto mediático que estos animales fósiles han tenido en los medios de prensa mundial, incluimos un libro de divulgación para niños como parte de nuestras actividades doctorales. Algunos de los principales resultados de estos trabajos se encuentran relacionados con el estudio de la ontogenia en el género *Isostylomys*, y sus potenciales consecuencias en la taxonomía y sistemática de Eumegamyinae. También reportamos un nuevo género de dinómido para el Uruguay, proveniente del Mioceno tardío, y realizamos estudios paleobiológicos y biomecánicos de dos géneros (*Josephoartigasia* y *Tetrastylus*) fundamentalmente centrados en la estimación de la fuerza de mordida de estos taxones.

Introducción

Los roedores constituyen uno de los grupos de mamíferos actuales más exitosos, tanto en lo que se refiere a su distribución como a su diversidad taxonómica. Presentes en todos los continentes con excepción de la Antártida y con unas 2300 especies descriptas son quizás los animales no domesticados que más han influido en la historia del hombre. A manera de ejemplo, en la Edad Media los roedores causaron indirectamente la desaparición de casi la mitad de la población europea durante la peste bubónica. Dentro de la gran diversidad del orden Rodentia se encuentran los denominados "Hystricognathi del Nuevo Mundo", un grupo muy característico de la Región Neotropical incluido en el suborden Caviomorpha (Huchon & Douzery, 2001). Hasta el momento el grupo incluye más de 170 géneros agrupados en unas 17 familias y se registra a partir del Eoceno-Oligoceno (Mones, 1986). Una de las peculiaridades de las distintas especies vivientes incluidas en el suborden Caviomorpha (y en todo el orden Rodentia) es el reducido tamaño, ya que en la actualidad la masa corporal máxima alcanzada por un roedor es de aproximadamente 60 kg (Mones & Ojasti, 1986). El animal que alcanza este tamaño, se conoce con el nombre de "Carpincho" o "Capibara" (*Hydrochoerus hydrochaeris*) y es considerado como el gigante del grupo ya que la gran mayoría de los roedores vivientes no alcanzan el kilogramo de masa corporal.

Es también en Sudamérica donde se encuentra la "Pacarana" (*Dinomys branickii*) (Fig1.), un extraño roedor caviomorfo que habita zonas selváticas de Brasil, Bolivia, Colombia, Ecuador y Perú (Fig. 2). Se trata del único representante viviente de una familia (Dinomyidae) que en el pasado geológico tuvo una notable diversidad (Frailey, 1986; Mones, 1986).


Figura 1: *Dinomys branickii*

Si bien la Pacarana es uno de los roedores vivientes de mayor tamaño con una masa corporal que varía entre los 10 y los 15 kg (White & Alberico, 1992), muchos taxones fósiles de la familia Dinomyidae alcanzaron tamaños corporales extraordinarios para un roedor, especialmente los pertenecientes a la extinguida subfamilia Eumegamyinae.


Figura 2: Distribución actual de *Dinomys* (sombreado oscuro) y registro fósil de Dinomyidae (puntos).

Registrados indudablemente a partir del Mioceno medio, la diversidad de los Dinomyidae ha sido ampliamente corroborada con una gran cantidad de hallazgos y hasta el momento se conocen aproximadamente 60 especies fósiles todas ellas distribuidas en Sudamérica (Mones, 1986; Krapovickas & Nasif, 2011) (Fig. 2).

A esta diversidad de roedores gigantes sudamericanos deben agregárseles unas 15 especies agrupadas en la familia Neoepiblemidae (Mones, 1986).

Si bien la gran mayoría de las especies de dinómidos descriptas provienen de Argentina (Ameghino, 1883b; Kraglievich, 1926), en el Uruguay se ha registrado una importante cantidad de taxones los cuales se agrupan en las subfamilias Potamarchinae, Gyriabrinae y Eumegamyinae (Kraglievich, 1930; Perea *et al.*, 1989; Rinderknecht & Blanco, 2008; Rinderknecht *et al.*, 2010).

Lamentablemente, hasta el momento es muy poco lo que se conoce sobre la anatomía y paleobiología de estos animales ya que la gran mayoría de los fósiles recuperados son dientes aislados y fragmentos de maxilares.

En relación a esta problemática, nuestro país se encuentra en una posición privilegiada ya que en los últimos años se ha colectado una importante cantidad de materiales fósiles de Dinomyidae, algunos de los cuales constituyen los registros fósiles más completos y mejor preservados del grupo.

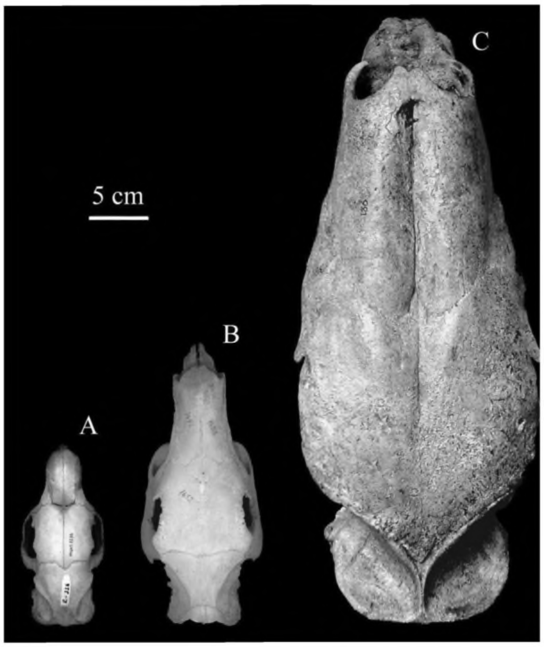

Figura 3: Cráneos en vista dorsal de: *Dinomys branickii* (A), *Hydrochoerus* (B) y *Josephoartigasia* (C)

A modo de ejemplo, la reciente publicación del cráneo más completo de un dinómido Eumegamyinae (Rinderknecht & Blanco, 2008) (Fig. 3; Lám. 1), alcanzó difusión mundial, apareciendo en todos los medios de prensa importantes alrededor del mundo, entre los que se destacan: *CNN*, *BBC*, *The Times*, *National Geographic; Discovery; CBS*, Diarios *Clarín* y *La Nación*, *Nature*, *The New York Times*, *American Scientist*, etc. Esta publicación se convirtió en uno de los descubrimientos paleontológicos que más impacto mediático ha causado en los últimos años, habiendo generado decenas de miles de artículos en la prensa mundial.

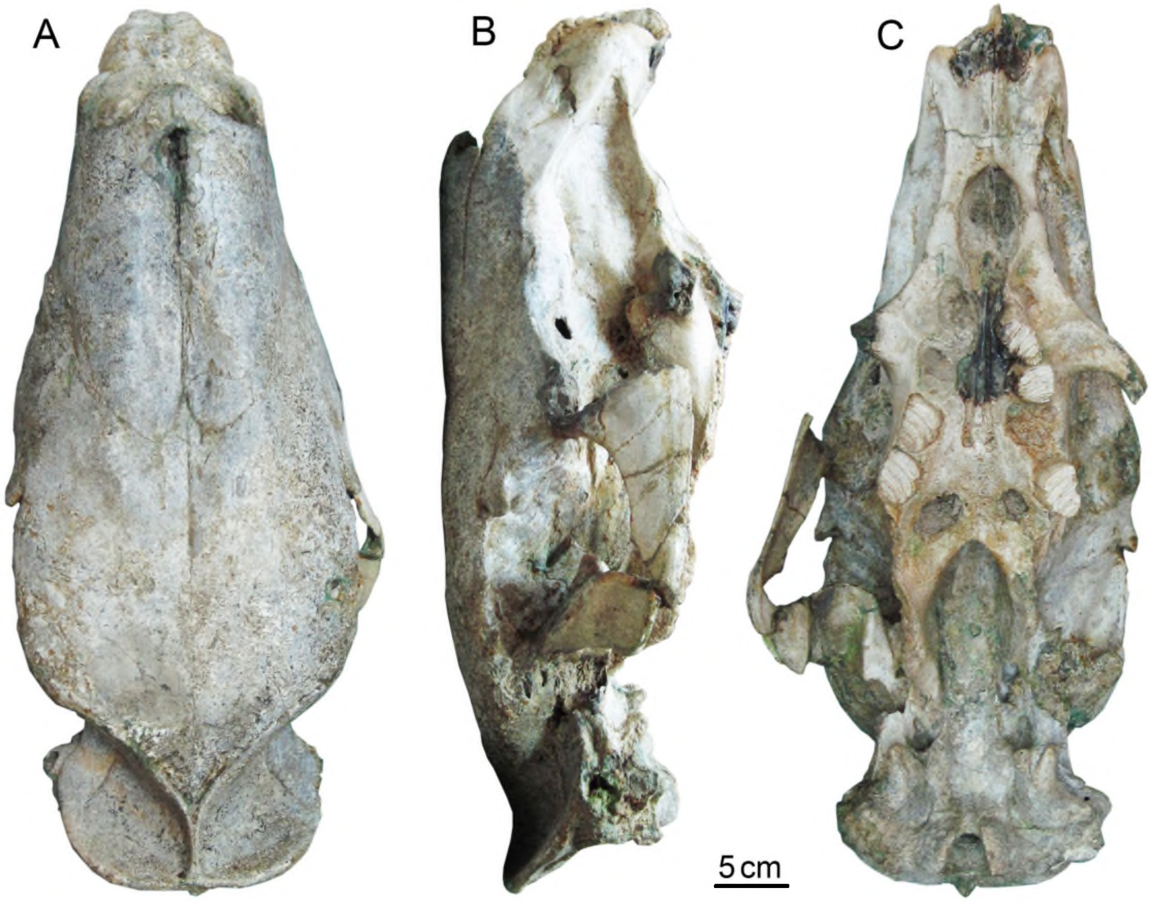

Lámina 1: Cráneo de *Josephoartigasia monesi* (MNHN: 921, holotipo) en vistas dorsal (A), lateral derecha (B) y ventral (C).

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Objetivos y estructura de la tesis

Ya se mencionó que pese a haber sido un grupo muy diverso y ampliamente distribuido por Sudamérica, los dinómidos fósiles son conocidos por restos muy fragmentarios. Por otra parte, durante el siglo XX los estudios sobre la familia (incluyendo su representante actual) han sido escasos. Esto último, sumado al hecho de que en el Uruguay se han colectado algunos de los restos más completos y mejor preservados de Eumegamyinae, nos coloca en una posición privilegiada para intentar profundizar en el conocimiento sobre esta subfamilia y sobre los dinómidos en general. Como principal objetivo de esta tesis entonces se pretenden analizar los distintos materiales fósiles de la familia Dinomyidae pertenecientes a la subfamilia Eumegamyinae y Tetrastylinae (la gran mayoría de ellos inéditos hasta el momento), registrados en el lapso Mioceno-Plioceno de Uruguay y Argentina, a fin de poder esclarecer las características anatómicas, paleobiológicas y sistemáticas de este grupo de roedores gigantes.

Todos los materiales de Eumegamyinae analizados en esta tesis se encuentran depositados en el Museo Nacional de Historia Natural de Montevideo (MNHN). Mientras que los de las subfamilias Tetrastylinae se encuentran en el Museo Argentino de Ciencias Naturales (Argentina) y en la Facultad de Ciencias (Uruguay). Los fósiles de Uruguay provienen todos de la misma localidad y formación geológica (Arazatí, Formación Camacho) y una descripción de los atributos litológicos y paleontológicos de dicha formación puede verse en dos de los trabajos aquí presentados. Para la realización de esta tesis fue fundamental contar con materiales comparativos de roedores actuales; especialmente del único representante moderno de la familia Dinomyidae (*Dinomys branickii)* y del roedor viviente de mayor tamaño (*Hydrochoerus hydrochaeris*). En el segundo artículo de esta tesis se da un listado completo de estos materiales y de las instituciones en las que se encuentran depositados. Debido a lo complejo de la historia del estudio de la familia Dinomyidae, en el capítulo de antecedentes se resumirán los principales estudios realizados sobre la misma así como también las diferentes propuestas de clasificaciones supragenéricas. Para ello se ha dividido al mencionado capítulo en 3 partes. En la primera parte (Los primeros hallazgos) se detalla el devenir histórico de los estudios sobre dinómidos fósiles; en la segunda parte (Los últimos hallazgos) se recuentan los últimos publicados dentro del grupo, para luego detallar las propuestas de ubicación sistemática para la subfamilia Eumegamyinae (Sistemática de la subfamilia Eumegamyinae). Es importante aclarar que mucha de la información dada en estos tres capítulos ha sido publicada en formato capítulo de libro y dicho trabajo se incluye como parte de los resultados de la presente tesis. No obstante, consideramos de utilidad incluir algunas de estas informaciones en los antecedentes de la tesis, fundamentalmente para aclarar lo más posible este tema tan poco comprendido de la clasificación sistemática y el devenir histórico en los estudios del grupo. Terminado el capítulo de Antecedentes se da un listado bibliográfico de los principales trabajos paleontológicos publicados para la familia Dinomyidae. Este listado se organizó cronológicamente comentando (en negrita) cada uno de los trabajos. Algunos de los artículos referidos en este capítulo no están citados en el texto. Continuando con la tesis se incluye la bibliografía completa y se adjuntan 5 artículos; 4 de ellos recientemente publicados y un quinto que se encuentra en prensa. Finalmente se incluye un libro de divulgación en relación a los dinómidos fósiles y la paleontología en general.

Para concluir se incluyen los capítulos "Conclusiones finales y perspectivas" y "Agradecimientos".

Antecedentes

Los primeros hallazgos

El descubrimiento de los primeros fósiles de la familia Dinomyidae es sin duda uno de los eventos más peculiares en la historia de la paleontología sudamericana.

Entre los años 1827 y 1828 el naturalista francés Alcides D'Orbigny colectó en la "Ensenada de Ross" al sur de la Provincia de Río Negro (Argentina) una tibia y una rótula de un mamífero fósil cuyas dimensiones debieron ser comparables a las de un caballo. Estos materiales fueron posteriormente descritos por el paleontólogo francés Charles Léopold Laurillard en la obra de D'Orbigny sobre su viaje por Sudamérica (ver Laurillard, 1848) y, en base al parecido de dichos huesos con los que poseen las vizcachas, fueron identificados como pertenecientes a un gigantesco roedor. Es así como Laurillard crea el género *Megamys* (con la especie tipo *Megamys patagoniensis*) y enciende una controversia que duraría casi un siglo. Es que el gran tamaño de los materiales tipo del género *Megamys* sumado al hecho de que se conocieran únicamente dos huesos poscraneanos, hizo que algunos científicos de la época cuestionaran la asignación de estos fósiles como pertenecientes a un roedor. El principal investigador en tratar de refutar las conclusiones de Laurillard fue el paleontólogo y zoólogo alemán Germán Burmeister, quien afirmó que la tibia y rótula provenientes de la Ensenada de Ross debieron pertenecer realmente a un mamífero notoungulado del género *Nesodon* (Burmeister, 1879). Esta afirmación se sustentaba en que *Nesodon* es un taxón próximo al género *Typotherium*, el cual presenta algunas similitudes morfológicas con los roedores. A este trabajo de Burmeister le seguirá la réplica de Henri Gervais y del principal adversario científico del paleontólogo alemán: Florentino Ameghino (ver Gervais & Ameghino, 1880; Ameghino 1883a). Si bien Gervais y Ameghino no discuten las afirmaciones de Burmeister, sí consideran la asignación de Laurillard como correcta y se refieren al género *Megamys* como un gigantesco roedor perteneciente a la fauna extinguida de Argentina: *"Lo que hasta ahora se conocía de la fauna mamalógica de este horizonte (Piso Mesopotámico del Oligoceno inferior) se reduce a poca cosa: 2 mamíferos* (...); *un roedor gigantesco del Río Negro, poco menos enigmático, conocido con el nombre de Megamys* (...)" (Ameghino 1883a).


Figura 4: Germán Burmeister

La aparente resolución de este debate comenzaría unos años más tarde con algunos notables hallazgos provenientes de Paraná. En la segunda mitad del siglo XIX la región del Paraná sería objeto de un emprendimiento cultural del Gobierno de la Argentina, emprendimiento que tuvo como uno de sus principales logros la creación de la "Escuela Normal del Paraná" entre cuyos docentes se encontraba el profesor Pedro Scalabrini. Este investigador emprendería la tarea de colectar fósiles provenientes de las barrancas de la zona del Río Paraná y formaría una pequeña colección cuyas piezas más significativas serían enviadas a Buenos Aires para así poder ser estudiadas por Ameghino (ver Ameghino 1883a). Inmediatamente después de que Ameghino terminara sus estudios sobre los fósiles de dicha colección, Scalabrini le enviaría una segunda colección de fósiles, en la cual se encontraba el fragmento anterior de una rama mandibular derecha, la parte anterior de un incisivo inferior y dos molares aislados de un gigantesco roedor. Estos últimos fósiles serían asignados por Ameghino a la especie *Megamys patagoniensis* (Ameghino, 1883b) y se transformarían en una prueba irrefutable de que en Argentina existieron roedores cuyos tamaños corporales sobrepasaron ampliamente los de cualquier otro roedor conocido hasta la fecha. Este trabajo (Ameghino, 1883b) aparentemente pondría fin a la controversia generada en torno a la tibia y rótula descriptas por Laurillard, tal como sería expresado por el propio Ameghino: "*Unos cuantos golpes de pico dados en las barrancas del Paraná, poniendo a la luz del día una página inédita de la historia de nuestro globo que nos da a conocer toda una fauna perdida, han arrancado a la vez de las entrañas de la tierra varias partes características del enigmático roedor, que se nos aparece respondiendo al llamado que de él hiciera el ilustre sabio cuarenta años ha, cuando el nombre de Laurillard es de ultra-tumba y sus sucesores se elevan incrédulos ante las inducciones del genio y de la ciencia!*" (Ameghino, 1883b).


Figura 5: Florentino Ameghino

En el mencionado trabajo Ameghino también describe el fragmento de una mandíbula inferior izquierda sobre la cual se crea la especie *Megamys laurillardi*: "*Designaré esta nueva especie con el nombre de Megamys laurillardi, como pobre tributo de respeto por mi parte al sabio de cuyas inducciones científicas el acaso me ha designado a demostrar exactitud.*" (Ameghino, 1893b).

Finalmente Ameghino se encargaría de hacerle llegar a Burmeister un copia en yeso de la mandíbula descripta bajo la denominación de *Megamys patagoniensis*.

Ante estas evidencias el paleontólogo alemán reconoce su error: "*No vacilo conceder que mi conjetura ha sido errónea; el animal llamado Megamys, es, en verdad, no solamente un roedor gigantesco, sino también el más parecido á la vizcacha, aunque de tamaño sorprendente, casi del tamaño de una vaca pequeña ó del asno.*" (Burmeister, 1885).

En el citado trabajo Burmeister también describe la porción posterior del cráneo de un dinómido donada en 1867 al Museo Argentino de Ciencias Naturales (ex Museo Público de Buenos Aires) y también proveniente del Río Paraná. Sobre este material (MACN 4007) Burmeister realiza importantes observaciones, especialmente referidas a la conformación de la región occipital.

Pese a haber reconocido su error, este último trabajo de Burmeister no está exento de criticas para con Ameghino; de hecho las últimas páginas de la mencionada obra consisten en una serie de duras apreciaciones sobre el desempeño científico del paleontólogo argentino: "*Como un aviso al público, agrego que no contestaré jamás á quejas y nuevas inventivas del señor Ameghino, tratándole como individuo que no existe, dejando en olvido sus obras y su persona.*" (Burmeister, 1885).

Un año más tarde Ameghino se defendería de las críticas efectuadas por Burmeister, especialmente de la referida a la propensión que tendría el paleontólogo argentino de dedicarle especies fósiles a sus "(…) *diferentes amigos personales* (…)" (Burmeister, 1885). En el mencionado trabajo (Ameghino, 1886) se describen numerosos fósiles de roedores gigantes entre los cuales se destacaba una rama mandibular considerada por Ameghino como perteneciente al roedor de mayor tamaño jamás descubierto. El nombre elegido por Ameghino para denominar a este taxón fue el de *Megamys burmeisteri*.

Luego de terminado el debate sobre la existencia de estos roedores se continuarían describiendo especies y estudiando las peculiaridades anatómicas del grupo (ver Ameghino, 1889; 1891a,b; Rovereto, 1914).

Sin embargo la discusión sobre la correcta asignación de los materiales colectados por D'Orbigny en la Ensenada de Ross sería retomada en el año 1926 por el paleontólogo argentino Lucas Kraglievich con resultados inesperados. Es así como casi ochenta años después de que Laurillard descubriera al gigantesco *Megamys*, Kraglievich demostraría que sin lugar a dudas la tibia y la rótula de este taxón no correspondían realmente a un roedor y sí a un mamífero ungulado posiblemente de la familia Macraucheniidae (ver Kraglievich, 1926). Por lo tanto casi un siglo después de que se reportaran los primeros fósiles de un roedor gigante para Sudamérica quedaría demostrado que dichos restos no pertenecieron a un roedor. Sin embargo y debido a una extraordinaria coincidencia los fósiles descritos posteriormente por Ameghino (1883b) y utilizados por este investigador para demostrar la supuesta equivocación de Burmeister sí pertenecieron a un gigantesco roedor. Es por esta razón que Kraglievich (1926) propone cambiar el nombre de todos los fósiles publicados por Ameghino bajo la denominación genérica de *Megamys* (*Megamys* es un mamífero ungulado) por la de *Eumegamys*. En este trabajo también se traspasan todos los restos de roedores gigantes incluidos en la familia "Viscaccidae" a las familias "Eumegamyidae" (ver Kraglievich, 1926) y Neoepiblemidae. Esta última familia fue creada por Kraglievich (1926) para

Figura 6: Lucas Kraglievich

agrupar a los géneros *Neoepiblema* y *Dabbenea*. Es también en este último trabajo en donde se establecen los criterios generales de clasificación de la familia Dinomyidae; criterios que permanecen hasta el presente, pese a que Kraglievich no reconoce la existencia de la familia Dinomyidae a la que él llama Eumegamyidae. A partir de 1926 se avanza significativamente en el conocimiento de los dinómidos fósiles los cuales han sido registrados en gran parte de Sudamérica, habiéndose descrito unas 60 especies fósiles (ver Mones, 1986).

Los últimos estudios

Es a partir de comienzos del siglo XXI cuando algunos investigadores, fundamentalmente de Argentina, Brasil y Uruguay, comienzan a estudiar pormenorizadamente fósiles de dinómidos, e incluso algunos aspectos anatómicos de *Dinomys*.

La investigadora Norma Nasif realiza su tesis de doctorado sobre dinómidos fósiles del Mioceno tardío de Argentina (Nasif, 2009) aportando datos sobre la sistemática, taxonomía y evolución del grupo (ver Nasif *et al.*, 2013). También realiza un importante análisis del desarrollo ontogenético cráneo-dental en *Dinomys branickii* (Nasif & Abdala, 2015) el cual ha sido tomado como base para uno de nuestros trabajos.

En Uruguay, a partir del año 2008 se han realizado numerosos estudios sobre el grupo. Sumado a la descripción de *Josephoartigasia monesi* (Rinderknecht & Blanco 2008) se han realizado estudios de la región auditiva en la subfamilia Eumegamyinae (Rinderknecht *et al.*, 2011), descripto un nuevo género (Rinderknecht *et al.*, 2011) y realizado estudios biomecánicos que analizan la fuerza de mordida de *Josephoartigasia monesi* (Blanco *et. al.*, 2011).

Finalmente se han realizado importantes descubrimientos en Brasil, liderados por el investigador Leonardo Kerber. Los estudios incluyen descripciones de nuevos taxones de Potamarchinae, registros de dinómidos en el cuaternario de Brasil y consideraciones sistemáticas sobre el grupo (Kerber *et al.*, 2016, 2018).

Sistemática de la familia Dinomyidae

Como ya hemos visto, los primeros restos indudables de un dinómido fósil son dientes aislados y un fragmento de mandíbula descritos por Ameghino (1883b) bajo la denominación incorrecta de "*Megamys patagoniensis*". Luego de este trabajo todos los investigadores anteriores a Kraglievich considerarían a los dinómidos como un grupo dentro de la familia Chinchillidae *(antea* Viscaccidae): "*Estas analogías con la vizcacha son fundamentales y no dejan absolutamente duda alguna de que Megamys á pesar de la enorme talla de alguna de sus especies, pertenece á la misma familia*" (Ameghino, 1889). El criterio de la época fue el de agrupar a todos los roedores de gran tamaño dentro de un mismo grupo y excluir a la mayoría de los de pequeño tamaño; tal es el caso de los Potamarchinae (hoy considerados una subfamilia de Dinomyidae) los cuales fueron incluidos en una familia propia (Kraglievich, 1926) o considerados como emparentados con los Myocastoridae (Burmeister, 1883). Los estudios pormenorizados sobre la sistemática de los dinómidos comienzan con el trabajo del año 1926 de Lucas Kraglievich (ver Tabla 1). En este trabajo el paleontólogo argentino demuestra que la denominación "*Megamys*" para los restos de roedores gigantes es incorrecta y crea las familias Eumegamyidae (con la subfamilia Phoberomyinae), Neoepiblemidae y Potamarchidae. Por último se establece la separación a nivel familiar de estos tres grupos con respecto a los roedores fósiles de gran tamaño descritos para las islas de las Antillas.

Cuatro años más tarde Kraglievich (1930) describe nuevos restos de dinómidos fósiles y crea (siempre dentro de Eumegamyidae) la subfamilia Gyriabrinae, a la que le seguirían las subfamilias Tetrastylinae (Kraglievich, 1931), Eumegamyinae (Kraglievich, 1932) y Dinomyinae (Kraglievich, 1934).

Pese a que Kraglievich siempre mantuvo como válida la designación de Eumegamyidae para la familia que hoy se conoce bajo el nombre de Dinomyidae, el notable descubrimiento de que este grupo de mamíferos fósiles tiene un representante viviente también se debe al paleontólogo argentino: *"El subgrupo de los tetrastilinos, al que pertenece T. montanus, tenía los molares casi exactamente conformados como el actual género Dinomys Peters, pero el cráneo poseía paracóndilos, y por esta causa debe aislarse subfamiliarmente de este animal."* (Kraglievich, 1931).

Ésta es la primera vez que se menciona en la literatura científica que los roedores fósiles agrupados dentro de la familia Eumegamyidae no están completamente extinguidos; de hecho la única distinción que Kraglievich hace entre *Dinomys* y *Tetrastylus* (un "Eumegamyidae" fósil descrito por Ameghino en 1886) es la presencia de paracóndilos en este último género. Hoy sabemos que *Dinomys* también tiene paracóndilos (ver Mones, 1997) por lo que si seguimos el criterio de Kraglievich *Dinomys* debería ser incluido en la subfamilia Tetrastylinae. Ante tal descubrimiento resulta curioso el poco énfasis con que Kraglievich da a conocer sus resultados, y es seguramente por esto que el mencionado descubrimiento ha sido incorrectamente atribuido al paleontólogo estadounidense Robert W. Fields (ver Fields, 1957; Bondesio, 1978). Tres años más tarde Kraglievich en una publicación póstuma (Kraglievich, 1934) incluirá a *Dinomys* en su familia Eumegamyidae creando la subfamilia Dinomyinae: *"Me parece que la familia Potamarchidae debe aislarse de la precedente. Comprende los precursores de la familia Eumegamyidae. Esta última familia debe considerarse subsistente en la actualidad, pues el género Dinomys Peters, parece pertenecer a ella."* (Kraglievich, 1934). El próximo autor que se ocupará pormenorizadamente de la clasificación de los dinómidos será Robert W. Fields, quien en su trabajo sobre roedores fósiles del Mioceno de Colombia (Fields, 1957) realizará una importante serie de observaciones taxonómicas y sistemáticas sobre la mencionada familia. Fields considera de forma explícita que las familia Eumegamyidae y Dinomyidae son sinónimas (consideración ya hecha por Kraglievich), siendo esta última la denominación correcta (ver Tabla 1). Es en este trabajo en donde se incluye a la familia Potamarchidae como una subfamilia (Potamarchinae) de Dinomyidae. Según la clasificación de Fields la familia Dinomyidae quedaría compuesta por tres subfamilias: Potamarchinae, Eumegamyinae (que incluye Tetrastylinae y Gyriabrinae, pese a que estas tienen prioridad sobre Eumegamyinae) y Dinomyinae. No existe mención de la subfamilia Phoberomyinae en el trabajo de Fields.

La inclusión de las subfamilias Tetrastylinae y Gyriabrinae dentro de Eumegamyinae no ha sido completamente reconocida en investigaciones posteriores; es así como Pascual (1967) reconoce a Gyriabrinae como subfamilia válida pero comparte con Fields la idea de que los Tetrastylinae son un grupo dentro de Eumegamyinae (pese a que Tetrastylinae tiene prioridad nomenclatural). Mones (1981) reconoce cuatro subfamilias dentro de Dinomyidae: Potamarchinae, Gyriabrinae, Dinomyinae (con las tribus Dinomyini y Eumegamyini) y Phoberomyinae (que incluiría los géneros *Eusigmomys* y *Phoberomys*). Unos años más tarde, Jean Bocquentin y Pedro Bondesio (1987) demuestran que los restos conocidos de *Phoberomys* (restos mandibulares) se corresponden con los molares superiores conocidos de *Dabbenea*; al establecerse esta identidad el género *Dabbenea* pasa a ser sinónimo de *Phoberomys* y los taxones incluidos en la subfamilia Phoberomyinae pasan a integrar la familia Neoepiblemidae (ver Mones, 1989). En la actualidad la mayoría de los autores incluyen en la familia Dinomyidae al menos dos subfamilias: Potamarchinae y Eumegamyinae, quedando las restantes subfamilias propuestas (Gyriabrinae, Tetrastilinae y Dinomyinae) pendientes de una revisión sistemática. Las relaciones de la familia Dinomyidae con la superfamilia

Chinchilloidea (tema largamente debatido durante el siglo XX) ha quedado demostrada gracias a los estudios moleculares (ver Huchon & Douzery, 2001; Blanga-Kanfi *et al.*, 2009).

Autor	**Familia**	**Subfamilias**
Ameghino (1883-1889)	Viscaccidae	No se reconocen
Kraglievich (1926-1934)	Eumegamyidae	Tetrastylinae Eumegamyinae Gyriabrinae Phoberomyinae Dinomyinae
Fields (1957)	Dinomyidae	Eumegamyinae Potamarchinae Dinomyinae
Pascual (1967)	Dinomyidae	Eumegamyinae Potamarchinae Gyriabrinae Phoberomyinae Dinomyinae?
Mones (1981)	Dinomyidae	Potamarchinae Gyriabrinae Phoberomyinae Dinomyinae

Tabla 1: Clasificaciones de Dinomyidae según distintos autores.

Bibliografía fundamental comentada

LAURILLARD, C. L. (IN D'ORBIGNY, A) 1848. Voyage dans l'Amérique Meridional. Paleontología, 4éme. partie. Paris. **Laurillard describe una tibia y una rótula colectadas por D'orbigny en la "Ensenada de Ross" al sur de la Provincia de Río Negro (Argentina) y llega a la conclusión de que se trata de los huesos de un gigantesco roedor fósil al que denomina *Megamys patagoniensis*.**

PICTET, F. J. 1853. Traité élémentaire de Paléontologie des animaux fossiles considérés dans leurs rapports zoologiques et géologiques. 1: xvii + 1-371, láms. 1-18. Langlois et Leclerq, Paris. **En este trabajo se pone en duda la asignación taxonómica hecha por Laurillard de la tibia y la rótula y se recomienda poner dicha determinación como provisoria hasta no encontrar restos dentales.**

BRAVARD, A. 1858. Monografía de los terrenos marinos terciarios de las cercanías del Paraná. Imprenta del Registro Oficial, Paraná, Argentina, 107 pp. **Este trabajo fue publicado en 1858 en el Diario oficial del Gobierno: "*El Nacional Argentino*" y Bravard le regaló algunos ejemplares impresos separadamente a sus amigos. Posteriormente el trabajo se vuelve inhallable pero Burmeister en 1885 da una "*reimpresión verbal con algunas alteraciones*" del trabajo original. En el mencionado trabajo se habla de los fósiles de *Megamys* colectados por D'Orbigny y se cita el hallazgo de un molar asignado a la especie europea *Theridomys americanus*. Este molar podría ser el primer registro de un dinómido fósil y pertenecer al género *Potamarchus*; sin embargo el material estaría perdido o su identificación en la colección Bravard (realizada**

tentativamente por Burmeister en 1885) sería dudosa por lo que hasta el momento no es posible confirmar esta asignación taxonómica.

"*No se ha encontrado en su colección ningún hueso ó diente con ese nombre, y ningún objeto que exactamente cuadre con la descripción y las figuras de los dientes del género Theridomys*" Burmeister (1885: 109)

BURMEISTER, G. 1879. Description physique de la République Argentina d'après des observations personnelles et étragères. 3 (animaux vertébrés, 1: Mammifères vivants et éteins): vi+1-555. P. E. Coni, Buénos Ayres. **En este trabajo Burmeister considera que la tibia y rótula descriptas por Laurillard no son de un roedor sino que pertenecen a un Notoungulado del género *Nesodon*.**

GERVAIS, H. & F. AMEGHINO. 1880. Los mamíferos fósiles de la América del sud. Pps. xi + 1-225. F. Savy-Igon., París-Buenos Aires. **Los autores consideran que la tibia y rótula colectadas por Laurillard pertenecieron a un roedor emparentado con las vizcachas.**

AMEGHINO, F. 1883a. Sobre una colección de mamíferos fósiles del piso mesopotámico de la formación patagónica, recogidos en las barrancas del Paraná, por el profesor Pedro Scalabrini. Boletín de la Academia Nacional de Ciencias en Córdoba 5: 101–116. **Ameghino valida nuevamente la teoría de Laurillard de la existencia de roedores gigantes: "*Lo que hasta ahora se conocía de la fauna mamalógica de este horizonte (Piso Mesopotámico del Oligoceno inferior) se reduce a poca cosa: 2 mamíferos.....; un roedor gigantesco del Río Negro, poco menos enigmático, conocido con el nombre de Megamys*". En este trabajo no se cita o se describe ningún fósil de dinómido, Ameghino simplemente se refiere a la tibia y la rótula descriptas por Laurillard.**

AMEGHINO, F. 1883b. Sobre una nueva colección de mamíferos fósiles recogidos por el Profesor Scalabrini en las barrancas del Paraná. Boletín de la Academia Nacional de Ciencias en Córdoba 5: 257–306. **Ameghino por primera vez describe restos fósiles de dinómidos que serían los primeros conocidos**

para la ciencia (por lo menos hasta que se confirme si el *Theridomys americanus* de la colección Bravard es realmente *Potamarchus*); dichos materiales son descritos bajo la denominación de *Megamys patagoniensis* (tipo de *Eumegamys scalabrinianus*). En este trabajo también se crea la especie *Megamys laurillardi*.

AMEGHINO, F. 1885. Nuevos restos de mamíferos fósiles oligocenos recogidos por el profesor Pedro Scalabrini y pertenecientes al Museo Provincial de la Ciudad del Paraná. Boletín de la Academia Nacional de Ciencias en Córdoba 8: 5–207. **El autor describe nuevos restos de *Megamys patagoniensis* y crea la especie *Megamys depressidens*, *M. holmbergi*, *M? laevigatus* (que Ameghino pasa a *Tetrastylus laevigatus* en 1886), *M. racedi*. También afirma que *Megamys* pertenece a la familia de las vizcachas y describe un molar proveniente de la colección Bravard que sospecha puede ser el asignado a la especie *Theridomys americanus* por Bravard en su trabajo de 1858. Este molar es indudablemente de un dinómido perteneciente a la subfamilia Potamarchinae.**

BURMEISTER, G. 1885. Examen crítico de los mamíferos y reptiles fósiles denominados por D. Augusto Bravard y mencionados en su obra precedente. Anales del Museo Público, Buenos Aires, 3: 95–174. **Burmeister admite que estaba equivocado al pensar que la tibia y la rótula recogidas por D'Orbigny y descriptas por Laurillard eran de un *Nesodon* aceptando entonces la existencia de roedores gigantes; el autor dice también que la afinidad de *Megamys* con *Lagostomus* propuesta por Ameghino es correcta. También aclara que cambió de opinión cuando, en el año 1884, Ameghino le regaló un calco de la mandíbula de *Megamys patagoniensis*. Burmeister también describe la porción posterior de un cráneo (MACN 4007) y dice que antes él lo citó como *Anoplotherium* (un ungulado) o un taxón afín. El cráneo MACN 4007 fue donado al Museo de Bs As. el 1867 por D. M. D. Savoyat y procede de Paraná. En este trabajo Burmeister crea el género *Potamarchus* y considera que sería afín al coypo actual; este último fósil no viene de la colección de Bravard pero en un apéndice Burmeister describe fósiles que son de Paraná y que están en el Museo de**

Bs. As. y que sería una lástima no publicar ya que vendrán de la misma "Formación Terciaria" de la que proceden los fósiles de Bravard.

AMEGHINO, F. 1886. Contribuciones al conocimiento de los mamíferos fósiles de los terrenos terciarios antiguos del Paraná. Boletín de la Academia Nacional de Ciencias en Córdoba 9: 5–228. **Se da la diagnosis del género *Megamys* y se describen nuevos restos de varias especies ya descriptas de *Megamys.* Ameghino afirma también que el cráneo MACN 4007 podría ser asignado a *M. laurillardi* y no a *M. patagoniensis* como afirmó Burmeister. En este trabajo también se crean las especies *M. praependens*, *M. burmeisteri, Epiblema* con la especies *E. horrídula*, el género *Tetrastylus* con las espeies *T. laevigatus*, *T. diffisus*. También se invalida al género *Potamarchus* y se sostiene que *P. murinus* es en realidad *Megamys holmbergii.***

AMEGHINO, F. 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. Actas de la Academia Nacional de Ciencias 6: XXXII + 1–1027. Córdoba. **En este trabajo se realiza un recuento histórico y taxonómico de los fósiles de dinómidos conocidos hasta la fecha.**

ROVERETO, C. 1914. Los estratos araucanos y sus fósiles. Anales del Museo Nacional de Historia Natural de Buenos Aires 25: 1–247. **Se describen por primera vez cráneos completos de dinómidos fósiles (géneros *Telicomys* y *Tetrastylus*)**.

KRAGLIEVICH, L. 1926. Los grandes roedores terciarios de la Argentina y sus relaciones con ciertos géneros pleistocenos de las Antillas. Anales del Museo Nacional de Historia Natural 34:121-135. Buenos Aires.

Este es el trabajo de referencia sobre dinómidos fósiles; Kraglievich tiene en preparación una extensa monografía sobre el grupo pero los trabajos de autores como Matthew, Anthony y Miller sobre roedores gigantes de las Antillas lo motivan para publicar este adelanto. En este trabajo se demuestra que la tibia y rótula descriptas por Laurillard no pertenecen a un roedor y sí probablemente a un macrauquénido, por lo que

Kraglievich cambia la denominación genérica de todos los fósiles de roedores descritos bajo el nombre de *Megamys* (como por ejemplo *Megamys laurillardi*) por el de Eumegamys, creando la familia Eumegamyidae. Se crea el género *Phoberomys* sobre la base de la especie *Euphilus burmeisteri* de Ameghino (1886). Crea la familia Neoepiblemidae con los géneros *Neoepiblema* y *Dabbenea* –género este último creado en este trabajo-. Crea la familia Potamarchidae con los géneros *Potamarchus* y *Simplimus*. No comparte propuestas anteriores de incluir a roedores de las Antillas dentro de la familia Eumegamyidae.

KRAGLIEVICH, L. 1930. Descripción de un interesante roedor eumegámido descubierto en el Uruguay. *Gyriabrus teisseirei*, n. sp. Revista de la Sociedad de Amigos de la Arqueología 4: 219-224. **Kraglievich crea la subfamilia Gyriabrinae.**

KRAGLIEVICH, L. 1931. Cuatro notas paleontológicas (sobre Octomylodon aversus Amegh., Argyrolagus palemeri Amegnh., Tetrastylus montanus Amegh., y Muñizia paranensis n. gen. n. sp.). Physis, 10 (36): 242-266. Buenos Aires. **Crea la subfamilia Tetrastylinae y por primera vez se considera a *Dinomys* como integrante de los Eumegamyidae.**

KRAGLIEVICH, L. 1932. Diagnosis de nuevos géneros y especies de roedores cávidos y eumegámidos fósiles de la Argentina. Rectificación genérica de algunas especies conocidas y adiciones al conocimiento de otras. Anales de la Sociedad Científica Argentina, 114(4): 155-181; (5-6): 211-237. **El autor crea a la subfamila Eumegamyinae.**

KRAGLIEVICH, L. 1934. La antigüedad pliocena de las faunas de Monte Hermoso y Chapalmalal, deducidas de su comparación con las que les precedieron y sucedieron. Pps 17-133. El Siglo ilustrado, Montevideo. **En este trabajo póstumo por primera vez se afirma de manera explícita que los roedores gigantes de la familia Eumegamyidae tienen un representante viviente:** *Dinomys branickii*. **Pese a esta afirmación Kraglievich incluye a esta última**

especie en la familia Eumegamyidae sin percatarse que Dinomyidae tiene prioridad. También se crea la subfamilia Dinomyinae.

KRAGLIEVICH, L. 1940. Los roedores de la Familia Extinguida Neoepiblemidae. **Este trabajo es póstumo y se publicó tomando las notas y borradores que dejara inconclusos Kraglievich. Se detallan las características de los roedores incluidos dentro de esta familia.**

FIELDS, R. W. 1957. Hystricomorph rodents from the late Miocene of Colombia, South America. University of California Publications in Geological Sciences 32: 273-404. **En este trabajo se incluye de forma explícta a los Eumegamyidae dentro de la familia Dinomyidae y se considera a la famila Potamarchidae como un grupo dentro de los Dinomyidae. Pese a que comunmente se considera á este el trabajo en donde se afirma por primera vez que los grandes roedores fósiles "eumegamidos" tienen un representante viviente, este descubrimiento corresponde a Kraglievich (1931; 1934). También se realizan sinonimias en base a consideraciones sobre el desarrollo ontogenético.**

PASCUAL. R. 1967. Familia Dinomyidae. Pp. 123–127 in Paleontografía Bonaerense (A. V. Borrello, ed). Comisión de Investigación Científica, volumen 4 (vertebrata), La Plata. **Se dan diagnosis de las subfamilias Potamarchinae, Gyriabrinae y Eumegamyinae.**

MONES, A. 1981. Sinopsis sistemáticva y preliminar de la familia Dinomyidae (Mammalia: Rodentia: Caviomorpha). Anais 2° Congreso Latinoamericano de Paleontologia, 2: 605-619. Porto Alegre. **Se hace un recuento sobre las clasificaciones de la familia reconociendo 4 subfamilias (Potamarchinae, Gyriabrinae, Phoberomyinae y Dinomyinae). Se dan diagnosis de todas las subfamilias y las tribus y se presenta una lista taxonómica enumerando 28 géneros y 58 especies.**

MONES, A. 1986. Palaeovertebrata Sudamericana. Catálogo Sistemático de los Vertebrados Fósiles de América del Sur. Parte I. Lista preliminar y bibliografía. Courier Forschungsinstitut Senckenberg 82: 1-625. **Se realiza un listado sistemático de todos los taxones fósiles de Dinomyidae conocidos hasta la fecha.**

BOCQUENTIN-VILLANUEVA, J. & P. BONDESIO. 1987. Novedosos restos de Neoepiblemidae (Rodentia, Caviomorpha) del Mioceno de Venezuela. Inferencias paleoambientales. Boletín Informativo, Asociación Paleontológica Argentina, 16: 11. **Se demuestra que los restos conocidos de *Phoberomys* se corresponden con los molares superiores conocidos de *Dabbenea*; al establecerse esta identidad el género *Dabbenea* pasa a ser sinónimo de *Phoberomys* y los taxones incluidos en la subfamilia Phoberomyinae pasan a integrar la familia Neoepiblemidae.**

MONES, A. 1997. Estudios sobre la familia Dinomyidae, II. Aportes para una osteología comparada de *Dinomys branickii* Peters, 1873 (Mammalia: Rodentia). Comunicaciones Paleontológicas del Museo Nacional de Historia Natural de Montevideo 29: 1-40. **Se describe por primera vez la osteología de *Dinomys*.**

NASIF, N. 2009. Los Dinomyidae (Rodentia, Caviomorpha) del Mioceno superior del noroeste argentino. Su anatomía cráneo-dentaria, Tucumán: Facultad de Ciencias Naturales and Instituto Miguel Lillo, Universidad Nacional de Tucumán, Tesis de doctorado (inédita). **Por primera vez se realiza un análisis filogenético de la Familia Dinomyidae. Además se estudian numerosos fósiles y se efectúan reordenamientos sistemáticos y taxonómicos.**

NASIF, N.L. & ABDALA, F. 2015. Craniodental ontogeny of the pacarana *Dinomys branickii* Peters 1837 (Rodentia, Hystricognathi, Caviomorpha, Dinomyidae).

Journal of Mammalogy, **26**: 1224-1244. **Importante trabajo sobre el desarrollo onetogenético en el único dinómido viviente.**

NASIF, N.; CANDELA, A.M.; RASIA, L.; MADOZZO-JAÉN, M.C. & BONINI, R. 2013. Actualización del conocimiento de los roedores de la Mesopotamia Argentina: aspectos sistemáticos, evolutivos y paleobiogeográficos. In: D. Brandoni &J.I. Noriega (eds.) El Neógeno de la Mesopotamia Argentina. Asociación Paleontológica Argentina, Publicación Especial, Buenos Aires, p.153-169. **Se publican algunos de los resultados de la tesis de Nasif y se realizan consideraciones taxonómicas en relación al género *Tetrastylus*.**

RINDERKNECHT, A. & BLANCO, R.E. 2008. The largest fossil rodent. *Proceedings of the Royal Society of London*, **275**: 923-928. **Descripción del primer cráneo completo de un Eumegamyinae y del roedor más grande del mundo.**

RINDERKNECHT, A.; BOSTELMANN, E.& UBILLA, M. 2011. New genus of giant Dinomyidae (Rodentia: Hystricognathi: Caviomorpha) from the late Miocene of Uruguay. *Journal of Mammalogy*, **92**: 169-178. **Descripción de un nuevo género de Eumegamyinae y estudio de la región auditiva en dinómidos.**

BLANCO, R. E., RINDERKNECHT, A. & G. LECUONA. 2011. The bite force of the largest fossil rodent. *Lethaia*, 45: 157-163, figs 1-2, 3 tablas. **Primer estudio biomecánico sobre un integrante de la familia Dinomyidae.**

KERBER, L.; NEGRI, F.R.; RIBEIRO, A.M.; NASIF, N.; SOUZA-FILHO, J.P. & FERIGOLO, J. 2016. Tropical fossil caviomorph rodents from the southwestern brazilian Amazonia in the South American faunas: systematics, biochronology, and paleobiogeography. *Journal of Mammalian Evolution.*

DOI: 10.1007/s10914-016-9340-2. **Contribución al estudio de los dinómidos fósiles de Brazil.**

KERBER, L.; NEGRI, FR.; RIBEIRO, A.M.; VUCETICH, M.G. & SOUZA-FILHO, J.P. 2016. Late Miocene potamarchine rodents from southwestern Amazonia, Brazil: with description of new taxa. *Acta Paleontologica Polonica*, **6**: 191-203. **Análisis de potamarchinos fósiles con descripción de nuevos taxones.**

KERBER, L.; MAYER, E.L.; GOMES, A.C. & NASIF, N. 2018. On the morphological, taxonomic, and phylogenetic status of South American Quaternary dinomyid rodents (Rodentia: Dinomyidae). *PalZ*, DOI: 10.1007/s12542-018-0435-3. **Confirmación de la existencia de fósiles de dinómidos en el cuaternario, y descripción de una nueva especie del género *Tetrastylus*.**

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Primer artículo

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En este trabajo se realiza una puesta a punto del estado del conocimiento sobre los dinómidos fósiles. Esta tarea incluye aspectos históricos, taxonómicos, sistemáticos y morfológicos además de una lista bibliográfica básica sobre el grupo.

Consideramos esta tarea de suma importancia ya que el trabajo está escrito en inglés y en el mismo se resume mucha información hasta el momento publicada únicamente en castellano. La publicación en cuestión, incluye algunos de los capítulos de esta tesis, sobre todo las secciones de: “Los primeros hallazgos” y “Sistemática de la familia Dinomyidae”

6

History, taxonomy and palaeobiology of giant fossil rodents (Hystricognathi, Dinomyidae)

ANDRÉS RINDERKNECHT AND R. ERNESTO BLANCO

Introduction

Among the great diversity of the order Rodentia, the "New World Hystricognathi", or caviomorphs are a very characteristic group from the Neotropical region. This group, whose fossil record begins in the late Eocene (Antoine *et al.*, 2011), and is included in the infraorder Hystricognathi (Huchon and Douzery, 2001; Woods and Kilpatrick, 2005), comprises more than 50 genera in 13 families. One of the peculiarities of the extant caviomorphs is their wide range of size, between ~200 g and ~60 kg (Sánchez-Villagra *et al.*, 2003). The latter is the maximum body mass among extant rodents (Mones and Ojasti, 1986) and occurs in *Hydrochoerus hydrochaeris* (known colloquially as capybaras), considered the giant of the group. South America is also home of the pacarana, *Dinomys branickii*, a large, enigmatic caviomorph rodent that can be found in the rainforests of Brazil, Bolivia, Colombia, Ecuador and Peru (Figure 6.1). This is the only living member of the family Dinomyidae, which is notorious for its great past diversity (Frailey, 1986; Mones, 1986; Rinderknecht *et al.*, 2011).

With a body mass that varies from 10 kg to 15 kg (White and Alberico, 1992), the pacarana is one of the biggest living rodents. However, dinomyid rodents used to be much larger. Many taxa from this family achieved extraordinary body sizes, especially those that belong to the extinct subfamily Eumegamyinae (Rinderknecht and Blanco, 2008). This subfamily contains the biggest rodents that ever existed (see Figures 6.2–6.4).

Recorded since the middle Miocene (but see Krapovickas and Nasif, 2011), the diversity of the Dinomyidae has been repeatedly corroborated with a great number of findings. Nowadays, approximately 60 extinct species are known, all of them distributed within South America (Mones, 1986; Rinderknecht and Blanco, 2008; Rinderknecht *et al.*, 2011). In this chapter we summarize the principal aspects of the history, anatomy, systematics and taxonomy of these enigmatic rodents. All texts shown in square brackets and italics are translations from Spanish.

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Figure 6.1 Map of South America showing the approximate current distribution of *Dinomys branickii* (black) and the locations (points) with a fossil record of the Dinomyidae. Modified from Rinderknecht *et al.* (2011).

First findings

The finding of the first fossils of the Dinomyidae family is without a doubt one of the most peculiar events in the history of South American paleontology. Between 1827 and 1828, the French naturalist Alcides D'Orbigny collected in the "Ensenada de Ross", south of the Río Negro province (Argentina), a tibia and a patella of a fossil mammal whose dimensions seemed to be comparable to those of a horse. These fossils were later described by the French palaeontologist Charles Léopold Laurillard and

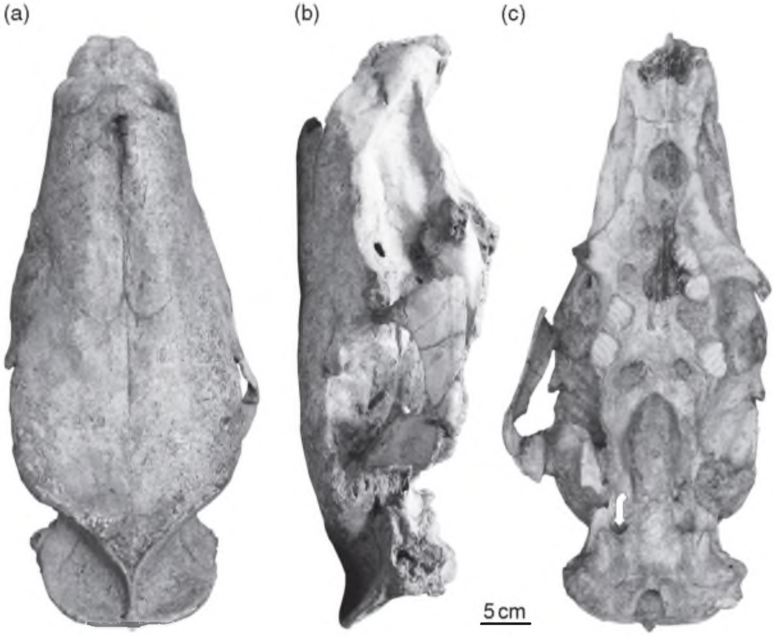

Figure 6.2 Skull of †*Josephoartigasia monesi* (holotype) in (a) dorsal, (b) lateral and (c) ventral views. White arrow shows the location of right pretympanic fossa.

published in the work of D'Orbigny about his trip to South America (see Laurillard in D'Orbigny, 1848). Owing to their similarities to the bones of the viscachas (Chinchillidae), these bones were identified as belonging to a giant rodent. This is how Laurillard created the genus †*Megamys* (with the type species †*Megamys patagoniensis*), beginning a controversy that would last almost a century. The size of these materials, added to the fact that only two postcranial bones were known, made it hard for some scientists to accept the assignation of those fossils to a rodent. The paleontologist and zoologist Germán Burmeister was the main antagonist to Laurillard's conclusions. He asserted that those fossils had to belong to a notoungulate mammal of the †*Nesodon* genus (Burmeister, 1879), a proximal taxon to the genus †*Typotherium*, which shows some morphological similarities with rodents. This article (Burmeister, 1879) was followed by a reply made by Henri Gervais and Florentino Ameghino, the biggest scientific adversary of Burmeister (see Gervais and Ameghino, 1880; Ameghino, 1883a). Notwithstanding Burmeister's interpretation, they considered Laurillard's characterization as correct and referred to the genus †*Megamys* as a giant rodent belonging to the extinct Argentinian fauna.

The apparent resolution of this debate would begin a few years later along with some remarkable findings from Parana. In the second half of the nineteenth century, the Parana region would become the object of a cultural endeavour from the Argentinean government, one of whose main achievements was the creation of the "Escuela Normal del Paraná". One of its members was Professor Pedro Scalabrini. This researcher started the task of collecting fossils from the ravines near the Paraná River area, beginning a

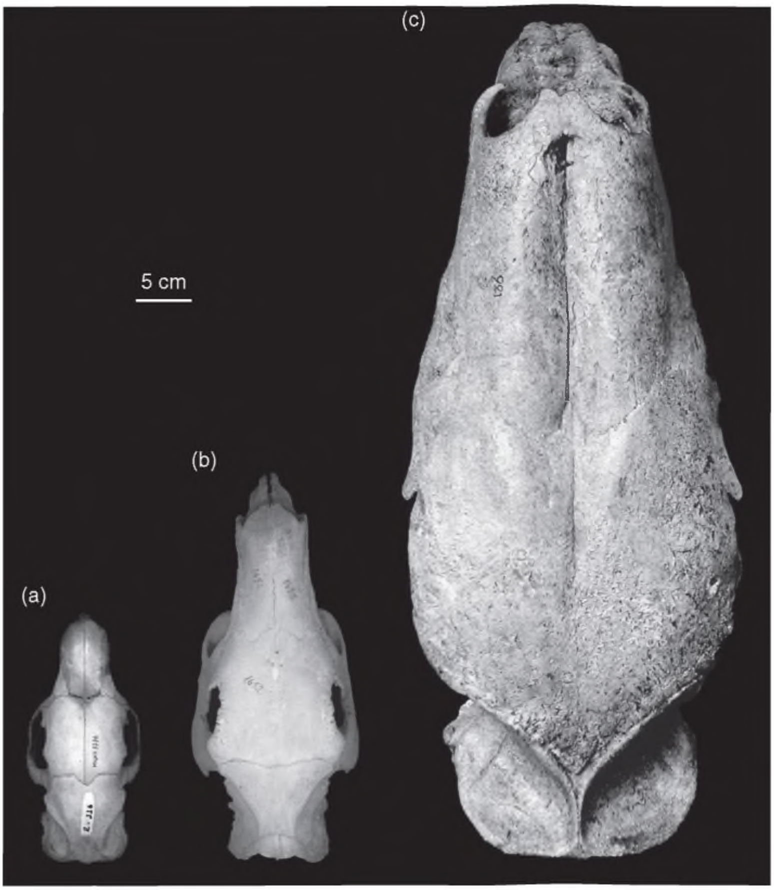

Figure 6.3 Dorsal views of the skulls of (a) *Dinomys branickii*, (b) *Hydrochoerus hydrochaeris*, and (c) †*Josephoartigasia monesi* (holotype). Modified from Rinderknecht and Blanco (2008).

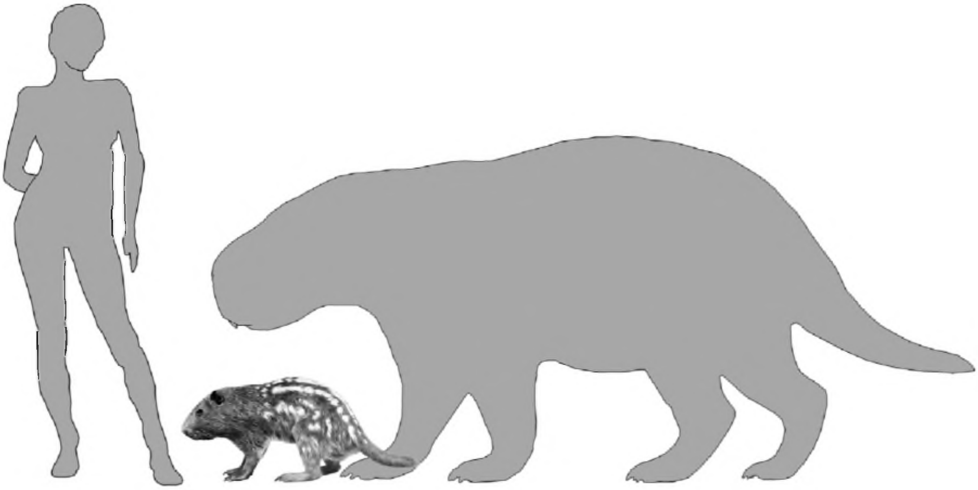

Figure 6.4 Palaeobiological reconstruction of †*Josephoartigasia monesi* (right), in comparison with *Dinomys branickii* (centre) and a human (left).

small collection whose most important pieces would be sent to Buenos Aires for further studies by Ameghino (see Ameghino, 1883a). After Ameghino finished analysing the first shipment of fossils, Scalabrini sent him a second shipment, which included the anterior portion of mandibular ramus and three isolated teeth of a giant rodent. These latter fossils were to be assigned by Ameghino to the species †*Megamys patagoniensis* (Ameghino, 1883b), becoming proof of the existence of fossil rodents in Argentina whose size was enormous in comparison to any other rodent known at that date. This article would put an end to the controversy generated by those fossils described by Laurillard.

In the quoted article, Ameghino (1883b) also described the fragment of a left mandibular ramus which led to the designation of the species †*Megamys laurillardi*. After this finding, Ameghino sent a cast of one jaw of a giant rodent to Burmeister. On receipt of these findings, the German palaeontologist had to recognize his error: ['*My conjecture was undoubtedly wrong; the animal called* Megamys *is, in fact, not only a giant rodent but also the rodent most similar to the viscacha, although its size is overwhelming: almost as big as a small cow or a donkey.*'] (Burmeister, 1885).

In his article, Burmeister also described a posterior portion of the skull of a dinomyid rodent donated in 1876 to the Museo Argentino de Ciencias Naturales (former Museo Público de Buenos Aires), also from the Paraná River. Burmeister made some remarkable observations on this material (MACN 4007), especially in reference to the conformation of the occipital region. Although Burmeister recognized his mistake, he was not comfortable with Ameghino's attitude and he showed that in his article; the last pages of his bibliography consist of a series of rough criticisms to the scientific performance of the latter palaeontologist (Burmeister, 1885). A year later, Ameghino responded to these criticisms made by Burmeister, especially those referring to his tendency to dedicate fossil specimens to his ['. . . *many personal friends* . . .'] (Burmeister, 1885). In this work, Ameghino (1886) described numerous fossils of giant rodents, among which a mandibular ramus was of special interest, as it was considered as belonging to the biggest rodent ever found. The name Ameghino chose for this taxon was †*Megamys burmeisteri*.

After the debate concerning the existence of these rodents was resolved, the description of species and study of their anatomic peculiarities continued (Ameghino, 1889, 1891a, b; Rovereto, 1914). Nevertheless, the discussion over the correct assignation of the materials collected by D'Orbigny in the Ensenada de Ross would be resumed in the year 1926 by the paleontologist Lucas Kraglievich, with surprising results. Almost 80 years after Laurillard's finding of the giant †*Megamys*, Kraglievich proved that neither the tibia nor the patella corresponded to any kind of rodent, but to an ungulate mammal, possibly from the Macraucheniidae family (Kraglievich, 1926). Therefore, almost a century after the first report of giant rodent fossils in South America, it would be demonstrated that these findings did not belong to a rodent after all; nevertheless, due to an extraordinary coincidence, the fossils described later by Ameghino (1883b) and used by him to show the apparent confusion of Burmeister did indeed belong to a giant rodent. This is why Kraglievich (1926) proposed to change the name of all the fossils published by Ameghino under the generic denomination †*Megamys* (†*Megamys* is an ungulate mammal) for the term †*Eumegamys*. Accordingly, all the giant rodents included in the family "Viscaccidae" are transferred to the families "Eumegamyidae" (see Kraglievich, 1926) and Neoepiblemidae.This is also the article that establishes the general criteria for the classification of the Dinomyidae family, criteria that would remain until the present, despite the fact that Kraglievich did not recognize the existence of the Dinomyidae family, which he called as Eumegamyidae.

Systematics of the Dinomyidae family

Since 1926, significant advances have been made in the identification of the fossil dinomyids recorded throughout much of South America. They comprise approximately 60 described species (see Mones, 1986). Despite this great diversity, palaeoecological studies of this group remain scarce and there still is not a consensus regarding the systematics of the family (see Rinderknecht *et al.*, 2011; Blanco *et al.*, 2011).

As we have already seen, the first true dinomyid fossils are isolated teeth and a mandible fragment described by Ameghino (1883b) under the wrong name "†*Megamys patagoniensis*". From the late nineteenth century, and until 1926, all researchers considered the giant fossil dinomyids as a group of the Chinchillidae (*antea* Viscaccidae) family (Ameghino, 1889). The criteria of the time was to group all the bigger-size rodents together and leave most of the small ones out; such is the case of the Potamarchinae (today considered a subfamily of Dinomyidae), which were either considered as a single family (Potamarchidae Kraglievich, 1926) or as relatives of the Myocastoridae (Burmeister, 1885). Detailed studies concerning the systematics of dinomyids began in 1926 with the article by Kraglievich. In his work, Kraglievich proposed the families Eumegamyidae (including the subfamily Phoberomyinae), Neoepiblemidae and Potamarchidae. This study also established the separation at familial level between these three groups and the gigantic fossil rodents found in the Antilles islands (Kraglievich, 1926).

Kraglievich (1930) described new dinomyid fossil fragments and named (inside the Eumegamyidae) the subfamily Gyriabrinae, which would be joined by the subfamilies Tetrastylinae (Kraglievich, 1931), Eumegamyinae (Kraglievich, 1932), Phoberomyinae (Kraglievich, 1926), and Dinomyinae (Kraglievich, 1934). Despite the fact that Kraglievich always kept the designation Eumegamyidae as valid for the family known today as Dinomyidae, the remarkable finding that this group of fossil mammals has a living representative is also due to this Argentinean palaeontologist: ['*The subgroup of the tetrastilines, to which* Tetrastylus montanus *belongs, presented molars almost exactly formed as the extant genus* Dinomys *Peters; but, due to the fact that its cranium presented paracondyles, they have to be a separate subfamily from this animal*'] (Kraglievich, 1931). Thus, this article represents the first recognition in the scientific literature of dinomyids as a not fully extinct group; in fact, the only difference that Kraglievich identifies between *Dinomys* and †*Tetrastylus* (a fossil "Eumegamyidae" described by Ameghino in 1886) is the presence of paracondyles in the latter genus. Today, we know that

Dinomys also possesses paracondyles (see Mones, 1997) and thus, following Kralievich's criterion, should be included in the subfamily Tetrastylinae.

It seems curious how little emphasis Kraglievich gave to the great discovery of one living taxon related to the giant fossil rodents, and this is probably the reason why this finding is usually wrongly attributed to Robert W. Fields (see Fields, 1957; Bondesio, 1978). In a posthumous publication, Kraglievich (1934) again included the genus *Dinomys* among the Eumegamyidae, creating the Dinomyinae subfamily: [*'I think that the Potamarchidae family should be separate from the previous one. It encompasses the precursors of the Eumegamyidae family, which should be considered as valid, since the* Dinomys *Peters genus seems to belong to it.'*] (Kraglievich, 1934). The next author to focus in detail on the classification of dinomyids would be Robert W. Fields, who made an important series of taxonomic and systematic observations on this family in his work concerning fossil rodents from the Colombian Miocene (Fields, 1957). Fields asserts, in agreement with Kraglievich, that the families Eumegamyidae and Dinomyidae are synonyms. In this article, the family Potamarchidae is included as a subfamily of Dinomyidae (Potamarchinae). According to Fields' classification, the family Dinomyidae comprises three subfamilies: Potamarchinae, Eumegamyinae (which includes Tetrastylinae and Gyriabrinae, although these now have priority over Eumegamyinae), and Dinomyinae. There is no mention of the Phoberomyinae subfamily in Fields' work. The inclusion of the representatives of the subfamilies Tetrastylinae and Gyriabrinae in Eumegamyinae was not fully recognized in later research; Pascual (1967) recognizes Gyriabrinae as a valid subfamily but does not share with Fields (1957) the idea that Tetrastylinae is not a valid group (Fields transferred the genera †*Tetrastylus*, †*Telicomys* and *Dinomys* to the Eumegamyinae, although Tetrastylinae has nomenclatural priority). Mones (1981) recognizes four subfamilies inside the Dinomyidae (Table 6.1): Potamarchinae, Gyriabrinae, Dinomyinae (with the tribes Dinomyini and Eumegamyini) and Phoberomyinae (which would include the genera †*Eusigmomys* and †*Phoberomys*). Some years later, Bocquentin-Villanueva and Bondesio (1987) demonstrated that the presumed mandible fragments referred to †*Phoberomys* correspond to maxillae of †*Dabbenea*; thus, the genus †*Dabbenea* is a junior synonym for †*Phoberomys*, and taxa included in the subfamily Phoberomyinae become members of the Neoepiblemidae family (see Mones, 1989). Nowadays, most authors include at least two subfamilies in the Dinomyidae family: Potamarchinae and Eumegamyinae, while the other candidates (Gyriabrinae, Tetrastylinae and Dinomyinae) are on hold pending systematic revision. The last revision of the family (Rinderknecht *et al.*, 2011) recognized at least four subfamilies: Potamarchinae (including the oldest known representatives of the family, recorded with doubts from the middle Miocene, and to the early Pliocene); Gyriabrinae (late Miocene to late Pliocene); Tetrastylinae (late Miocene to late Pliocene); and Eumegamyinae (late Miocene to late Pliocene). The inclusion of the family Dinomyidae in the Chinchilloidea superfamily (a topic hotly debated during the twentieth century) has been strongly sustained by many molecular studies (see Huchon and Douzery, 2001; Blanga-Kanfi *et al.*, 2009).

Table 6.1. Summary of the main systematic schemes proposed for Dinomyidae.

Author	Family	Subfamilies
Ameghino (1883–1889)	Viscaccidae	Not recognized
Kraglievich (1926–1932)	Eumegamyidae	Tetrastylinae Eumegamyinae Gyriabrinae, Phoberomyinae
Fields (1957)	Dinomyidae	Eumegamyinae Potamarchinae Dinomyinae
Pascual (1967)	Dinomyidae	Eumegamyinae Potamarchinae Gyriabrinae Phoberomyinae Dinomyinae?
Mones (1981)	Dinomyidae	Potamarchinae Gyriabrinae Phoberomyinae Dinomyinae

Modern definition of Dinomyidae

So far, there has been no morphological diagnosis of the Dinomyidae that considers every subfamily and tribe included in the family, although there are some studies where general anatomical characteristics of the group, and even some of the subfamilies, are described (Miller and Gidley, 1918; Ellerman, 1940; Fields, 1957; Pascual, 1967; Mones, 1981, 1997). One of the most exhaustive characterizations of the Dinomyidae family is the one given by Fields (1957: 358). This first characterization of Dinomyidae was based on previous definitions (see Miller and Gidley, 1918; Ellerman, 1940), primarily from studies of the *Dinomys* genus; therefore, caution should be taken, as the great morphological diversity of the family registered in extinct forms was not considered (e.g. Fields does not mention the presence of paracondyles in Dinomyidae).

The first characterization of the Dinomyidae family that takes most of the taxonomic and systematic diversity of extinct and extant species into consideration was given by Pascual (1967). While this article does not define the Dinomyidae family, it does provide a diagnosis for many subfamilies and genera described. The diagnoses given by Pascual for the Potamarchinae and Gyriabrinae genera are based strictly on dental characteristics, while the characterization of Eumegamyinae also takes cranial morphological characteristics into account. Pascual does not recongnize the Tetrastylinae and considers taxa such as †*Tetrastylus* and †*Telicomys* to be in Eumegamyinae.

An improved diagnosis for the family was given by Mones (1981), who expanded Fields' (1957) diagnosis by adding some characteristics related to larger dinomyids. Subfamilial characterizations made by Mones (1981) were based mainly upon those given by Pascual (1967).

Osteological characteristics of Eumegamyinae

The Eumegamyinae subfamily includes the biggest known rodents and it is the subfamily (if we consider the Tetrastylinae as a group inside Eumegamyinae) that has the best preserved fossil record. Despite the fact that this group was created by Kraglievich (1932), the first explicit diagnosis of this subfamily was given by Pascual (1967): [*'Specialized rodents that include, along with the Hydrochoeridae, the biggest sizes known among rodents. Skulls with a morphology generally similar to that of* Lagostomus *among Chinchillidae: a flat superior surface, with great expansion of the frontal bones, presenting a transverse diameter bigger than or equal to the bimastoid breadth; a lateral expansion of the frontals that corresponds to internally immense sinuses, reaching the fronto-parietal suture, sometimes even outdistancing it; a braincase restricted superiorly by the extent of the parietals; parasagittal crests that give shape to a short sagittal crest, (. . .), delimiting a deep, though constrained, temporal fossa; an occipital very similar to that of* Lagostomus, *with a semicircular shape, almost flat and vertical, but with very externally spread exoccipital bones, not including the mastoid bones; transversal eminences located next to the occipital condyles, almost reaching the paraoccipital processes, limited superiorly by a deep pit, equipped with an accessory joint (paracondyle), which is unique among mammals; relatively swollen and kidney-shaped bullae; wide, horizontal basioccipital and basisphenoid; foramen lacerum posterius located in a deep retrotympanic fossa; foramen lacerum medium and eustachian tube located in a deep and wide pretympanic fossa; a bony palate, usually nearly flat, (. . .); two oral crests originating in the lower roots of the zygomatic process of the maxilla, spreading almost until the lingual border of the incisor alveoli; palatine foramina that extend in convergent grooves beyond the premolars, terminating in the incisive foramina; a diastema between incisors and premolars usually one and a half times the length of the whole cheek-teeth; lower anterior zygomatic root behind the back of the* P^4*. Lower jaw with coronid process absent, or diffusely represented by an inconspicuous roughness, located around the last molar; a very high condyle; a practically non-existent masseteric crest; masseteric fossa shallow, with an inflected lower border; incisors spread posteriorly reaching the back of the* m^3*, defining an internal flange, in a very prominent surface in comparison to the ascendant branch. Robust and triangular-sectioned incisors, generally equilateral; the uppers highly curved, with the base located just above the beginning of the anterior zygomatic root; lowers reaching the level of the rear surface of* m^3*. Uniformly-sectioned and constantly growing cheek-teeth, constituted by concentric, bent, transversal laminar lophs, whose convexities are toward the front in the upper teeth and the back in the lower teeth; junctures among lophs are variable in number among different genera, but the posterior lophs are always joined in the upper teeth, on the lingual side, and the anterior lophs are always joined in the lower teeth, via the buccal side; usually, the internal face of each superior cheek-tooth prism is thicker, as is the posterior on the inferiors; anterior lophs are wider in the upper cheek-teeth, and posterior lophs are wider in the lower teeth.'*].

This definition presents some anatomical terms, such as paracondyle, pretympanic fossa and retrotympanic fossa that led to confusion and misapplication among many authors (see Pascual, 1967; Mones, 1981). Even though some of these morphological attributes have been considered to be of great systematic importance since the late nineteenth century, these terms have not even been mentioned by many authors (e.g. Fields, 1957). Below, some of these morphological characteristics are explained, in order to dispel any confusion that might exist concerning the cranial morphology of Eumegamyinae.

What is a paracondyle?

Some mammals present extensions of the occipital condyles, but they are never developed as convex surfaces. Despite this fact, some authors have misnamed these kinds of structures "paracondyles" (see Gaudin and Wible, 2006). By definition then, a paracondyle has an articular convex surface that allows the articulation of the skull with the atlas. Dinomyids are the only mammals that possess this kind of articulation in their skull (Ameghino, 1916; Pascual, 1967), as convex elongations that articulate with the atlas next to the external side of each occipital condyle (Figure 6.5). These articular structures were first mentioned by Burmeister (1885) while describing the posterior portion of a Eumegamyinae cranium: [*'Those thick protuberances, which are joined by condyles, do not exist in the viscacha, and are a unique feature of* Megamys *(. . .)'*]. It is important to note that Burmeister misused the name †*Megamys* by referring to the skull of a dinomyid (see Kraglievich, 1926).

While Burmeister was the first author to mention the presence of occipital paracondyles in mammals, the peculiarity of these accessory articular structures would finally be discussed in Carlos Ameghino's work concerning a †*Tetrastylus* cranium (see Ameghino, 1916). This article was the first to propose hypotheses concerning the functionality of the paracondyles; according to Ameghino, these structures would be necessary to hold up a disproportionately large cranium. The peculiarity of paracondyles as unique structures among mammals has led to their use as one of the most important characteristics in the Dinomyidae intrafamilial classification.

As previously mentioned, Kraglievich (1931) misused paracondyles in his differentiation between Tetrastylinae and *Dinomys* (as he did not know that *Dinomys* has paracondyles), while Fields (1957) did not mention them and Pascual (1967) used them as a diagnostic element of the Eumegamyinae subfamily (which includes the Tetrastylinae according to Pascual). Subsequently, Mones (1981) considered them as a diagnostic element of the Dinomyinae subfamily (constituted by the Dinomyini and Eumegamyini tribes), becoming the first researcher who noticed the presence of these structures in the *Dinomys* genus. Posteriorly Mones (1997) described these structures in *Dinomys* and demonstrated that other groups of large-bodied rodents, such as Hydrochoeridae, "Heptaxodontidae" and Neoepiblemidae, do not have paracondyles.

Paracondyles are observed in all dinomyids that retain their occipital region (Rinderknecht *et al.*, 2011); the taxa in which the presence of these structures can be confirmed include: *Dinomys*, †*Tetrastylus*, †*Telicomys*, †*Eumegamysops*, †*Josephoartigasia*, †*Arazamys* and material assigned to †*Eumegamys* by Kraglievich (1926). Paracondyles are also present in the †*Drytomomys* genus (Potamarchinae), according to Fields' drawing of a cranium (Fields, 1957: 325) assigned to †*Olenopsis*. With regard to the presence of underdeveloped paracondyles in *Dinomys* (see Mones, 1997), our research shows that the degree of development of these structures is variable within the genus, ranging from taxa with very little development to taxa with a development similar to that observed in the †*Tetrastylus* genus. We have also analysed several juvenile *Dinomys* skulls which do not present paracondyles, and therefore we believe these structures are

Figure 6.5 Right occipital region (nucal plane, not to scale) of (a) *Lagostomus maximus*, (b) *Dinomys branickii*, (c) †*Eumegamysops praependens*. Abbreviations: oc, occipital condyle; pc, paracondyle. Modified from Rinderknecht *et al.* (2011).

only present on adult specimens. The presence of paracondyles in all dinomyid specimens (belonging to different subfamilies) that preserve their braincase suggests that the presence of paracondyles is a diagnostic feature of the Dinomyidae family (Rinderknecht *et al.*, 2011).

What is a pretympanic fossa?

In the basicranium of caviomorphs, right behind the hard palate and in front of the auditory bullae, there is a window limited by the alisphenoid, basisphenoid,

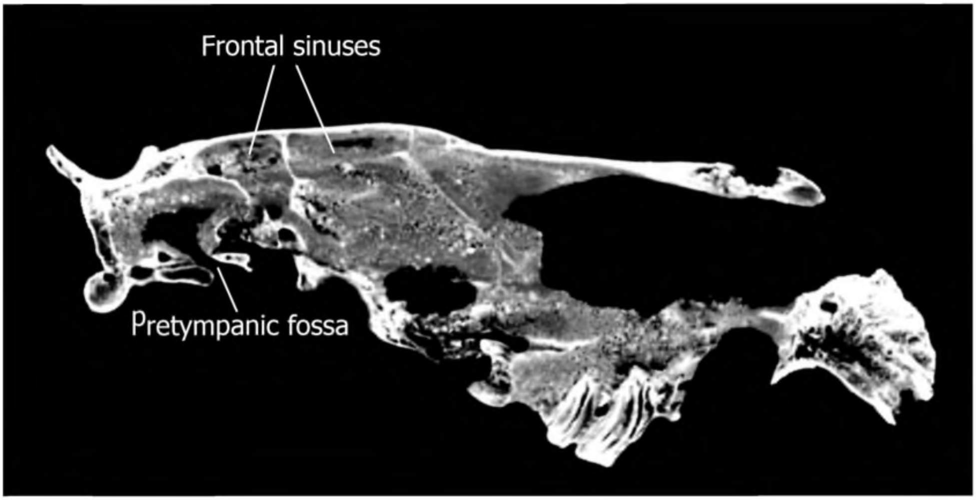

Figure 6.6 Sagittal skull tomographic slice of †*Josephoartigasia monesi* (holotype).

pterygoid and palatine bones. It is in this window that the eustachian tube and the *foramen lacerum medium* meet (Figure 6.2). In some dinomyids, a posterior extension of the alisphenoid (and probably also of the pterygoid) takes place, rising above the auditory bulla and transforming this window into a kind of deep pit in whose interior the eustachian tube and the *foramen lacerum medium* lie; this pit is known as the pretympanic fossa (Figure 6.6). These structures were first described by Fernández de Álvarez (1958) in his description of the †*Eumegamysops* genus. There is no mention of this structure in either Fields' (1957) or Frailey's (1986) publications; however, Pascual (1967) considers it to be a diagnostic characteristic of Eumegamyinae, and Mones (1981) associates it directly with the *Dinomys* genus by including it as a diagnostic characteristic of the Dinomyinae subfamily. Nonetheless, a detailed study of the cranial anatomy of *Dinomys* and †*Tetrastylus* (the only tetrastyline whose skull allows determination of the presence of a pretympanic fossa) suggests that neither of these taxa has a pretympanic fossa, thus this structure only seems to be found on larger dinomyids (Eumegamyinae).

What is a retrotympanic fossa?

According to Pascual (1967), the taxa included in the Eumegamyinae subfamily are characterized by the presence of the *foramen lacerum posterior* (= *foramen jugulare* = *foramen metoticum*) and the *foramen hypoglossi* (= *canalis n. hypoglossi*) inside a deep pit called the retrotympanic fossa. This pit is located immediately in front of the occipital condyle and behind the auditory bullae. The first to describe this structure was Fernández de Álvarez (1958), although he did not elaborate on its systematic utility. By including the retrotympanic fossa as a diagnostic character of Eumegamyinae, Pascual (1967) implied that both †*Tetrastylus* and †*Telicomys* presented it, while Mones (1981) indirectly recorded it in *Dinomys* by including it as a diagnostic characteristic of the Dinomyinae subfamily. Our studies show that *Dinomys*, †*Tetrastylus* and probably †*Telicomys* do not present a true retrotympanic fossa; therefore this characterization should be considered as diagnostic of Eumegamyinae as long as this category does not include the subfamily Tetrastylinae and the *Dinomys* genus (see Rinderknecht *et al.*, 2011).

In our opinion, the intrafamilial systematics of Dinomyidae are highly problematic. The fact that complete skulls are not known for two of the subfamilies (Potamarchinae and Gyriabrinae) makes robust anatomical and phylogenetic analyses not possible (see Rinderknecht *et al.*, 2011). Beyond this, our bibliographical analysis allows us to detect certain incongruences in the characterization of two Dinomyidae groups (or one according to each author): Tetrastylinae and Eumegamyinae. A morphological detailed analysis of a skull of †*Tetrastylus intermedius* (the only Tetrastylinae whose cranium allows such a detailed analysis) confirms that this species does not present either a pretympanic fossa or a retrotympanic fossa, opposite to the descriptions by Pascual (1967) and Mones (1981). Neither does it present other usual characteristics of large-sized Eumegamyinae such as the presence of a sagittal crest nor an optic foramen located very posteriorly in the skull. This makes the inclusion of Tetrastylinae among the Eumegamyinae subfamily currently unsupported. Additionally, there do not even seem to be differences separating †*Tetrastylus* from *Dinomys* at subfamilial level: contrasting with the assertion by Kraglievich (1931, 1934), *Dinomys* does present paracondyles, which are as well-developed as those of †*Tetrastylus*. This means that, if we follow the criteria established by the different authors to classify Dinomyidae, there are three clearly defined groups: Potamarchinae, Tetrastylinae (which includes *Dinomys*) and Eumegamyinae, pending analysis of Gyriabrinae monophyly.

What is an ectotympanic cavity?

All eumegamines in which the auditory region is preserved except †*Josephoartigasia* present a pit in front of the *meatus acusticus externus*, which Rinderknecht *et al.* (2011) named the ectotympanic cavity (Figure 6.7). The function of this structure is not yet known. The ectotympanic fossa has been wrongly interpreted as either a part of the *meatus acusticus externus* (Fernández de Álvarez, 1958) or an epitympanic recess that became exposed when the exterior surface was damaged (MacPhee, 2011).

Palaeobiology

The pacarana (*Dinomys branickii*) is a poorly studied forest-dwelling caviomorph (see Fields, 1957). The pacarana is also one of the largest extant rodents, with a body mass of approximately 15 kg (White and Alberico, 1992). Most rodents have body masses of less than one kg; the largest living rodent, the capybara (*Hydrochoerus*

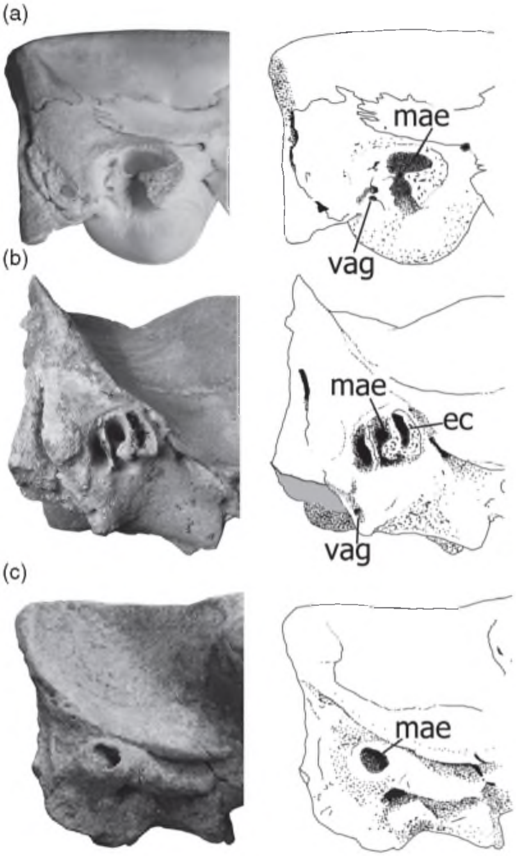

Figure 6.7 Right auditory region (not to scale) of (a) *Dinomys branickii*, (b) †*Eumegamysops praependens* and (c) †*Josephoartigasia monesi* (holotype). Abbreviations: ec, ectotympanic cavity, mae, *meatus acusticus externus*, vag, *vagina processus hyoidei*. Modified from Rinderknecht *et al.* (2011).

hydrochaeris), has a body mass of approximately 60 kg (Mones and Ojasti, 1986). A few studies have been published on pacarana behaviour and maintenance in captivity (Mohr, 1937; Crandall, 1964; Collins and Eisenberg, 1972). Females have four nipples, and give birth to one or two young at a time. The gestation period is estimated at 223–283 days (Collins and Eisenberg, 1972) but probably does not exceed 252 days (Meritt, 1984). Nest-building behaviour by females has not been observed. The newborns are precocious, and stay close to the mother. Mass at birth is between 570 and 660 g. *Dinomys* are thought to be nocturnal and captive animals are primarily active after dark (Collins and Eisenberg, 1972). Although most of their activities are terrestrial, pacaranas will also climb (Woods, 1984), using their long claws to aid them in ascending tree trunks. The pacarana has many morphological characteristics of a semi-arboreal animal: it has about equal musculature in the forelimbs and hindlimbs and a relatively small back extensor muscle, and its limb muscles are not developed for linear propulsive thrust. Its terrestrial walk is plantigrade with a side-to-side waddle (Grand and Eisenberg, 1982). Arboreality is reduced throughout ontogeny, and climbing persists only in a limited capacity in adults (Collins and Eisenberg, 1972).

Since the first discoveries of fossil dinomyids, the large size of these mammals was the characteristic that impressed researchers the most. Nevertheless, the fragmentary state of the giant dinomyid (Eumegamyinae) fossils did not allow detailed studies on body mass and paleobiology. This would finally change with the discovery of the cranium of †*Josephoartigasia monesi*, the only eumegamyine whose cranium is fully known (Rinderknecht and Blanco, 2008). Body mass is an important ecological variable because it is related to locomotory capabilities, reproductive strategies and other biological features. The body mass of †*J. monesi* was estimated in the first report of the species (Rinderknecht and Blanco, 2008) using allometric relationships between body masses and seven standard skull measurements from a sample of hystricognath rodents.

The average of all seven body mass estimates for †*J. monesi* gives 1211 kg with a standard deviation of 753 kg, when each of the estimates is given equal strength. The largest and smallest estimates of the mass of †*J. monesi* obtained are 2586 kg (from the extremely large width of the incisors) and 468 kg (from the very small zygomatic arches). Body mass estimation following Reynolds (2002) gives extreme values of 716 kg and 2250 kg (Rinderknecht and Blanco, 2008).The body mass estimation methods in Rinderknecht and Blanco (2008) were discussed by Millien (2008). This publication gave a technical contribution to the body mass study, concluding that †*J. monesi* does not fit a body mass estimation model for any extant rodents. Millien (2008) established that† *J. monesi* must have had a very elongated skull or a much reduced tooth row. In Rinderknecht and Blanco (2008) it was assumed that the tooth row was very short and this measurement was excluded from the body mass estimation. Exclusion of any cranial measurement in body mass estimation is problematic. However, prior studies of body mass proxies for the extant *Dinomys*, found that actual body mass was closely approximated by all cranial measurements except for tooth row length and total occlusal surface, both of which yielded a severe underestimate of body mass (Blanco, 2008). This suggests that tooth row size might be reduced relative to body size in Dinomyidae, which is consistent with the results obtained by Millien (2008) who found the lowest body mass value was predicted by tooth row length. A direct observation of the skull of *Dinomys* is enough to suggest that its tooth row is very small. But whether this is true for †*J. monesi* is unknown (Millien, 2008).

There are allometric effects of rostral length in rodents (Lessa and Patton, 1989, and references therein) and †*J. monesi* goes even beyond the predictions of these models (Millien, 2008). Some body mass estimates for †*J. monesi* obtained by Millien (2008) are smaller than those obtained by Rinderknecht and Blanco (2008), but the mean value of Millien (2008) is approximately 900 kg which is similar to the 1211 kg estimate of Rinderknecht and Blanco (2008). The fragments available for the cranium of the largest previously known rodent †*Phoberomys* (Family Neoepiblemidae) (Horovitz *et al.*, 2006) indicate a skull of approximately

Figure 6.8 Anatomical reconstruction of skull, jaw and main jaw adductor muscles of †*Josephoartigasia monesi*. Dark areas were not present in the original fossil. Modified from Blanco *et al.* (2011).

65% the size of that of †*Josephoartigasia*. We can thus conclude, with a high degree of confidence, that †*J. monesi* had a body mass larger than that of †*Phoberomys*, making it the largest rodent known to have existed.

Although several fossil species of Dinomyidae have been described (Kraglievich, 1926, 1930; Mones, 1986) our knowledge of anatomy and palaeobiology of these animals is far from satisfactory due to the lack of associated cranial and postcranial material. In fact, most specimens are found as isolated teeth and/or small fragments of the skull or mandibles (Mones, 1986). Thus, the locomotory capabilities can be only speculated upon until postcranial remains are discovered.

The complete skull of †*Josephoartigasia monesi* provides an oportunity to study the bite mechanics of this species. Bite force is an important aspect of mammal ecology and can shed light on the palaeobiology and ecological niche of some species (Christiansen and Meers, 2002; Vizcaíno and De Iuliis, 2003; Therrien, 2005a, b; Wroe *et al.*, 2005; Wroe, 2007). In rodents, the well-developed incisors and powerful bite forces generally have been related to very strenuous functions, such as durophagy, excavating burrows and processing wood, among others. The bite force of †*J. monesi* was estimated using three different methods: a biomechanical model involving a reconstruction of the jaw abductor muscles (Figure 6.8); allometric equations using body mass; and from the section modulus of incisors (Blanco *et al.*, 2011). A sensitivity analysis was conducted for each of these methods. The mean bite force obtained from the reconstructed model was 959 N with the variation in bite force obtained from the sensitivity analysis of 799–1199 N. The expected bite force calculated from estimated values of body mass ranged from 630 to 1515 N, with a value of 991 N for a body mass of 1000 kg. The expected bite force calculated from the section modulus of the incisors was 3214 N, a value much larger than all the other estimations (Blanco *et al.*, 2011).

The discrepancies in bite force estimates could be due to the fact that †*J. monesi* had a larger safety factor in comparison to that of other rodents. Safety factors can be larger in situations where the loads in the structure are more unpredictable or if the cost of failure is too large (Alexander, 1981). The former situation would imply that the incisors were subjected to highly variable forces, such as biting through heterogeneous materials with variable compositions. Another possibility is that bite force was achieved not only by closing of the jaw but also through skull movements, an action that produces more variable forces. A high cost of failure could be related to a strong dependency on the incisors in maintaining fitness, for example if they were necessary for obtaining food or some other valuable resource. However, as rodents' incisors grow continuously, it seems unlikely that the cost of failure would be extraordinarily large.

The large incisor strength could instead be a consequence of some structural difference between †*J. monesi* and the living rodents from which the predictive equation was constructed (Freeman and Lemen, 2008). In a series of studies on living fossorial rodents, incisor procumbency has been shown to be strongly related to two factors: body mass and tooth-digging behaviour (Lessa and Patton, 1989; Lessa and Stein, 1993). A study of scaling has shown that, if rostral length exhibits a strong positive allometry, as is the general tendency in mammals, incisor procumbency increases with body size (e.g. Lessa and Patton, 1989). Millien (2008) has proposed that, in †*J. monesi*, positive allometry of rostral length is stronger than usual for mammals. The procumbency of the incisors of †*J. monesi* can only be roughly estimated because the incisors are broken at the alveoli. However, it is clear from the rostral geometry and the curvature of the incisor roots that †*J. monesi* incisors are procumbent. Lessa and Patton (1989) considered the allometry of procumbency and predicted the extreme procumbency that is observed in giant rodents. As greater procumbency implies a wider angle between the incisor and the direction of the bite force, the moment of force is also larger. This produces larger bending stresses than would the same bite force in a smaller rodent. Then the incisor strength (strongly dependent on the section modulus) must be larger even at the same bite force value because a larger moment of force, produced by a larger lever arm, would increase the bending stress. It is expected that larger procumbency must produce an increase of section modulus in order to maintain stresses at a proper functional level. We therefore expect that extreme procumbency would produce an overestimation of bite force from incisor strength indicators, which may explain the discrepancies in the estimated bite force values between the incisor strength analysis and the other two methods.

The bite force of †*J. monesi* seems to be close to the predicted value obtained based on body size. This estimated bite force value is much larger than that calculated by similar methods for almost every extant carnivore (Wroe *et al.*, 2005; Christiansen, 2007). For large-bodied herbivores, bite aperture seems to be a more relevant value for fitness than bite force (Shipley *et al.*, 1999). The †*Josephoartigasia monesi* skull has a very long diastema; long diastemas are associated with large rostral lengths. The toothless diastema enables rodents to gnaw without ingesting unwanted material, as the lips can be drawn into the space behind the incisors, to close off the rear part of the mouth. A squirrel can gnaw through the shell of a nut but ingest nothing until it reaches the kernel, a beaver can fell a tree without filling its mouth with wood shavings, and a tooth-digging rodent can create a burrow without filling its mouth with sediments. This diastema also enables grazing mammals to eat long blades of grass (Alexander, 1990 and references therein). The relatively small size of the tooth row of †*Josephoartigasia monesi* in comparison to other skull measurements has been interpreted to suggest that this animal was not a good grazer and that it probably fed primarily on soft plants. Therefore, it is possible that †*J. monesi* used its diastema to process non-alimentary items as tooth-digging rodents and nut-eating squirrels do (Blanco, 2008).

We think that the large bite force of †*Josephoartigasia monesi* yields additional palaeobiological clues. Freeman and Lemen (2008) discussed possible reasons for animals to have very large bite forces, and the only possibilities that seem consistent with their statistical results are fossoriality and durophagy. Both of these habits could have been employed by †*J. monesi* as the long diastema also suggests. Fossoriality may be unlikely due to the large size of this animal, but †*J. monesi* could have used digging for other purposes, such as feeding on roots. The incisors were probably also the main defensive weapon against predators such as terror birds, if we consider that rodents are generally not well-suited for fast running and do not have natural weapons such as the horns or antlers possessed by other large herbivores. Many living rodents use their small size to avoid predators by hiding from them, but large rodents such as †*J. monesi* probably needed some other defensive strategy and a powerful incisor bite force, such as the one estimated here, could have been a deterrent. If the incisors were used against charging predators, the safety factor of the incisors may be attributable to extremely unpredictable loads. The long rostrum would have kept the eyes and other delicate parts of the head and neck far from the predator's weapons as the defensive bite was applied (Blanco *et al.*, 2011).

Procumbency due to large body size, tooth-digging behaviour and defence against predators are three hypotheses consistent with the strange association of large absolute bite force, excessive strength of the incisors and a long diastema in †*J. monesi* (Blanco *et al.*, 2011). Although, from our observations and arguments, it seems clear that the incisor diameter of †*J. monesi* could exceed the values expected for its overall skull size (similarly, the length of the upper molar series seems to be relatively short), further more-detailed studies of cranial and dentary allometries for this species in the context of caviomorphs must be made to verify the degree of validity of this observations.

Summary

The Dinomyidae is one of three known families of giant rodents from South America. Nowadays the family only includes the pacarana (*Dinomys branickii*), a quite peculiar but poorly studied "long headed" cursorial Amazonian caviomorph, considered among the largest living rodents with a body mass that approximates 15 kg.

Contrary to this impoverished present record, the past diversity of the group was notable, with an astonishing number of fossil genera and species reaching body sizes even larger than the pacarana. The biggest was the Pliocene †*Josephoartigasia monesi*, the largest rodent ever recorded. Until now, fossil members of the Dinomyidae have been described from almost every South American country, the collections of Argentina, Colombia, Venezuela and Uruguay being the most important ones. Despite this great diversity, it has been more than half a century since the last time detailed studies of fossil mammals were performed on this group. Fortunately, in recent years our research team has made significant progress related to the knowledge of the fossil dinomyids, in areas such as biomechanical analysis, morphological characterizations and taxonomic arrangements within the family. In this chapter we summarize the principal aspects of the history, anatomy, systematics and taxonomy of these enigmatic rodents.

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Segundo artículo

RINDERKNECHT, A., BOSTELMANN, E. & M. UBILLA. 2018. Making a giant rodent: cranial anatomy and ontogenetic development in the genus *Isostylomys* (Mammalia: Hystricognathi: Dinomyidae). *Journal of Systematic Palaeontology*, 16 (3): 245-261, 11 figs., 3 tablas.

Se trata del principal trabajo de la tesis. En el describimos dos notables fósiles de la subfamilia Eumegamyinae, pertenecientes al género *Isostylomys*. Ambos provenientes de la misma localidad y Formación geológica (Arazatí, Fm. Camacho). El primero de ellos es un gran cráneo asociado con su mandíbula. Se trata de un adulto de gran tamaño y constituye la primera asociación cráneo-mandibular reportada para la subfamilia, además de ser uno de los dos restos craneanos más completos conocidos para este grupo. El segundo fósil son dos ramas mandibulares con un calcáneo asociado, y es identificado como un ejemplar juvenil.

En base a la comparación entre estos dos ejemplares se sinonimizan todas las especies dentro del género, reconociendo como válida solamente la especie *Isostylomys laurillardi*. También se realiza un análisis sobre el crecimiento ontogenético dental, y se testean anteriores propuestas a ese respecto. Es de destacar la propuesta de no validar, o, al menos, de poner en duda la validez de la subfamilia Gyriabrinae, un grupo hasta ahora considerado como clave para comprender la evolución de los dinómidos.

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Making a giant rodent: cranial anatomy and ontogenetic development in the genus *Isostylomys* (Mammalia, Hystricognathi, Dinomyidae)

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South American giant fossil rodents represent a notable example of an extreme evolutionary trend towards size differentiation among caviomorph lineages. Although spectacular, fossil remains of these animals are uncommon and usually highly incomplete. We here describe fully grown adult and juvenile fossil specimens from the rodent family Dinomyidae Alston, 1876, collected from the same location, lithostratigraphical formation and fossiliferous horizon: the coast of the Río de la Plata of southern Uruguay in pelitic sediments assigned to the late Miocene Camacho Formation. The adult remains consist of an almost complete skull with partial jaw and represent the first published description of associated craneo-mandibular remains of a giant rodent within the subfamily Eumegamyinae. The juvenile specimen is the first to be recognized as such for the entire subfamily, and consists of a complete mandible and a right calcaneus. Based on the homologies observed in the configuration of the teeth, the new specimens are assigned to *Isostylomys laurillardi* Kraglievich, 1926, thus demonstrating that the general morphology of the teeth (including the binding pattern) of Eumegamyinae remained unchanged throughout most of their growth. The dental ontogeny of large-sized rodents casts doubt on the validity of the subfamily Gyriabrinae, which may be composed of juveniles of different taxa within other subfamilies of Dinomyidae.

Keywords: Dinomyidae; giant rodent; ontogeny; Miocene; Uruguay

Introduction

During most of the Cenozoic, the continental isolation of South America was one of the main reasons for the limited faunal exchange with other regions of the world. This isolation resulted in reduced and discontinuous migrations, and the promotion of local diversification in many endemic and 'new-arriving' lineages (Simpson 1940; Pascual *et al.* 1996). One of these groups includes the endemic mid-sized rodents of the infraorder Caviomorpha (Wood 1955; Huchon & Douzery 2001; Poux *et al.* 2006; Sallam *et al.* 2009, Patton *et al.* 2015), which represent an important part of the current diversity of rodents on the subcontinent (Woods 1982; Woods & Kilpatrick 2005; Solari *et al.* 2012). The first undisputed caviomorph record of the group comes from the middle Eocene deposits at Contamana, in the Peruvian Amazonia, from which tiny primitive forms closely related to some African Oligocene hystricognaths have been identified (Antoine *et al.* 2012). The group experienced an *in situ* early radiation, achieving a multiplicity of ecomorphotypes whose most remarkable aspects include the independent appearance (during the Miocene) of large-sized to gigantic forms in several lineages. One of these is the Family Dinomyidae, Alston 1876, which includes the largest rodent ever recorded, currently placed in the superfamily Chinchilloidea (Rinderknecht & Blanco 2008; Rinderknecht *et al.* 2011).

Although the fossil record of Dinomyidae is diverse and extensive (see Rinderknecht *et al.* 2011), it currently includes only the pacarana (*Dinomys branickii*), a cursorial and enigmatic Amazonian caviomorph considered to be among the largest living rodents (Collins & Eisenberg 1972; White & Alberico 1992; Nasif & Abdala 2015). Fossil Dinomyidae are putatively known from as early as the middle Miocene (Friasian: South American Land Mammal Age (SALMA)), showing a clear increase in abundance and diversity during the middle-to-early late Miocene (Laventan to Huayquerian SALMAs). Although the first described fossils of the family date back to the late 19th century (Ameghino 1883, 1885, 1886, 1889, 1891a, b; Burmeister 1885), the phylogeny of Dinomyidae has never been addressed or tested using a modern cladistics approach (but see Nasif 2009 for an unpublished phylogeny of the group). A brief review of the history and

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Figure 1. Unedited original portrait of the great Argentine palaeontologist Lucas Kraglievich (1886–1932) who, among many contributions to the field of South American vertebrate palaeontology, established the general criteria for the current systematic arrangement of Dinomyidae.

scientific knowledge of fossil dinomyds was provided by Rinderknecht & Blanco (2015).

Almost all current knowledge of Dinomyidae is based on the remarkable work done by the Argentine palaeontologist Lucas Kraglievich (Fig. 1), whose main contributions on the topic were reported at the beginning of the twentieth century. Kraglievich's investigations, published as detailed notes, communications and extended monographs, some posthumous, gave rise to the present systematic arrangement of the entire family, addressing diverse aspects of the anatomy and taxonomy of the Dinomyidae (Kraglievich 1926, 1930, 1932, 1934). His review of the group included almost all known specimens deposited in the collections of national history museums in both Argentina and Uruguay, leading to the description of new species, genera and subfamilies, and the fundamentals of systematic stability for more than the 60 fossil species currently recognized (Kraglievich 1926, 1930; Fernández de Álvarez 1947; Bondesio 1978; Mones 1986). Following this historical arrangement, later complemented and corrected by Fields (1957) and Pascual (1967), the family was subdivided into four or five subfamilies: Potamarchinae (including the oldest known representatives of the family, which extends from the middle Miocene to the late Pliocene); Gyriabrinae (late Miocene to late Pliocene, medium-sized forms); Dinomyinae (which includes only the extant pacarana, *Dinomys branickii*); Eumegamyinae (late Miocene to late Pliocene forms, including the largest representatives of the family); and Tetrastylinae (late Miocene to Pliocene, also medium-sized tetralophodont forms), which many authors consider to be a subgroup of the Eumegamyinae or Dinomyinae (Fields 1957). Although this systematic scheme has been sustained over the years with minimal changes, it is important to note that current knowledge of the anatomy of these animals is clearly insufficient. This is due to the lack of associated cranial and postcranial remains, with almost all of the named species being based on fragmentary remains, mostly consisting of isolated teeth and/or small fragments of skulls or mandibles (Mones 1986). Such an incomplete record limits any possibility of developing a comprehensive comparative analysis of the different lineages within Dinomyidae, hindering the understanding of the phyletic trajectory experienced by this notable group of rodents during their evolution.

Fortunately, in recent years, our research team has made significant progress on fossil dinomids, including the naming of a new genus and recognition of the potential of the auditive region for taxonomic characterization (Rinderknecht *et al.* 2011). In addition, we described *Josephoartigasia monesi* Rinderknecht & Blanco, 2008, the largest rodent ever recorded, providing a detailed palaeobiological investigation (Rinderknecht & Blanco 2008; Blanco *et al.* 2011; Cox *et al.* 2015). In this new contribution, we report the discovery of a new giant, nearly complete skull and mandible of a full-growth adult of the Miocene genus *Isostylomys* Kraglievich, 1926. This is the first description of an almost complete skull of this genus and its associated mandible. We also present the first known remains of an undisputable juvenile Eumegamyinae, composed of an exceptionally well-preserved mandible with complete dentition and the associated right calcaneum. This specimen is also assigned to the genus *Isostylomys*. All of the fossils were exhumed at the same locality and stratigraphical position at the base of the local exposures of the late Miocene Camacho Formation, and they represent some of the best-preserved remains of giant dinomids known to date. The new materials allow us to perform a detailed investigation of the dental morphology and its variation during growth in this genus. The different hypotheses proposed since the nineteenth century related to the dental ontogenetic development in these rodents are tested for the first time. Based on our results, we also review the taxonomic status of all of the species described within the genus *Isostylomys*, proposing a new taxonomic arrangement for the genus and extending our comments in relation to the systematic validity of one of the most enigmatic subfamilies – Gyriabrinae – within the dinomids.

Materials and methods

As a comparative framework oriented toward analysing the ontogenetic development of the Eumegamyinae, we studied specimens in different stages of growth from the genus *Dinomys* (the only living Dinomyidae), along with the largest living rodent, the capybara (*Hydrochoerus hydrochaeris*). The criteria selected for determining the age range/stage of the samples in the case of *Hydrochoerus hydrochaeris* were taken from Ojasti (1971), who related degree of cranial sutures with age. In *Dinomys*, ontogenetic stages were addressed through the direct observation of collection specimens, examination of high-quality photographs taken from materials deposited in scientific collections from Peru, Colombia, Argentina, England, France and Uruguay, and recently published descriptions (Nasif & Abdala 2015). The upper teeth are designated using capital letters (P4, M1–M3), and the lower teeth designated with lowercase letters (p4, m1–m3).

The traditional ontogenetic stages of eutherian mammals (prenatal, infant, juvenile, adult and senile) were deduced from the fusion of the epiphyses, sutures in the skeleton, the tooth eruption sequence and the degree of wear (Sánchez-Villagra 2010; Nasif & Abdala 2015). Because most fossil dinomids are only known from isolated teeth or fragmentary dentitions, any proposed model devoted to determining the age of these rodents must rely on the characteristics observed in the teeth. Unfortunately, these kinds of models are somewhat limited for extant caviomorph rodents with ever-growing hypselodont teeth, as many of them are born with permanent dentition that undergoes little change throughout their life. For these reasons, this study considers three stages of ontogenetic development: prenatal, juvenile, and full-growth adult stages.

All of the new fossil specimens reported here were collected by Luis R. Castiglioni and are housed in the palaeontological collection of the Museo Nacional de Historia Natural in Montevideo, Uruguay (**MNHN**). The examined specimens that were used in the comparisons and their institutional abbreviations are listed in the online Supplementary material.

Institutional abbreviations

Fossil and extant specimens utilized in this analysis belong to the following institutions. **NHMUK**: Natural History Museum, London, UK; **MACN**: Colección paleontológica del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; **MACN-A**: Colección Ameghino del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; **MACN-M**: Colección Mastozoológica del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; **MNHN**: Museo Nacional de Historia Natural, Montevideo, Uruguay; **MLP**: Museo de La Plata, La Plata, Argentina; **UDCA-UIFS:** Unidad de Investigación en Fauna Silvestre de la Universidad de Ciencias Aplicadas y Ambientales, Bogotá, Colombia; **UNMSM-MUSM**: Colección de Mastozooología del Museo de Historia Natural de la Universidad Nacional de San Marcos, Lima, Peru.

Geological setting

The fossil-bearing strata are located in south-western Uruguay (San José Department; 34° 34′ S, 56° 58′ W) in exposures located on the coastal cliffs and littoral platform of the Río de La Plata. Here, the lithostratigraphical units recognized from base to top are the Camacho (late Miocene), Raigón (Pliocene and Pleistocene) and Libertad (Pleistocene) formations (Bossi & Navarro 1991; Tófalo *et al.* 2009). The first two units yield many vertebrate fossils, including a variety of dinomids currently under study.

The Camacho Formation is the Uruguayan representation of an extended, late Miocene, eustatic event regionally known as the 'Paranean transgression' or 'Paranean Sea'. In the San José department, this includes facies related to the regressive phase, characterized as estuarine and/or paralic environments. Terrestrial and freshwater vertebrates in association with marine invertebrates and ichnofossils compose the fossil assemblage of the unit (Ubilla *et al.* 1990; Perea *et al.* 1996; Sprechmann *et al.* 2000; Verde 2002; Perea 2005). Sediments of the Camacho Formation are formed by greenish-grey, friable and medium compressed pelite that becomes greenish-brownish towards the top of the formation. The mammalian fossil assemblage includes marsupial carnivores, xenarthrans, hystricognath rodents, notoungulates, litopterns and cetaceans, showing affinities with the late Miocene Chasicoan and Huayquerian Ages/Stages of Argentina, especially with the stage informally known as the 'Mesopotamiense' (formerly considered as a Huayquerian age local fossil fauna) of Entre Ríos Province (Perea *et al.* 1994, 2013; Perea 2005; Cione and Tonni 2005; Brandoni 2013). ^{40}Sr/^{39}Sr dated levels of the Paraná Formation and its southern correlative, the Puerto Madryn Formation, give a late Miocene 9.5–10 Ma (Tortonian) age for the top of the 'Paranean Sea' in Argentina. Recently, Bostelmann & Rinderknecht (2010) reported the presence of *Hemihegetotherium achataleptum*, a common early late Miocene biostratigraphical indicator from these beds. In addition, Rinderknecht *et al.* (2011) described a new dinomid, *Arazamys castiglionii*, from outcrops of the San José Department.

The overlying Raigón Formation is considered fluviodeltaic (Bossi 1966) or fluvial (Tófalo *et al.* 2009), with swamp-related channel-filled and floodplain facies. Its lithology includes green-clayed, fine- and medium-grained white sands and conglomerate levels (Bossi 1966). It is considered to be of Pliocene age, but the occurrence of certain Ensenadan age mammals, such as *Catonyx tarijensis*, suggests that its deposition ended during the early Pleistocene (McDonald & Perea 2002). Fossil mammals, while less abundant than in the Camacho Formation, include ground sloths, cingulates, notoungulates, and Hydrochoerinae and Eumegamyinae rodents, particularly the largest known taxa (Francis & Mones 1966; Mones 1989; Rinderknecht & Blanco 2008). Large phorusrhacid (Tambussi *et al.* 1999) and anhingids (Rinderknecht & Noriega 2002) are notable fossil birds exhumed in this formation.

Systematic palaeontology

Order **Rodentia** Bowdich, 1821
Infraorder **Hystricognathi** Tullberg, 1899
Superfamily **Chinchilloidea** Kraglievich, 1940a
Family **Dinomyidae** Alston, 1876
Subfamily **Eumegamyinae** Kraglievich, 1932
Genus ***Isostylomys*** Kraglievich, 1926
Isostylomys laurillardi (Ameghino, 1883)
(Figs 2–8)

Holotype. MACN 5823, anterior portion of left mandible.

Synonyms. *Isostylomys ameghinoi* Kraglievich, 1932; *Isostylomys laevis* Rusconi, 1945; *Isostylomys intermedius* Mones & Castiglioni, 1979; and *Isostylomys magnus* Mones & Castiglioni, 1979.

Age. Late Miocene, Tortonian Age, ?Chasicoan/ ?Huayquerian SALMA.

Material. MNHN 2187, skull and mandible: an almost complete skull of an adult specimen, slightly distorted during diagenesis, lacking the posterior part of the braincase. Two dentaries of the same specimen (Figs 2–5). MNHN 2687, two dentaries and right calcaneum of a juvenile specimen (Figs 4–8).

Description. Skull and upper teeth (MNHN 2187). Gigantic size (Table 1); larger than any other known rodent except for *Josephoartigasia monesi*, which is slightly larger and more robust. As in all Eumegamyinae, the nasals are wide, with laterally expanded frontals. The lacrimal apophysis is robust, and the parasagital crest is strong and posteriorly convergent. Slender zygomatic arches compared with other caviomorph rodents like Ctenomyidae, Chinchillidae and Dasiproctidae, with the anteorbitarian bar posteriorly located beginning at M3 transverse plane. Both characters are also shared with *J. monesi*, the only one Eumegamyinae in which the zygomatic arch has been preserved. The foramen opticum is not visible laterally due to a marked posterior displacement, differing from all remaining caviomorph rodents, in which it is located anteriorly. This particular feature is also observed in both *J. monesi* and *Eumegamys paranensis*, leading us to considerer it as a new diagnostic character for the subfamily Eumegamyinae.

The incisors are well developed (Fig. 3), with tiny longitudinal ridges in the enamel face, which are difficult to appreciate at first glance. The upper cheek teeth present a typical prismatic shape, formed by lophs of dentine surrounded by a thin enamel lamina, wider on the anterior face of the tooth. A thin layer of cementum separates these lophs from each other, with the anterior lophs being more laterally expanded than the posterior ones (Fig. 4).

The P4 is pentalophodont, with the first three lophs free and constituting separate units, and the two posterior lophs joined by the lingual face (a diagnostic character of the genus *Isostylomys*). Both M2 and M3 are pentalophodont, with the first two lophs free and the three posterior lophs being joined at the lingual side. In the right M3, the fifth loph is composed of three small cylindrical enamel columns, more or less joined to each other. These characteristics were first considered by earlier scholars to represent a pathological condition or an atavism that naturally tended to be reduced during the ontogenetic process (or evolution) of the different species (Kraglievich 1940c). Another cylindrical, small, enamel column is present in the labial border of the third and fourth lophs on both M3.

Mandible and lower teeth (MNHN 2187). The two dentaries are preserved and fused with each other, lacking the ascending ramus and the angular process. The symphysis reaches the anterior border of m1. The notch for the insertion of the tendon of the masseter medialis pars infraorbitalis muscle (= deep masseter) is located in the external wall, under the transverse plane of m1 and m2. The left p4–m3 series is fully preserved and displays a similar, but inverted structure in relation to the arrangement and morphology of the upper teeth lophs, with the posterior lophs being more laterally developed than the anterior ones (Fig. 5). It is also apparent that the enamelled face of the upper lophs is wider on its anterior face, whereas in the lower teeth, the posterior face is the widest. In the upper teeth, the posterior lophs are lingually joined, but in the lower teeth, this condition is inverted, with the anterior lophs labially joined. Finally, in the upper teeth, the anterior face of each molar is concave, while it is convex in the lower teeth. Consequently, due to this symmetrical inversion, each lower tooth is similar to the respective upper tooth on the opposite side. Thus, the left p4 could be attached to the alveolus of the right P4 without causing any differences. This situation can occur in all of the teeth of the Eumegamyinae except in the last upper molar because M3 usually yields one more loph than m3. Additionally, M3 can present reduced enamel accessory columns in the posterior portion of the tooth. These

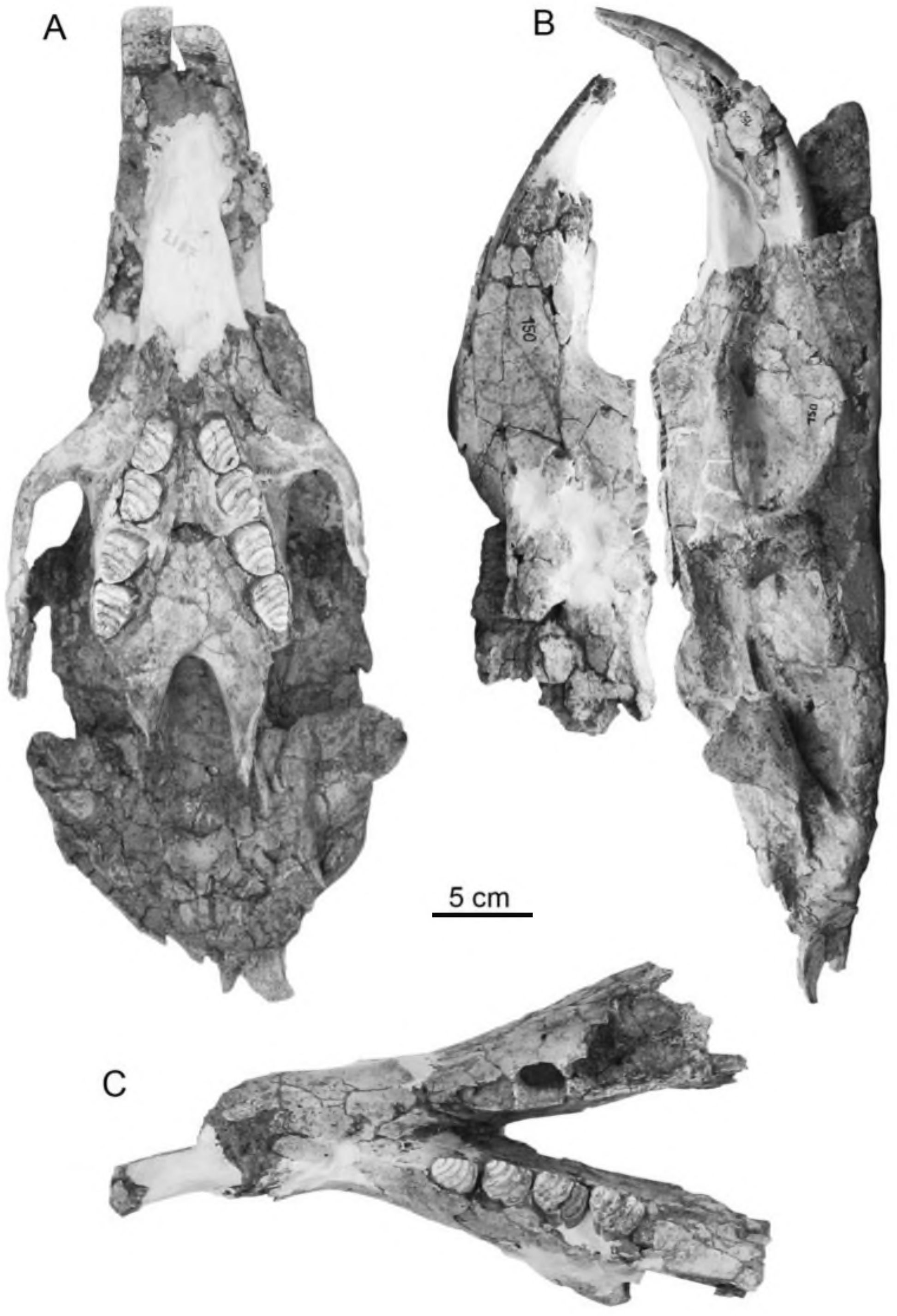

Figure 2. *Isostylomys laurillardi*, MNHN 2187. **A**, skull in ventral view; **B**, skull and mandible in left lateral view; **C**, mandible in occlusal view.

structures do not occur in m3, at least in the adult specimens. The m1 and m2 are pentalophodont, with the three first lophs labially joined and the two posterior lophs free. The m3 is also pentalophodont with the first three lophs labially joined and the two posterior lophs free. Both lower incisors were preserved, being similar to the upper ones. The conformation of each lower tooth, with five lophs, and the p4 with the two anterior lophs labially jointed, is a diagnostic feature of Isostylomys.

Juvenile mandible (MNHN 2687). The mandible includes both dentaries, which are nearly complete, exhibiting excellent preservation (Fig. 6). This material probably represents the most complete mandible ever recorded in a

Table 1. Dental measurements (in mm) of *Isostylomys laurillardi* (MNHN 2187).

	Mesiodistal length	Buccolingual width
Right P4	25.5	18.1
Right M1	25.2	20.0
Right M2	25.3	19.8
Right M3	25.3	19.0
Left P4	26.1	19.7
Left M1	25.1	21.3
Left M2	25.0	21.2
Left M3	27.6	20.2
Right I	—	24.8
Left I	—	24.3
Left p4	21.6	15.5
Left m1	24.1	21.3
Left m2	27.0	20.4
Left m3	26.7	22.0
Left i	—	23.3
Right i	25.1	23.2

fossil dinomyid. The most remarkable feature is its small size (half the size of the MNHN-2187 mandible, see Table 2) and the porosity of the bone surface, a condition commonly observed in juvenile rodents and mammals in general (see Ray 1964; Vucetich *et al.* 2005). The morphology of the mandible follows the overall pattern observed in Eumegamyinae, with: (1) a poorly developed horizontal crest; (2) the notch for the insertion of the tendon of the masseter medialis pars infraorbitalis muscle located under m1 and m2; (3) a low mandibular condyle; and (4) a barely visible reduced coronoid process, forming a small uneven surface on the posterolabial side at the m3 level.

The incisors are roughly similar to those of MNHN 2187. Except for the difference in size, each tooth of the p4–m3 series is equal to those described for the genus *Isostylomys*. This similarity extends to the pattern of fusion among the lophs and the proportions of the teeth. Both *rami* are unfused. An X-ray image allowed the observation that all teeth are permanent, with well-defined parallel margins (Fig. 7).

Juvenile calcaneum (MNHN 2687). The right calcaneum was collected in association with the juvenile mandible. Despite being almost complete (it lacks only the articular surface of the cuboid), it is not easy to describe, due to its low degree of ossification. Because of this, the articular surfaces are somewhat diffuse (Fig. 8). The bone is robust and massive, very similar to that observed in Dinomys, and presents an unfused tuber calcis separated from the rest of the bone, indicating a typical juvenile condition.

Figure 3. *Isostylomys laurillardi*, MNHN 2187. Right lower incisor.

Discussion

Dental development in the Eumegamyinae

The possibility for dinomids to change their dental morphology during ontogenetic development has been a topic of discussion for almost a century. The first researcher to address this issue in detail was Lucas Kraglievich, who warned about the likelihood that juveniles of the family

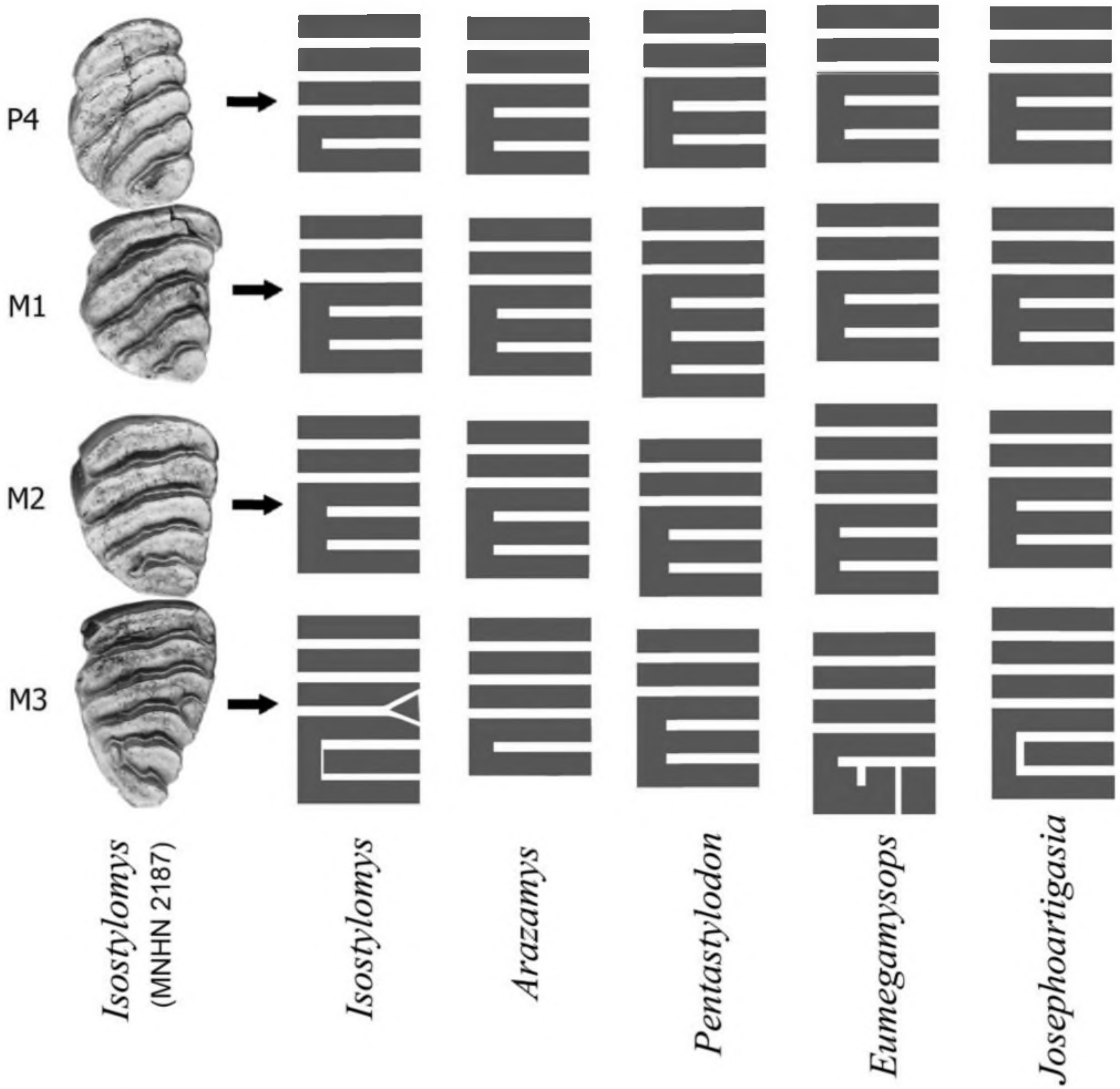

Figure 4. Left P4–M3 of *Isostylomys laurillardi*, MNHN 2187, in occlusal view, and schematics (not to scale) of upper cheek-tooth in different eumegamine genera.

'Eumegamyidae' (= Dinomyidae) might display a greater number of lophs in their teeth compared with full-growth adults (Kraglievich 1926). This statement was supported by observations of the juvenile molars of the genus *Phoberomys* (included within the dinomids at that time and currently located within the family Neoepiblemidae), which shows 'temporary enamel folds'. Wear of these temporary folds can lead to changes in the binding pattern between two lophs along the tooth, or even complete merger, forming just one loph. Thus, the occlusal surface of a tooth could present more lophs than the base, making reasonable to expect that putative juveniles could present teeth with more lophs than the adults.

Later, Kraglievich (1930) interpreted ontogenetic variations in the enamel folds of the teeth of Gyriabrinae but considered these changes to continue in the adults, presuming that members of this subfamily would experience changes in the structure of the teeth during much of their lifespan. Despite these observations, Kraglievich also indicated that Eumegamyinae would acquire the final conformation of the teeth very early in their ontogenetic development.

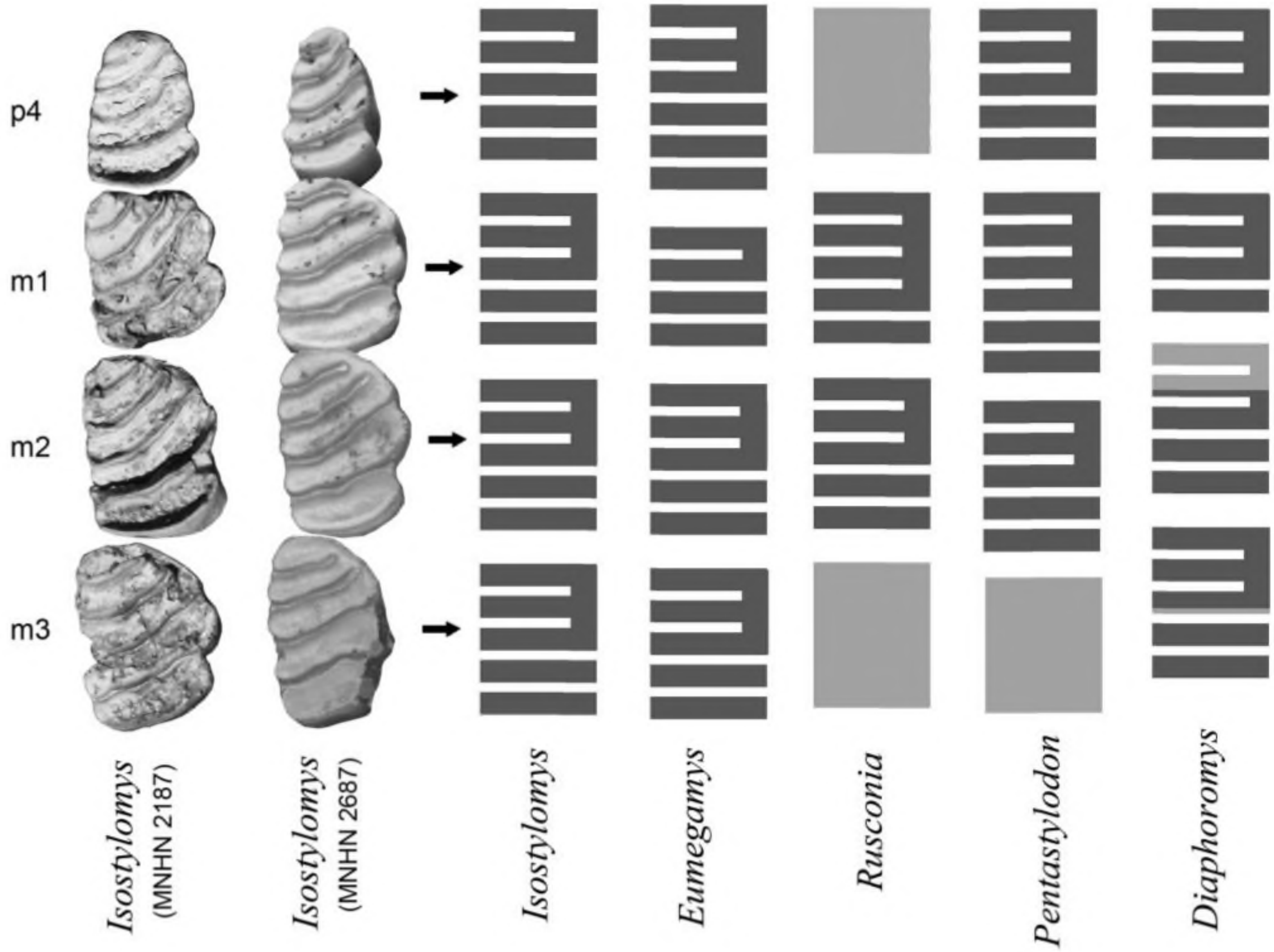

Figure 5. Right p4–m3 of *Isostylomys laurillardi*, MNHN 2187, reversed side, and MNHN 2687) in occlusal view, and schematics (not to scale) of upper cheek-tooth in different eumegamines.

The next palaeontologist who considered ontogenetic variation of the teeth of dinomids was Robert W. Fields, who produced an important series of observations on fossil Eumegamyinae and Potamarchinae in his work on the medium Miocene rodents from La Venta, Colombia (Fields 1957). In his opinion, Kraglievich's hypothesis was correct in relation to the greater number of lophs that are observable in juveniles compared to adults. Fields also suggested that each individual could experience differential degrees of wear, depending on the tooth position. This situation may arise because newly born dinomids retain a deciduous tooth (fourth premolar) and an un-erupted last molar. Hence, the wear on M1/m1 and M2/m2 begins before the wear on P4/p4 and M3/m3, making it reasonable to find juveniles that show the final conformation of M1/m1 and M2/m2, but still have a fourth premolar and third molar with accessory lophs. To support this explanation, Fields considered the holotype of *Eumegamys paranensis* (MLP 15-245), a partial small dentary that presents a p4 composed of six lophs, and interpreted it as a juvenile whose final dental conformation (relative to the number of lophs in the p4) had not yet been acquired. Based on these observations, Fields proposed formal synonymy of the vast majority of the taxa within the subfamily Eumegamyinae, including the genus *Isostylomys*, which he considered a junior synonym of *Eumegamys*.

Fields' proposals have not been taken into account by most subsequent researchers (see Mones & Castiglioni 1979; Mones 1981, 1986; Rinderknecht *et al.* 2011). However, MacPhee (2011) considered them valid based on subsuming *Eumegamysops* (one of the best-known dinomids) within *Eumegamys*. Our investigations show that Fields' proposal has inconsistencies related to the timing of eruption, number of lophs, and degree of wearing on the teeth, making it unreliable, at least for hypselodont Dinomyidae.

According to Fields, the p4 of the type material of *Eumegamys paranensis* shows six lophs (and not five, which is usual in most known Eumegamyinae) because it is expected to have belonged to a 'juvenile' individual in

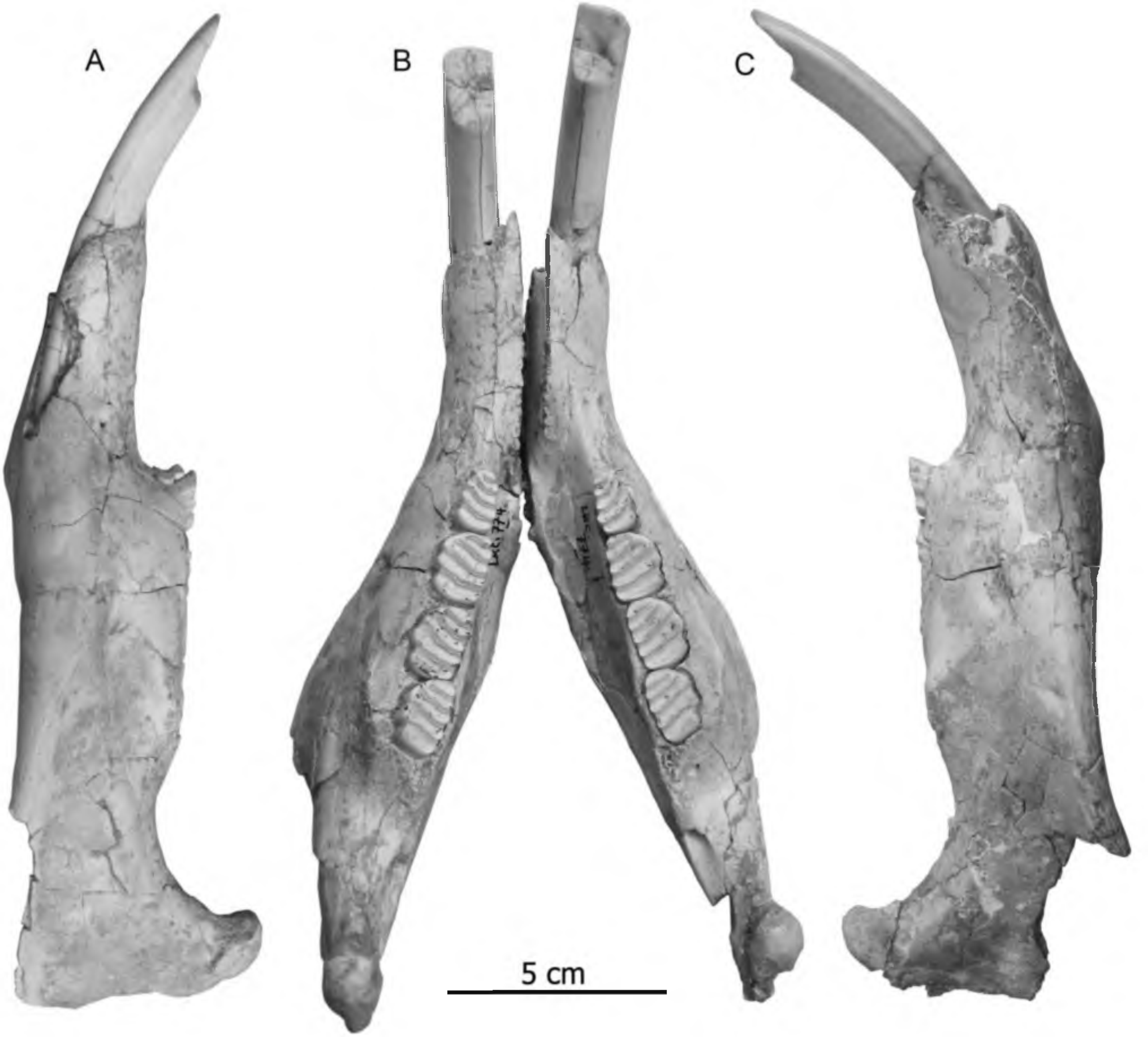

Figure 6. *Isostylomys laurillardi*, MNHN 2687. **A**, left dentary in lateral view; **B**, mandible in occlusal view; **C**, right dentary in lateral view.

Table 2. Dental measurements (in mm) of *Isostylomys laurillardi* (MNHN 2687).

	Mesiodistal length	Buccolingual width
Right p4	12.4	8.4
Right m1	15.0	12.0
Right m2	16.0	12.3
Right m3	15.9	10.9
Left p4	12.9	8.3
Left m1	14.5	11.4
Left m2	16.5	11.9
Left m3	15.7	10.8
Right i	10.4	11.8
Left i	10.2	11.5

which this tooth had recently erupted, without experiencing the loss of lophs that supposedly occurs during ontogenetic development. However, the m1 of the jaw has four lophs, and not five, as observed in all other eumegamines. Following Fields, if *Eumegamys paranensis* represents a juvenile individual, the mandible could not have presented an m1 with fewer lophs than the adult specimens assigned, for example, to *Isostylomys*. In summary, if the jaw of *Eumegamys paranensis* bears a p4 composed of six lophs due to the existence of an accessory loph, which Fields proposed as a characteristic of a less-worn tooth, it would also have been unlikely to lose one loph in m1, bearing in mind the pentalophodont condition observed in almost all eumegamyines.

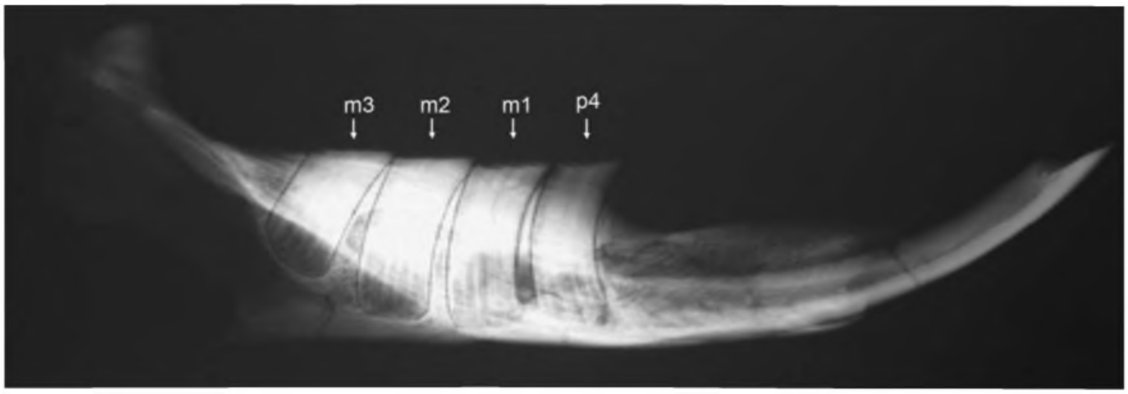

Figure 7. *Isostylomys laurillardi*, MNHN 2687. X-ray image of right dentary in lateral view.

It is important to note that some *Isostylomys* jaws described over a century ago are smaller than the type jaw of *Eumegamys paranensis* but show the same dental topology as the fully growth adults of the genus, with a p4 and m1 composed of five lophs. We consider that all of these contradictions challenge the proposed synonymy suggested by Fields. Moreover, recent studies on the anatomy of the auditory region in Eumegamyinae and its correlation with the dental morphology (Rinderknecht *et al.* 2011) also indicate a lack of support for this taxonomic scheme.

However, Fields' misconception does not mean that there may be named Eumegamyinae that are actually juvenile stages of other taxa. We have shown that, even accepting the thesis that juveniles of a referred taxon exhibited more lophs than the adults, *Eumegamys* cannot be a juvenile of *Isostylomys*. Our findings also call into question the notion that juveniles of Eumegamyinae have more lophs than the adults because the *Isostylomys* juvenile described here clearly shows the dental conformation of a full-growth adult. This implies that in the Eumegamyinae, the full dental conformation would be acquired very early in ontogenetic development, at least when great size differences exists between adults and juveniles.

There have been no previous reports of fossil Eumegamyinae as small as MNHN 2687, with the sole exception of MACN-A 5879, an isolated tooth assigned to *Isostylomys ameghinoi*, which shows a similar size compared with MNHN 2687. It is reasonable to consider that all of the specimens reported as Eumegamyinae in the scientific literature might then correspond to development stages within a single phyletic line. We indeed consider that all of the described specimens that currently constitute the subfamily Eumegamyinae may represent individuals that had attained the definitive condition of the tooth morphology at the time of their death, independent of their ontogenetic status (as adults or juveniles).

While there are few studies on the ontogenetic development of *Dinomys*, some published works (Ray 1964; Mones 1997; Nasif & Abdala, 2015) and specimens held in different collections allow us to speculate on the potential ontogenetic development of the fossil species, using it as an 'actualistic' model.

One remarkable feature of the mandibular ontogeny of the pacarana is related to the final configuration of the teeth, which are acquired when juveniles are almost the size of full-growth adults. When the jaws of a juvenile *Dinomys* reach 65–70% of their final size, m3 has not yet erupted, and dp4 is still present. MNHN 2187 is identical to MNHN 2687 but twice the size. Based on this size relationship, we can assume that *Dinomys* does not serve as a good analogue for the giant fossil forms. Another important feature to highlight is that *Dinomys* specimens do not experience loss of lophs during dental growth, with the sole exception of the m1, which may suffer, in some adult individuals, the incomplete fusion of the anteriormost two lophs. In newborn animals with recently erupted teeth, several unconnected enamel columns with rounded cusps make the occlusal surface. These structures merged to form the lophs, driven by progressive wear during the early ontogeny (Mones 1997; Nasif & Abdala 2015).

In contrast, the ontogenetic development of the capybara has been extensively studied (Kraglievich 1940b; Ojasti 1971; Vucetich *et al.* 2005; Aeschbach *et al.* 2016). Because it is the largest living rodent, we assume that dental growth in the capybara during its ontogeny could be of potential use as a model for comparisons with the Eumegamyinae. In the capybara, when the juveniles exhibit jaws with 60% of the size of the adult jaw, they acquire the final configuration of the dental topology (see Ray 1964). The maximum age reported for a capybara is approximately 12 years, and although the cranial configuration (and the rest of the skeleton) shows ontogenetic changes until approximately five years (Ojasti 1971), the jaw attains the general morphology of the adults (with the exception of the size and degree of ossification) between 17 and 19 months.

This situation implies that in the capybara, the general mandibular morphology forms very early in ontogenetic development, while a large difference in size remains between juveniles and adults. The same situation could

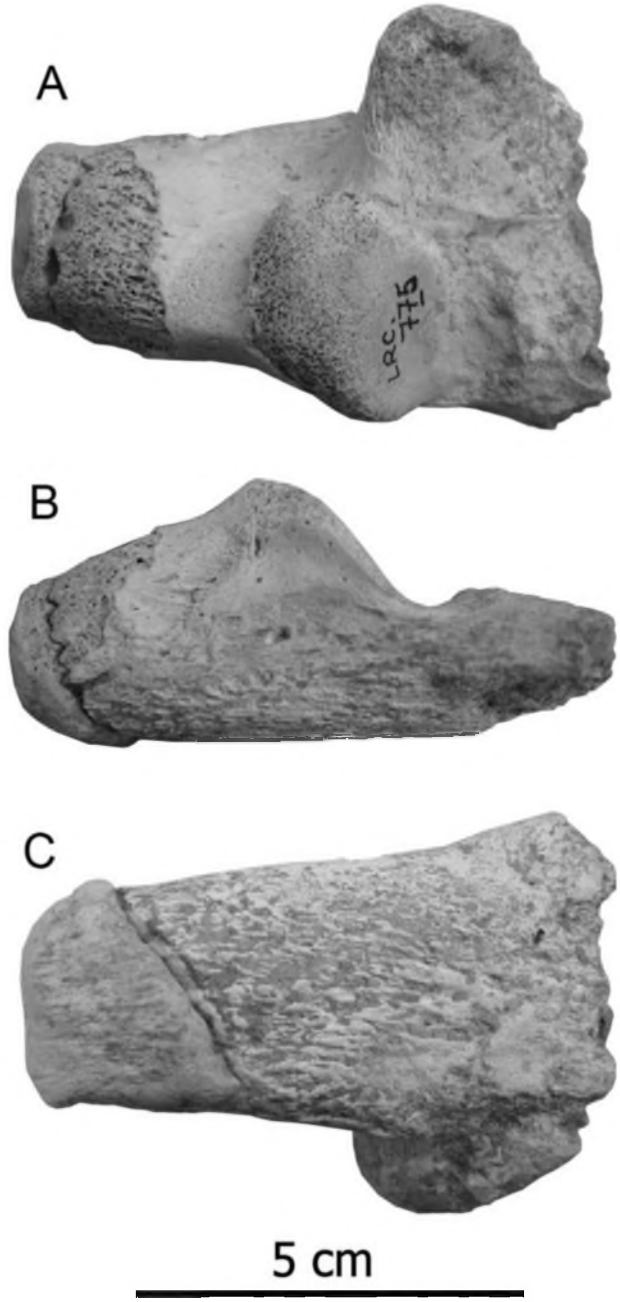

Figure 8. *Isostylomys laurillardi*, MNHN 2687. Right calcaneum in A, dorsal, B, external, and C, plantar views.

Table 3. Height of mandibles (in mm) in juvenile and adult specimens of *Isostylomys laurillardi* (MNHN 2187 and MNHN 2687).

Mandible height	MNHN 2187	MNHN 2687
At level of left p4	87	35.24
At level of left m3	62.9	36.8
At level of right p4	85	35.8
At level of right m3	—	37.8

have occurred in Eumegamyinae according to the characteristics observed in specimens MNHN 2687 and MNHN 2187.

Large body size may have been the main factor responsible for the mandibular growth of eumegamines during ontogeny, becoming more similar to *Hydrochoerus* than to *Dinomys*. We are aware that our assumptions are based on only two fossil specimens, and the discovery of more material will therefore be necessary to test these conclusions with greater confidence. Changes in mandibular proportions during ontogeny have been recorded in *Dinomys*, including alterations in the vertical orientation of the symphyseal region or the development of the angular process (Nasif & Abdala 2015). Nevertheless, the fragmentary nature of the Eumegamyinae fossil record makes it difficult to assess such changes in these fossil forms. We must also consider that size differences might exist within Eumegamyinae because of intraspecific variation and/or sexual dimorphism. The existence of significant differences in the adult sizes of large fossil rodents has been suggested previously (Biknevicius *et al.* 2003; Horovitz *et al.* 2006). Nevertheless, the differences between the two specimens of *Isostylomys* described herein (Table 3) surpass all intraspecific variations and/or sexual dimorphisms in size reported for any other rodent species (see MacPhee 1984; Patton *et al.* 2015). It is important to note the fact that even though an individual can acquire the final tooth shape very early in ontogenetic development, this does not mean that intraspecific variation may not exist in relation to the morphology of the teeth within Eumegamyinae. In fact, important intraspecific variations have been corroborated in adults *Dinomys*, especially with regard to degree of fusion in enamel columns and binding lophs patterns (see Nasif & Abdala 2015). These variations can be seen in the P4, M3 and p4.

On the species of the genus *Isostylomys*

The first report of the genus *Isostylomys* was based on a fragment of a jaw from Argentina, assigned by Ameghino (1883) to the species *Megamys laurillardi* (MACN-A 5823). Later, Kraglievich (1926) demonstrated that this genus (originally proposed by the naturalist Charles Léopold Laurillard) was erected on remains belonging to an ungulate mammal, and transferred all the fossil rodent material included by Ameghino in *Megamys* to the new genera *Eumegamys* (naming the species *Eumegamys paranensis* and *E. scalabrinianus*) and *Isostylomys* (recognizing one species, *Isostylomys laurillardi*).

Posteriorly, the species *Isotylomys ameghinoi* Kraglievich, 1932, *Isostylomys laevis* Rusconi, 1945, *Isostylomys intermedius* Mones & Castiglioni, 1979 and *Isostylomys magnus* Mones & Castiglioni, 1979 were proposed, all differentiated based exclusively on size.

Mones & Castiglioni (1979) did not recognize substantial differences between *Isostylomys laevis*, *I. ameghinoi* and *I. laurillardi* and therefore considered the first two species as synonyms of *I. laurillardi*. In their opinion, the genus *Isostylomys* was only composed of the species *I. laurillardi* (the smallest species), *I. intermedius* (named for an isolated tooth collected in Uruguay), and *I. magnus* (the largest species, also erected from isolated dental remains).

A particular case arises from the review of historical repositories. In the palaeontological collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" in Buenos Aires, one small isolated tooth (MACN 4708) is labelled as a new species of *Isostylomys*, although it was never formally published. This small ever-growing tooth is 1 cm long in the anteroposterior dimension and 3 cm tall. Five nearly horizontally projecting lophs form the occlusal surface of the tooth. The three anterior lophs are joined on the lingual side, and the labial sides remain free achieving the general pattern of *Isostylomys*. The first loph is the smallest and rounded, with a fragmented tip. The second loph is intermediate in size, with the labial side wider than the lingual side and both the first and third lophs being joined with narrow constrictions. The remaining two distal lophs are free, with the third being the most extended in the buccolingual (transverse) dimension. As is common in all eumegamines, all of the lophs are separated from each other by a thin layer of cement. There is no published record mentioning, or even announcing the existence of this proposed new species. Nevertheless, the adjoining hand-written label reads "(Type) 4708. *Isostylomys minimus* n.sp. Krag. (M) sup. der." and as such, it is recognized as a type specimen in the catalogue of the museum collection. The geographical origin of the specimen is the Barrancas del Río Paraná, Entre Ríos Province, Argentina, the same general locality for the majority of known records of eumegamyines (Nasif *et al.* 2013). Given the isolated nature of this tooth, almost certainly a juvenile, and the absence of adequate diagnostic characteristics, we consider it more appropriate to refer to this material as an undetermined Eumegamyinae.

Size differences, which are the only characteristic used to differentiate all the species within *Isostylomys*, are clearly inadequate for use as a specific characteristic, as *I. laurillardi* and *I. intermedius* are potentially juvenile specimens. Surprisingly, this consideration was never taken into account by previous researchers, probably because of a general belief that juvenile eumegamines should show differences in the number of lophs in relation to the adults. Our research demonstrates that the definitive lower dental morphology of the members of this subfamily is acquired early during ontogenetic development, and that *I. laurillardi*, which shows a remarkable difference in size from *I. magnus*, could indeed represent the same species.

Unfortunately, the meagre state of preservation of the type material of *Isostylomys laurillardi* (MACN-A 5823) does not allow an undisputed assignment regarding its adult or juvenile condition. However, a topotype of this species (MLP-15-247, consisting of a right mandibular ramus) shows the characteristic degree of ossification that suggests a juvenile condition similar to the one observed for MNHN 2687. Considering all this evidence, we propose the formal synonymy of the three present species within the genus – *I. laurillardi*, *I. intermedius* and *I. magnus* – which should be recognized uniquely as *Isostylomys laurillardi*.

On the validity of the subfamily Gyriabrinae

Previously, we concluded that all of the species described in the literature as eumegamines are individuals that had already attain the final configuration of their teeth. This does not mean that eumegamines whose dental configurations were not finally established at the time of death do not exist in the fossil record. However, if these fossils exist, they must have been erroneously placed in other groups.

The subfamily Gyriabrinae (Kraglievich 1930) has a biochron extending from the late Miocene to the late Pliocene and includes nine species assigned to the genera *Gyriabrus* and *Pseudosigmomys*. Gyriabrines are small-sized dinomids recorded in Argentina, Uruguay, Peru and possibly Colombia and Brazil (Paula Couto 1983; Mones 1986; Sant'Anna-Filho 1994). They have been classically considered as basal representatives in the transition to fully hypselodont forms. The subfamily includes all dinomids that have transitional enamel folds in the teeth as adults. According to Kraglievich (1930), these folds are evident on the occlusal surface but tend to disappear with wear, causing changes in the binding pattern and progressively reducing the number of lophs (Fig. 9). Young gyriabrines would therefore exhibit teeth with more lophs than the

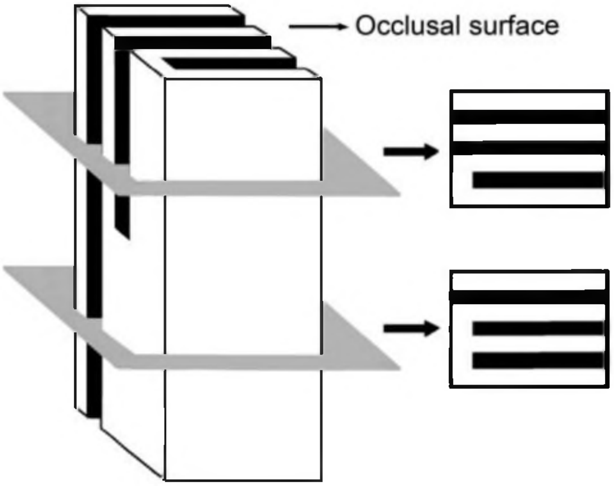

Figure 9. Schematic drawing of a Gyriabrinae tooth.

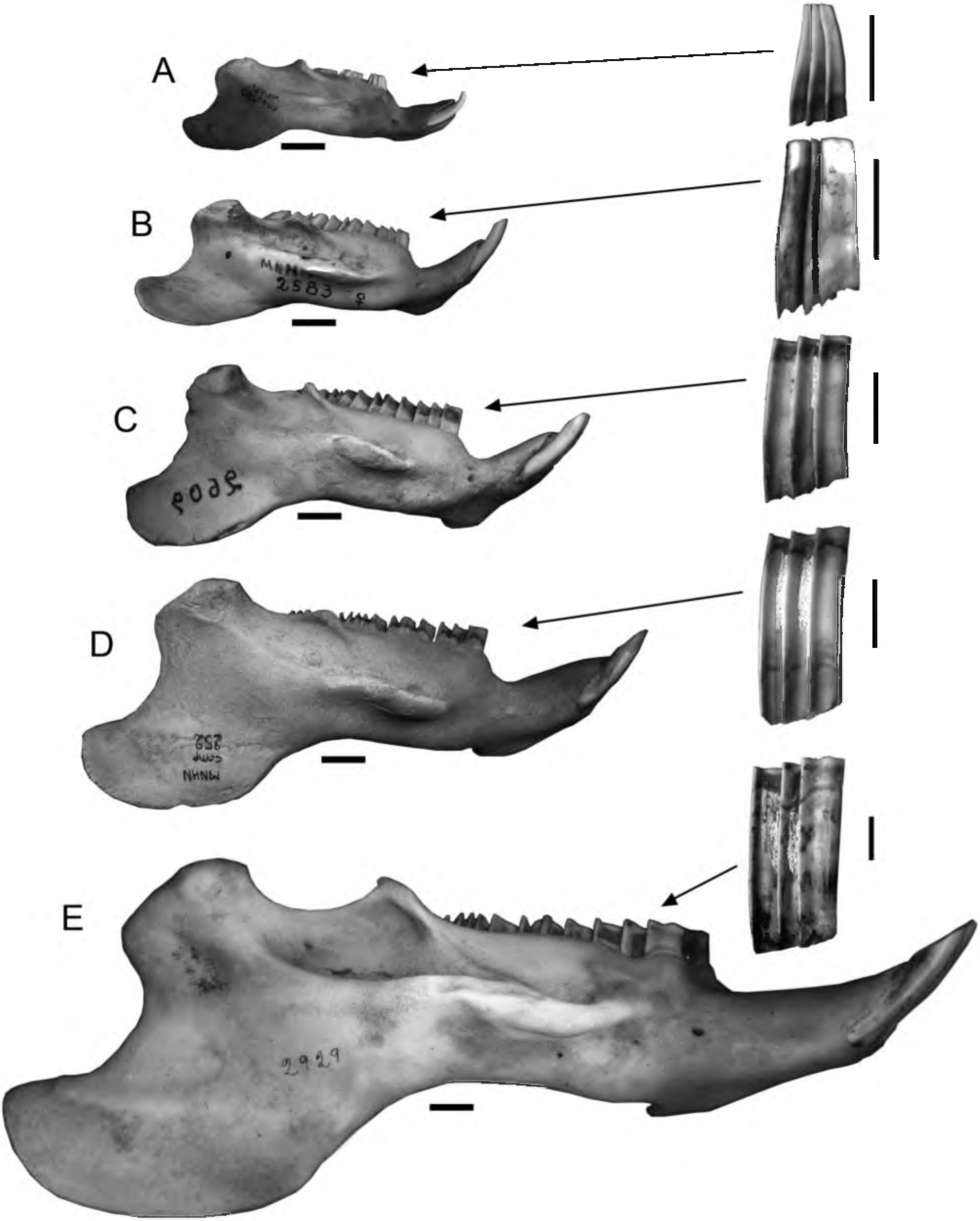

Figure 10. Right dentary of *Hydrochoerus hydrochaeris* and right p4 in different ontogenetic stages. **A**, MNHN 250, unborn specimen; **B**, MNHN 2583, nine days to seven months; **C**, MNHN 2609 (reversed side), seven to 10 months; **D**, MNHN 252 (reversed side), 18–21 months; **E**, MNHN 2929, specimen over four years old. Scale bars = 10 mm.

adults, whereas senile individuals would exhibit teeth with fewer lophs than the adults. The gyriabrines described thus far show a binding pattern of the lophs on the occlusal surface that is different from the one preserved at the base, but changes in the number of lophs along the tooth have only been recorded in the type material of *Gyriabrus glutinatus* (MACN-A 5881), consisting of a badly preserved isolated molar. Therefore, the claim that the gyriabrines showed a reduced number of lophs with wear is hypothetical for almost all known fossils assigned to the group.

It is within Gyriabrinae that the greatest morphological diversity of dental patterns in Dinomyidae is concentrated, although all of the fossils included in this subfamily are dramatically fragmentary and composed of only isolated teeth, fragments of jaws, and palates.

The fact that the morphology of a hypselodont tooth changed with wear (and therefore with the age of the animal) could indicate that the tooth belonged to a juvenile specimen. Kraglievich was aware of this observation, but in his opinion, the Gyriabrinae were not juveniles, but full-growth adults that exhibited morphological changes in their teeth throughout their life (the presumed main diagnostic feature of the subfamily). The argument put forth by the Argentine palaeontologist was that all Gyriabrinae teeth present an occlusal surface with the same width as the base, lacking the common 'cone' shape expected for juvenile hypselodont teeth (Kraglievich 1930, p. 222).

However, in accordance with Vucetich *et al.* (2005), our research shows that there are rodents that may exhibit parallel-sided teeth without completing their ontogenetic development. This occurs in the capybara, which bears cone-shaped teeth only during the early stages of its growth. A few months after birth, capybaras lose their cone-shaped teeth despite being much smaller than the adults (Fig. 10), while retaining morphological differences in the occlusal pattern of some of the teeth (Vucetich *et al.* 2005). This means that the largest living rodent passes through four stages during its ontogenetic dental development: a first stage with cone-shaped teeth, where the binding pattern of the lophs is not definitive; a second stage with parallel edges of the teeth, where the binding pattern of the lophs are still not definitive (the stage that potentially represents the Gyriabrinae); a third stage in which the teeth of the juveniles are indistinguishable from those of the adults except for their size (the stage of specimen MNHN 2687); and finally, the full-growth adult stage (Fig. 9). Following this, all the available evidence allows for an alternative hypothesis to Kraglievich's proposal that the Gyriabrinae represent adult animals. The question then arises of whether the subfamily in question can be maintained, as the only diagnostic feature proposed is precisely the existence of dental changes throughout much of the lifespan of the individuals. On the other hand, our observation shows that the vast majority of Gyriabrinae are almost indistinguishable (except for their small size and the presence of enamel folds) from other taxa allocated to different subfamilies of Dinomyidae. Gyriabrines would therefore not be juvenile specimens from a monophyletic group, as some taxa from this subfamily, such as *Gyriabrus teisseirei* (MNHN 1342), are remarkably similar to some members of Tetrastylinae (and, thus, *G. teisseirei* is likely a young specimen of a large form, such as *Telicomys*). Other taxa show great similarities to members of the Eumegamyinae (such as *Gyriabrus holmbergi* MACN-A 3956; MACN-A 5879). It seems that the false premise that juvenile rodents cannot have parallel-sided teeth led to inclusion of all the specimens showing this growing stage into an artificial group: the subfamily Gyriabrinae (see Fig. 11). The respective synonyms that might arise from our proposal are a subject that cannot be

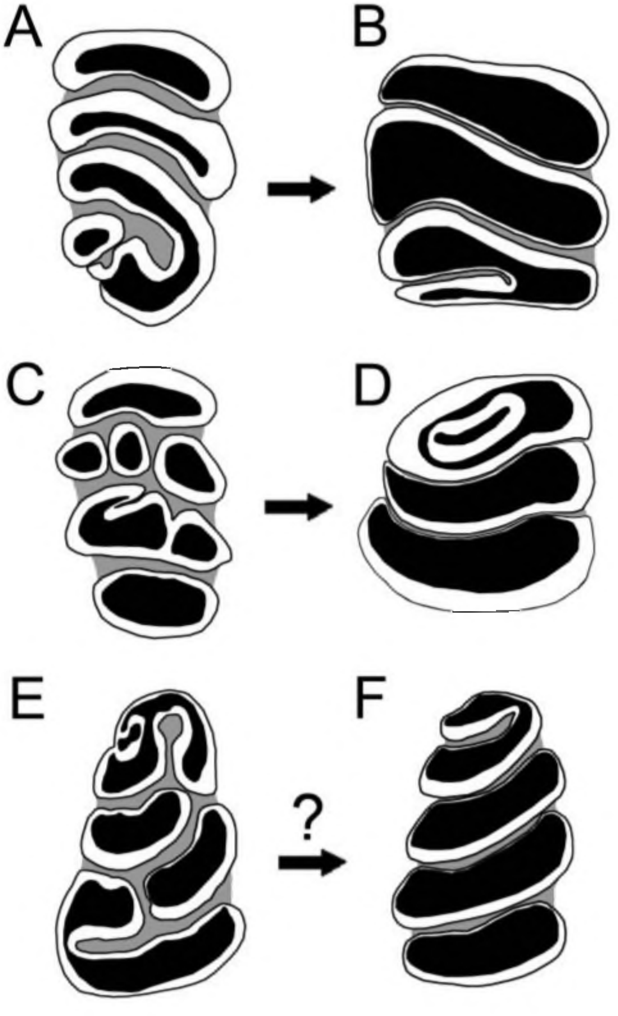

Figure 11. Occlusal view of Dinomyidae adult and juvenile teeth (not to scale). **A,** NHMUK 12.1.15.14, *Dinomys branickii* juvenile, right M1; **B,** NHMUK 3796, *Dinomys branickii* adult, right M1; **C,** MACN 12962, *Dinomys branickii* juvenile, left m1; **D,** NHMUK 34.9.10.191, *Dinomys branickii* adult, left m1; **E,** MACN 3954, *Gyriabrus holmbergi*, right p4; **F,** MNHN 2687, *Isostylomys laurillardi*, right p4.

securely resolved at present, due to the limited and fragmentary nature of the known fossil material. Hence, it is not possible to take the degree of ossification of the mandibular remains, for example, as a criterion for verifying the juvenile condition of fossils included in Gyriabrinae. Therefore, the known fossil remains assigned to this subfamily cannot be categorically placed as juveniles of already known taxa in other subfamilies, but our investigations do allow questioning of the validity of the subfamily Gyriabrinae as a natural group, pending new findings that could corroborate or refute this hypothesis.

Conclusions

A new fossil of an adult specimen of *Isostylomys laurillardi* (MNHN 2187) is described here, which represents the first known associated craneo-mandibular remains of a representative of the subfamily Eumegamyinae. We also report a juvenile specimen (MNHN 2687) of this species from the same location and lithostratigraphical unit. The two fossils exhibit a homologous morphology, where the sole difference is that MNHN 2187 is twice the size of MNHN 2687.

Based on comparisons between the Uruguayan remains and a detailed review involving specimens from different collections, we conclude that Eumegamyinae acquire the final form of their teeth very early during their ontogenetic development. The small size of the mandible of the juvenile specimen and the large size of the adult (only slightly smaller than that of *Josephoartigasia monesi*, the largest known rodent), suggests that all of the remains described thus far as Eumegamyinae correspond to individuals that had already attained the final configuration of the teeth. These findings allow the dismissal of earlier proposals of synonymy within Eumegamyinae (i.e. Fields 1957), based solely on presumed ontogenetic variation involving the number of lophs within the teeth. These findings do not exclude the possibility that intraspecific variation may exist (i.e. polymorphism) related to the binding pattern of lophs in the teeth of the Eumegamyinae.

Based on our observations, we propose formal synonymy of the three known species of the genus *Isostylomys* into just one species, *Isostylomys laurillardi*.

The analysis of the ontogenetic development of *Dinomys* and especially the capybara casts doubt on the validity of the subfamily Gyriabrinae, whose members could represent juvenile specimens of different taxa within the subfamilies Tetrastylinae, Eumegamyinae and Potamarchinae.

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Supplemental material

Supplemental material for this article can be accessed at: http://dx.doi.org/10.1080/14772019.2017.1285360

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Tercer artículo

RINDERKNECHT, A.,JONES, W.W., ARAÚJO, N., GRINSPAN, G. & R. E. BLANCO. 2017. Bite force and body mass of the fossil rodent *Telicomys giganteus* (Caviomorpha, Dinomyidae). *Historical Biology*. DOI: 10.1080/08912963.2017.1384475.

En este trabajo analizamos uno de los más interesantes taxones fósiles de Dinomidae: la especie *Telicomys giganteus*. Dicho taxón fue descripto hace más de un siglo en base a un cráneo completo y magníficamente preservado, depositado en el Museo Argentino de Ciencias Naturales "Bernardino Rivadavia". Al estar tan completo y presentar además algunas notables características (como su gran robustez o la presencia de unas profundas fosas premaxilares) sobre este taxón ha sido citado en libros sobre paleontología general, o sobre roedores fósiles, pero nunca se realizó un estudio científico sobre la paleobiología del taxón o sobre la significación de sus características anatómicas. Nosotros realizamos una estimación de la masa corporal, una reconstrucción de la musculatura craneana, y una estimación de la fuerza de mordida a nivel de los incisivos. Para esto último se siguieron tres metodologías. La primera de estas metodologías se basa en estimar la fuerza de mordida correlacionando este parámetro con la masa corporal; el segundo método considera las áreas de sección de los principales músculos involucrados en la mordida y los respectivos brazos de palanca, y por último se consideró un método fenomenológico que predice que la sección de los incisivos de los roedores se encuentra en relación directa con la fuerza de mordida.

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Bite force and body mass of the fossil rodent *Telicomys giganteus* (Caviomorpha, Dinomyidae)

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ABSTRACT
An exceptionally well-preserved skull of the Pliocene rodent *Telicomys giganteus* allowed the first estimation of body mass and analysis of the bite mechanics of this species of South American giant rodent. In this study, we reconstructed the main anatomical features of the skull of this Pliocene rodent and related them to the bite force at the incisors. The average of an estimation body mass gives 100 kg. We also estimated the bite force using three different techniques. Two methods suggest that bite forces at the incisors have a range of 500–1000 N. However, the incisors seem to be stronger than expected for this bite force, implying that the bite forces may have been greater than 2000 N. We consider the hypothesis of defense against predators or other agonistic behavior to explain our results.

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Giant rodent; Pliocene; body mass; bite force; incisors

Introduction

Dinomyids make up a family of caviomorph rodents that includes the largest rodents ever known (Bondesio 1978 and references therein). The first undisputed fossil from this family dates back to the middle Miocene (Friasian–Laventan South American Land Mammal Ages), although there are some records from the late Oligocene of Bolivia that may have affinities with this group (see Rinderknecht and Blanco 2015 and references therein).

Although the first descriptions of fossils of the family date back to the late nineteenth century (Ameghino 1883, 1885, 1886, 1889, 1891a, 1891b; Burmeister 1885), the phylogeny of Dinomyidae has never been addressed or tested using a modern cladistics approach. Nevertheless, the close relationship of Dinomyidae with the living Chinchillidae has been recently demonstrated (see Opazo 2005; Upham and Patterson 2015). In addition, a brief review of the history and scientific knowledge of fossil dinomyds is provided in Rinderknecht and Blanco (2015). Nowadays, the family includes only the 'pacarana' (*Dinomys branickii*), a peculiar but poorly studied 'long headed' cursorial Amazonian caviomorph (Pocock 1926; Sanborn 1931; Collins and Eisenberg 1972; White and Alberico 1992). There is a very poorly knowledge about the feeding behavioral and diet aspects in Dinomyidae, not only in relationship with the fossil forms, but also the living pacarana (see Higgins et al. 2011).

The most extreme Dinomyidae is the giant *Josephoartigasia monesi* recovered from Pliocene sediments in Uruguay (Rinderknecht and Blanco 2008). This is the only species of fossil Dinomyidae whose palaeobiology has been studied, especially the body mass and the bite force (Rinderknecht and Blanco 2008; Blanco et al. 2011; Cox et al. 2015). Although the accuracy of body mass estimations of *Josephoartigasia* has been debated (Blanco 2008; Rinderknecht and Blanco 2015), there is agreement that it is the largest fossil rodent discovered thus far. Although more than 60 fossil species have been described (Kraglievich 1926, 1930; Mones 1986; Rinderknecht et al. 2017), our knowledge of the anatomy and palaeobiology of these animals is far from satisfactory due to the lack of associated cranial and poscranial remains. In fact, most specimens are found as isolated teeth and/or small fragments of the skull or mandibles (Mones 1986; Rinderknecht et al. 2011; Rinderknecht and Blanco 2015).

Telicomys is a medium to large sized fossil dinomyd, reported from the Pliocene of Argentina and late Miocene of Peru (Ameghino 1904; Frailey 1986).

The type material of *Telicomys giganteus* is a complete skull (MACN 8011), the best preserved in the fossil record of the family (Figure 1). It was described by Ameghino (1904) as *Tetrastylus giganteus*, but later, Kraglievich (1926) re-examined this and other materials, and he erected the genus *Telicomys*, comprising *T. giganteus* (type species of the genus based on the skull previously described by Ameghino) and *T. gigantissimus*. This last taxon is based on an incomplete mandible (Figure 2), but some authors have expressed doubts about the taxonomical validity; *T. gigantissimus* could be a junior synonym of *T. giganteus* (see Vucetich and Verzi 1995).

Finally, Frailey (1986) described an incomplete skull from the Miocene of Peru and created the species *T. amazoniensis*.

Although *Telicomys giganteus* was much smaller than the largest representatives of the family (like *Josephoartigasia*, *Isostylomys*

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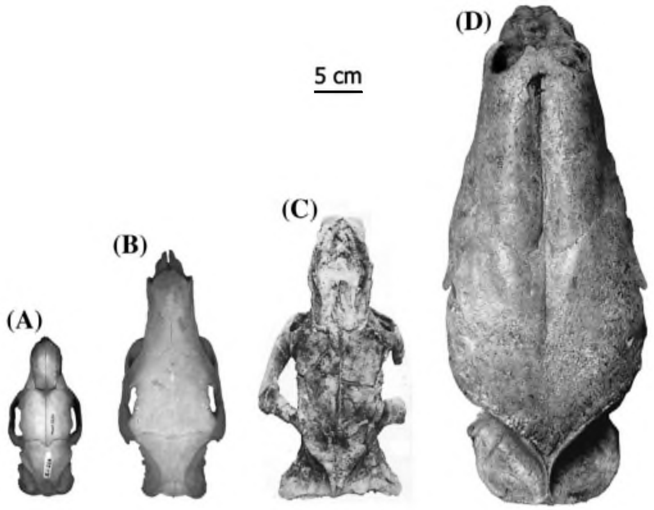

Figure 1. Skulls (in dorsal views) of *Dinomys branickii* (A), *Hydrochoerus hydrochaeris* (B), *Telicomys giganteus* (C; MACN 8011, holotype) and *Josephoartigasia monesi* (D; MNHN 921, holotype).

and *Arazamys*; see Figure 1), it has been suggested as an example of gigantism among the Dinomyidae family (Rovereto 1914; Kraglievich 1931; Dawkins 2004). On the other hand, the skull of this taxon shows very remarkable features that have caught the attention of several researchers (Ameghino 1904, 1916; Kraglievich 1926): the presence of remarkably wide incisors, the conformation of the occipital region (unique within the dynomids because it is flat and laterally expanded) and the presence of deep masseteric fossae in the premaxilla (Figure 2). These remarkable features make *Telicomys giganteus* one of the most interesting fossil rodents, and possibly the known Dinomyidae with the most bizarre cranial anatomy. Unfortunately, until now, no work has analyzed the function of these structures and the palaeobiology of this enigmatic taxon. The complete skull of *Telicomys giganteus* provides an opportunity to study for the first time the palaeoecology of this rodent, mainly based on body mass estimation and bite force mechanics.

Body mass is an important aspect of mammal ecology and sheds light on the palaeobiology and ecological role of some species (Damuth and Mc Fadden 1990; Meers 2002; Vizcaíno and De Iuliis 2003). There are several works about body mass estimation in fossil giant rodents using cranial (Reynolds 2002; Rinderknecht and Blanco 2008; Millien and Bovy 2010), dental (Hopkins 2008; Millien and Bovy 2010) and long bone measurements (Reynolds 2002; Sánchez-Villagra et al. 2003).

Another important ecological variable in mammals is the bite force, especially in species that use their mouth to hunt or as a tool. In rodents, the well-developed incisors and large bite force generally have been related to very strenuous functions such as durophagy, digging burrows, and wood processing among others (Lessa 1990; Van Daele et al. 2009; McIntosh and Cox 2016a, 2016b). Biomechanical methods have been developed to estimate the maximum bite force of mammals (Thomason 1991; Greaves 1995; Wroe et al. 2005; Christiansen 2007). Another study concludes that the body mass and section modulus of the incisors are very good predictors of maximum bite force in living cricetid rodents (Freeman and Lemen 2008).

In this work, we estimate the body mass of *Telicomys giganteus* based on an allometric relationship previously published. We also estimate bite force following three methods based on: (1) the expected body mass, (2) the incisor strength, and (3) a biomechanical model (following Thomason 1991). These three methods are those available in the literature to estimate bite force with the data that we have access. To apply the latter method, we have to reconstruct the jaw and the main jaw adductor muscles. We also expect to obtain a correlation between the bizarre cranial anatomy and the paleobiology of this species.

Materials and methods

Body mass estimations

We used allometric relationships previously applied to estimate the body mass of *Josephoartigasia monesi*, the largest rodent yet reported (Rinderknecht and Blanco 2008). These relationships are based on seven cranial measurements following Rinderknecht and Blanco (2008) (Figure 3). The body mass estimates are based on an allometric model that is expressed as a power function: $Y = aX^b$, where 'a' is a constant; 'b' is the allometric coefficient, 'Y' is the independent variable (body mass), and 'X' is the dependent variable (dental or skull measurements). All data

Figure 2. Skull of *Telicomys giganteus* (MACN 8011, holotype) in lateral view.
Note: The green areas indicate the position of the masseteric fossae in the premaxilla.

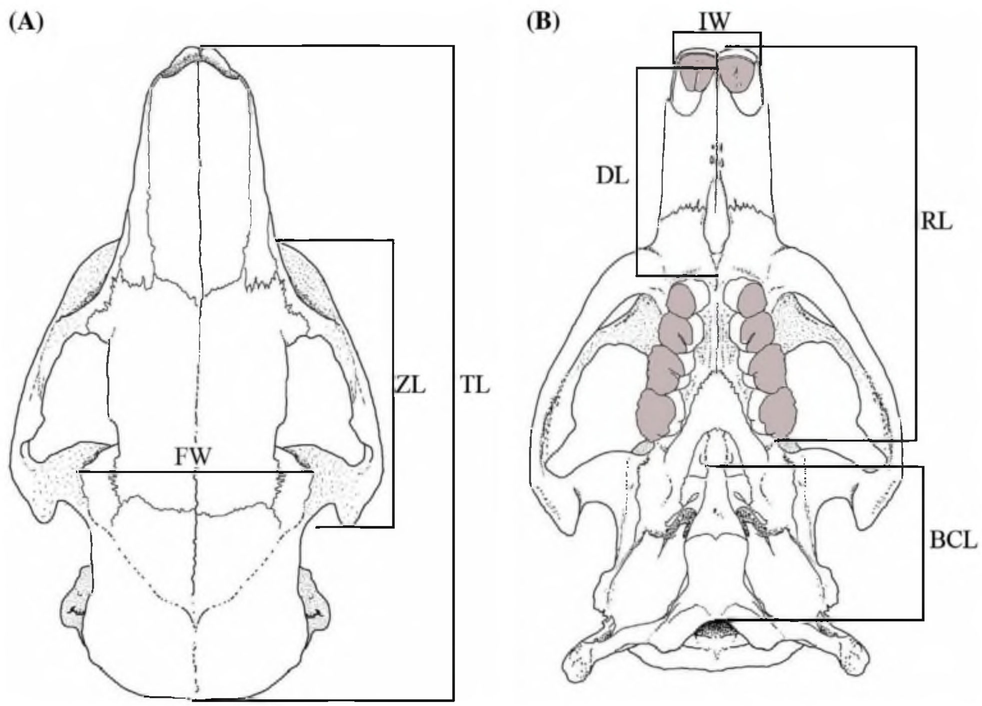

Figure 3. Skull of *Myocastor coypus* in dorsal (A) and ventral (B) views showing the skull variables used for allometric analysis.

Abbreviations: RL: rostral length; DL: diastema length; BCL: basicranial length (basioccipital + basispheniod); IW: incisors width; ZL: zygomatic arch length; FW: frontal width; TL: total length. Taken from Rinderknecht and Blanco (2008).

are log-transformed before regression. In order to compare our results with those obtained by other previous studies in living rodents, we applied the allometric equations given by Millien (2008) using the same cranial measurements. The per cent prediction error (%PE) indicates the per cent difference between the actual body mass and that predicted by the regression. In addition, the mean of the absolute values of the %PEs for a given regression provides a comparative index of predective accuracy among regressions (see Van Valkenburgh 1990 and references therein).

Recent works have suggested that two cranial measurements are the most reliable for estimating the body mass of extinct rodents: the total length of the skull and the grinding teeth area (Bertrand et al. 2015). Nevertheless, the latter is not a good indicator for Dinomyidae rodents because of the small size of the molars in comparison with the body size (see Pascual 1967; Rinderknecht and Blanco 2008, 2015). For this reason, we estimated the body mass of *T. giganteus* using the total length of the skull and other cranial measurements but not the grinding teeth area.

Cranial measurements and parameters of allometric equations are detailed in Table 1. Measurements were taken with digital calliper Mitutoyo, model: CD-6" CS (sensitive to 0.01 mm).

Musculature reconstruction and bite force

A cast was made from the original skull of *Telicomys giganteus* (MACN 8011) housed in the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (Figures 1 and 2). To reconstruct the mandibles (not preserved in the type material of *T. giganteus*), we based our model on a slightly bigger fossil specimen *Telicomys gigantissimus* (considered by some authors as a junior synonym of *T. giganteus*) (Figure 4). To reconstruct the muscles, we dissected the jaw muscles of *Hydrochoerus hydrochaeris* (the largest living rodent), *Myocastor coypus* and *Cavia pamparum*. All of these comparative materials are housed in the Museo Nacional de Historia Natural de Montevideo, Uruguay (MNHN). As the myology and biology of *Dinomys* are poorly known, we choose other living hystricognath rodents covering a broad size range.

Table 1. Measurements used for body mass estimation of *Telicomys giganteus*, with body mass estimation error ranges between parenthesis and %PE = average absolute value of per cent prediction error (from Rinderknecht and Blanco 2008/from Millien 2008); abbreviations are shown in Figure 3.

Measurement	*X* (mm)	Body mass estimation (kg) from Rinderknecht and Blanco (2008)	Body mass estimation from Millien (2008)	%PE
Diastema length	85.6	200 (150–267)	162.8	41.93/41.84
Frontal width	77.2	40 (30–53)	33.2	31.90/35.65
Incisors width	43.7	480 (261–881)	94.2	161.48/84.53
Zygomatic arch length	105.4	43 (36–53)	44.3	25.84/29.25
Basicranial length	65.1	109 (93–127)	106.6	22.85/19.70
Rostral length	165.1	94 (72–122)	105.4	32.67/31.75
Total length	269	91 (76–110)	93.3	20.85/23.84

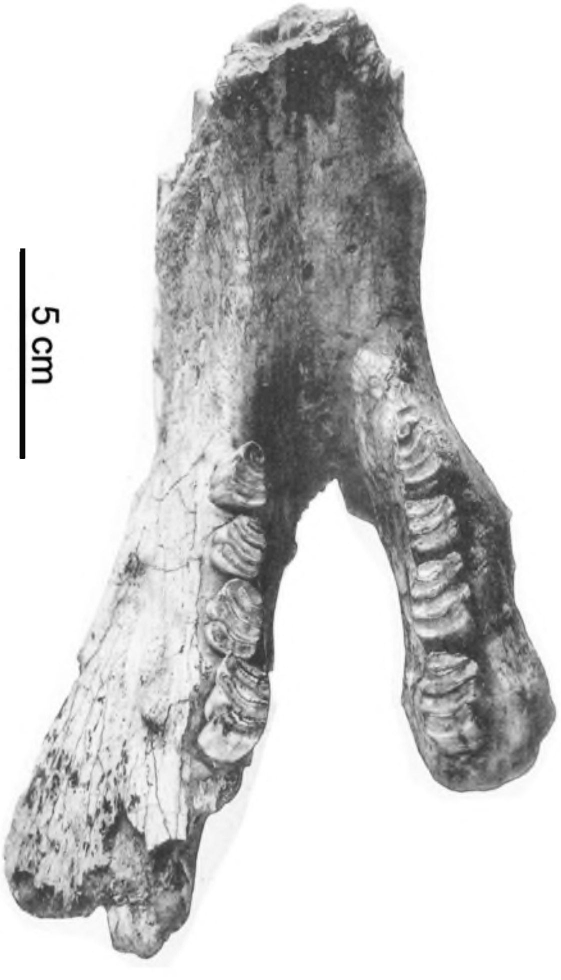

Figure 4. Occlusal view of the mandible of *Telicomys gigantissimus* (holotype). Note: Taken from Rovereto (1914).

The reconstruction of *m. temporalis* was relatively easy because the boundaries of the origin area in the skull of Dinomyidae are clearly visible (see Mones 1997; Blanco et al. 2011). Although in most rodents the *m. temporalis* origin is not clearly bounded, in the Dinomyidae, the origin area of this muscle in the deep temporal fossa is very clear (Kraglievich 1926, 1932; Fernández de Álvarez 1958; Rinderknecht and Blanco 2008). This muscle inserts in the coronoid process of the mandible, a structure absent in several dinomyds (Pascual 1967; Mones 1997). Fortunately, in the preserved mandible of *T. gigantissimus*, there is a very clearly rough region, located just under the last molar (Figure 5). Our model not considered the bippinate orientation of muscle fibres in this muscle. This bias would overestimate the muscle force. However, in most rodent masticatory muscles, the pennation angle is small, and thus the cosine is close to one (Druzinsky 2010b). Previously studies of bite force in fossil caviomorph rodents found that the temporalis muscle not have a large impact in bite force (Cox et al. 2015).

The *m. masseter* is divided into several branches (Windle and Parson 1899; Schulman 1906; Edgeworth 1935; Turnbull 1970; Naples 1987; Druzinsky 2010a, 2010b). The main branches considered here are *m. masseter superficialis*, *m. masseter lateralis* and *m. masseter medialis*. In addition, this last muscle is subdivided into the *m. masseter medialis anterior* (also called the infraorbital part of the *zygomatico-mandibularis* by Cox and Jeffery 2011 or *anterior lateral masseter* sensu Druzinsky 2010a) and the *m. masseter medialis posterior*. The cross section of the *m. masseter medialis anterior* can be accurately determined because in caviomorph rodents, this branch passes through the infraorbital foramen (Tullberg 1899–1900; Cooper and Schiller 1975; Woods and Hermanson 1985). In the case of *Telicomys giganteus*, a remarkable skull modification is observed in the infraorbital region: four deep premaxillary fossae that increase the volume (and cross-section) of this muscle (see Figure 2). This is a unique characteristic of this species and has never been studied in detail. The largest fossa is located posteriorly, and like the other their surfaces are completely smooth, without roughness or marks of muscular attachment (see Rovereto 1914). This last feature discarding that these are structures have some role in providing strong muscle attachment. There were also no channels for the passage of nerves or tendons. The cranial origin of *m. masseter medialis anterior* is located in the maxilla-premaxilla, and the mandibular insertion is in a small depression named the masseteric mandibular fossa. This fossa lies below p4–m1 in *Dinomys*, but in the giant Dinomyidae (Eumegamyinae subfamily), it is located between m1 and m2. The fossil of *Telicomys gigantissimus* shows this insertion located just below the m1. In this work, we consider the *m. masseter medialis posterior* and the *m. masseter lateralis* as a unit (with a single cross section) because the muscles fibers in both branches are aligned similarly.

The reconstruction of the other two branches of the *m. masseter* is more uncertain because the insertions and origins are not as well defined (see Saban 1968). The *m. masseter lateralis* inserts in the angular process of the mandible, and in the skull, the origin is marked by a jugal fossa. In our specimens, the insertions and origins can be roughly determined, but the different branches cannot be distinguished. The origins of the *m. masseter lateralis* muscles are along the zygomatic arch; thus, it is difficult to determine the muscle force direction. These errors were considered in our sensitivity analysis.

The *m. masseter superficialis* also inserts in the angular process of the mandible (superficial to the *lateralis*), forming the *pars reflexa* (Saban 1968; Cooper and Schiller 1975). The anterior limit of the origin of this muscle is located in the zygomatic apophysis of the maxilla located lateral to P4. The dissections of *Myocastor coypus*, *Cavia pamparum* and *Hydrochoerus hydrochaeris* show that the relative muscle mass of the *m. masseter superficialis* and *m. masseter lateralis* varies significantly among individuals. Our sensitivity analysis, described below, takes into account this effect.

The effects of the *m. masseter lateralis posterior* and *m. lateral pterygoid* were considered negligible in comparison with the other main adductor muscles. On respect to the *m. medial pterygoid* is very difficult to reconstruct the cross section of this muscle because the lack of anatomical information in Dinomyidae (included *Dinomys*) and osteological marks. Therefore, the absence of the *m. medial pterygoid* implies a source of error in our model. Nevertheless, it is important to note that this muscle has a considerable effect to the bite force at molar bites but less at incisor bites (see Cox et al. 2015).

Muscle cross-sectional areas were measured from sliced samples of the reconstructed muscles. We take the maximum cross-section of each muscle as the physiological cross-section.

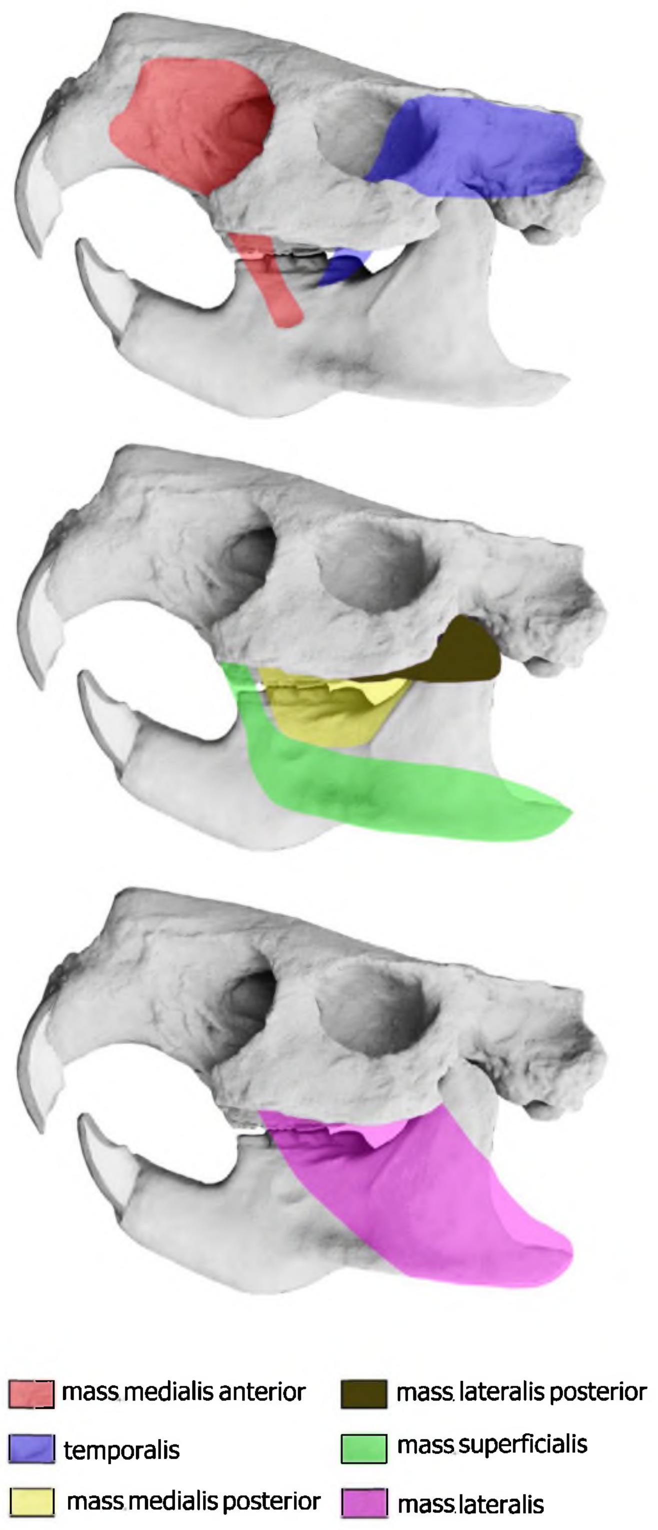

Figure 5. Anatomical reconstruction of skull, jaw, and main jaw adductor muscles of *Telicomys giganteus*.

To estimate the main action line in muscles we took into account the centroid of the origin and insertion areas of muscles. Muscles were made using mastic materials.

Lever arms were measured from a lateral picture of the skull with the reconstructed mandible using a digital vernier caliper. All data appear in Table 2. The maximum bite force was estimated from a quasistatic model of biting assuming that all the main muscles act together during maximum isometric force production:

$$F = \left(MS.s_{ms} + MMA.s_{mma} + ML.s_{ml} + MT.s_{mt}\right).\frac{300\text{ kPa}}{s_F}$$

where *MS* (*m. masseter superficialis*), *MMA* (*m. masseter medialis anterior* also known as *zygomatico-mandibularis*), *ML* (*m. masseter lateralis + m. masseter medialis posterior*) and *MT* (*m. temporalis*) are the cross section areas of main adductor muscles; s_{ms}, s_{mma}, s_{ml} and s_{mt} are the effective lever arms of the forces MS, MMA, L and T of the three muscle groups (see Figure 6), and s_F is the effective lever arm of the bite force. 300 kPa is a typical value of the maximum stress developed by skeletal muscles. The effective lever arms were measured as the perpendicular distances between the mandibular condyle and the line of action of the forces.

We employed sensitivity analysis to estimate the changes in bite force when the values for each reconstructed parameter varied by 20%.

We calculated bite force in these rodents based on two predictors, body mass and incisor strength, using equations obtained from data collected from extant rodents (see Freeman and Lemen 2008):

$$\log_{10}(\text{bite force}) = 0.430 \cdot \log_{10}(\text{body mass}) + 0.416$$

$$\log_{10}(\text{bite force}) = 0.566 \cdot \log_{10}(Z) + 1.432$$

where bite force is in newtons, body mass is in grams, and *Z* is the section modulus of incisors at the alveolar level with all dimensions measured in mm. Section modulus '*Z*' is a geometric property for a given cross-section used in the design of beams or flexural members. The section modulus is defined as: $Z = (wh^2)/6$ where *Z* is an index of a rectangular cross-section's ability to resist a bending moment (Freeman and Lemen 2008 and references therein). For estimated the cross-section we measured the anteroposterior length (23.8 mm) and width (21, 85 mm) of one incisor.

In order to remark on the reliability of this approach, it is important to consider that this methodology was previously applied in *Josephoartigasia monesi* (Blanco et al. 2011) and that the results were similarly matched with those obtained by applying other techniques (see Cox et al. 2015).

Results

The average of all seven body mass estimations based on Rinderknecht and Blanco (2008) gives 151 kg with a standard deviation of 154 kg. The largest and smallest estimates of the *Telicomys giganteus* obtained are 480 kg (from the width of incisors) and 40 kg (from the frontal width). The best predictors of body mass are the basicranial length and the total length of the skull because of their lower %PE values (see Table 1). Following the equations of best predictors, we consider the most likely body mass estimation around 100 kg. The reliability of this predictor was recently remarked upon by other authors (see Bertrand et al. 2015). The results obtained by our allometric equations are very close to estimations based on Millien (2008) using the same measurements. The only observed incongruence is between

Table 2. Data used in the biomechanical model for *Telicomys giganteus*.

	Measured value
Masseter superficialis cross section	8.35 cm^2
Masseter superficialis lever arm	7.86 cm
Masseter lateralis + *medialis posterior* cross section	33.63 cm^2
Masseter lateralis + *medialis posterior* lever arm	7.50 cm
Masseter medialis anterior cross section	25.61 cm^2
Masseter medialis anterior lever arm	11.29 cm
Temporalis cross section	13.29 cm^2
Temporalis lever arm	2.94 cm
Biting force lever arm	210.71 mm

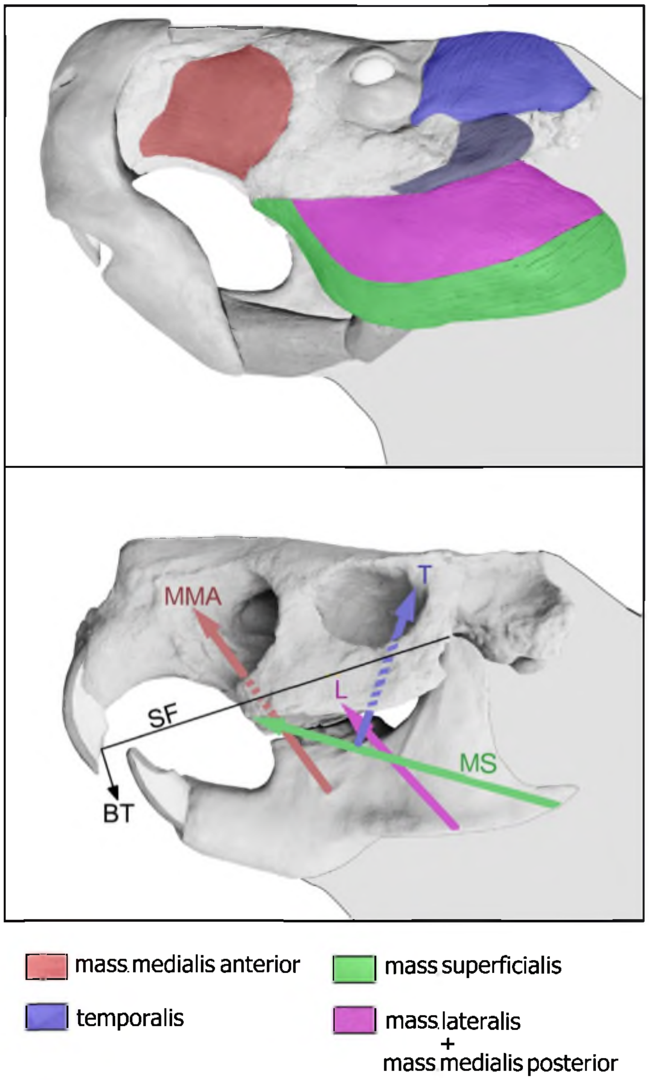

Figure 6. Skull of *Telicomys giganteus* showing the bite force direction and adductor main muscles forces directions (colored arrows).

Abbreviations: BT: bite force; SF: lever arm of the bite force; MMA: *masseter medialis anterior* force direction; MS: *masseter superficialis* force direction; L: *masseter lateralis* + *masseter medialis posterior* force direction; T: *temporalis* force direction.

both estimations based on the width of the incisors (IW), which show a difference that is five times larger (480 kg vs. 94 kg). The incongruence in the incisors width equation of Millen was discussed by Blanco (2008), which cautioned about a source of error. Leaving this aside, the average absolute value of per cent prediction error (PE%, see Table 1) of the equations based on the width of the incisors is the highest for both authors. Congruently, the statistical error range for the IW equation from Rinderknecht and Blanco (2008) is the largest (see Table 1).

The bite force obtained from the reconstructed anatomical model was 920 N, with the variation in bite force obtained from a sensitivity analysis of 736–1104 N (see Table 3). Bite force values varied widely in the sensitivity analysis with changes in the bite force lever arm, but fortunately, this measurement was fairly certain. The *m. masseter medialis anterior* cross-section and lever arm were also important parameters for this analysis. Fortunately, bite force was not very sensitive to variations in these parameters (a 20% variation in these parameters was associated with a less than 10% variation in bite force; see Table 3). Other parameters were not important in the sensitivity analysis; the effect of varying these parameters for the temporalis muscle was almost negligible (a 20% variation was associated with a 1% variation in bite force).

The expected bite force calculated from estimated values of body mass ranged from 229 to 723 N, with a value of 368 N for the most reliable estimated body mass (100 kg; see Table 4). The expected bite force calculated from the section modulus of the incisors was 2032 N, a much larger value than those of all the other estimations.

Discussion

Body mass estimation

Although the giant body size of *Telicomys giganteus* (see Rovereto 1914; Kraglievich 1931) has been described, the concrete body mass of this taxon never has been estimated. The skull studied here is clearly larger than that of any living rodent with the exception of the capybara (*Hydrochoerus hydrochaeris*). However, the skull of *Telicomys giganteus* is much more robust in comparison with that of the largest living rodent (see Figures 1 and 7). On the other hand, the fossil material that is known of *Telicomys giganteus* is very small in comparison with the largest representatives of the Dinomyidae, like *Josephoartigasia*, *Isostylomys* and *Arazamys* (Rinderknecht et al. 2011; Rinderknecht and Blanco 2015). Our results show that the Dinomyidae is one of the families with a broad body size range among rodents.

Bite force estimation

The results of the bite force estimations are the most remarkable and show very different data according to the applied method. The biomechanical model based on the anatomical reconstruction yields a value that is well above what is expected for its estimated body mass. Moreover, the estimate of bite force using the width of the incisors is even greater.

The bite force estimate from the biomechanical model and the anatomical reconstruction (736–1104 N) is much larger than the expected value for a rodent with a body mass in the range estimated for *Telicomys giganteus*. Even taking into account the upper limit of estimated body mass, the bite force from body mass (723 N) is lower than the lower limit of the biomechanical model (736 N). Moreover, the bite force estimation for *Telicomys giganteus* has almost the same value of that of *Josephoartigasia monesi* (Blanco et al. 2011) applying the same methodology. Noteworthy, the body mass of *Josephoartigasia* was estimated in

Table 3. Results of the mechanical model and sensitivity analysis for *Telicomys giganteus*.

Studied case	Maximum bite force (N)
Reconstructed anatomical model	919.97
+20% *masseter superficialis* area/lever arm	938.65
−20% *masseter superficialis* area/lever arm	901.29
+20% *masseter lateralis* + *medialis posterior* area/lever arm	991.79
−20% *masseter lateralis* + *medialis posterior* area/lever arm	848.15
+20% *masseter medialis anterior* area/lever arm	1002.33
−20% *masseter medialis anterior* area/lever arm	837.61
+20% *temporalis* area/lever arm	931.10
−20% *temporalis* area/lever arm	908.84
+20% biting force lever arm	1103.96
−20% biting force lever arm	735.98

Table 4. Results of the predictive indicators of bite force, body mass and section modulus of incisors for *Telicomys giganteus*.

Predictor	Bite force (N)
Body mass (33 kg)	228.54
Body mass (40 kg)	248.25
Body mass (100 kg)	368.13
Body mass (163 kg)	454.19
Body mass (480 kg)	722.66
Section modulus of incisors (2063 mm^3)	2032.39

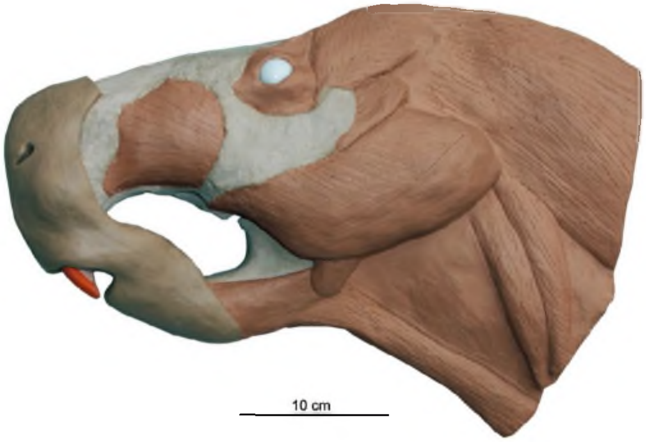

Figure 7. Anatomical reconstruction of the head of *Telicomys giganteus* showing the main adductor muscles.

nearly a tonne (Rinderknecht and Blanco 2008) and its estimated bite force is the expected for a mammal of that size.

The incisors seem to be much stronger than what is expected for such bite forces. The extreme body mass value of 480 kg (see Table 1) obtained from incisors width is other evidence of over-construction of these teeth. Beyond the uncertainties of bite force estimation from anatomical reconstruction and even taking into account the most robust abductor muscles of *T. giganteus* in comparison with other caviomorph rodents, the obtained value from the incisors section modulus (2032 N) indicates that this is an unlikely result for bite force. Similar discrepancies were obtained in a study of *Josephoartigasia monesi* bite forces, and potential sources of error from the methods were already discussed in Blanco et al. (2011). The great extrapolation beyond the data used to produce the predictive equation of Freeman and Lemen (2008) and the biomechanical lever models general underestimation of bite force are potential explanations. The unrealistic estimation of bite force applying the incisors section modulus could also be due to *Telicomys giganteus* having a larger safety factor in comparison with other rodents. Safety factors can be larger in situations where the loads in the structure are more unpredictable or if the cost of a failure is too large (Alexander 1981). As the rodent's incisors grow continuously, it seems unlikely that the cost of failure could be extraordinary large. It is more likely that these rodents' incisors were used for tasks with less predictable forces.

In relation to the putative tasks, one possibility is that the jaw bite is accompanied by skull movements. These movements increase the lateral stresses in the incisors and could explain its large section modulus. This kind of behavior is infrequent in rodents (but see Satoh and Fumihiko 2006) and generally implies skull anatomical modification. Moreover, when biting another animal (either as defense or attack), the bite force has to increase, as the struggle movements produce very large forces in the jaw that could become disarticulated. In *Telicomys giganteus*, the bite force using adductor muscles seems to be much larger than expected for the body size (but obviously not as large as the incisor modulus indicates), something that was not observed in the *J. monesi* case using the same method (see Blanco et al. 2011). This result is consistent with anatomical characteristics observed in the skull of *T. giganteus* (like the deep masseteric fossae in the premaxilla; see Figure 2) that seem to be adaptations that produced a large bite force increase in the cross section of the *m. masseter medialis anterior*. Perhaps the robust incisors and the strong bite was a defensive weapon against predators such as large 'terror birds' (Aves, Phorusrhacidae) or other agonistic behavior (see Ferraz et al. 2012; Zenuto et al. 2002 as examples on the use of incisors during social agonistic encounters among Caviomorpha).

Another possibility that would explain the robust incisors in rodents is procumbency. This topic was previously discussed for *J. monesi* (see Blanco et al. 2011). It is clear that *J. monesi* incisors are extremely procumbent, and this condition produces larger bending stresses than for the same bite force in a smaller rodent. We expect that extreme procumbency produces an overestimation of bite force from the incisors strength indicator. It was considered previously that for *J. monesi*, procumbency is the most likely explanation for the discrepancies in bite force between the incisor strength and the other two methods of estimation used in Blanco et al. (2011). But in *Telicomys giganteus*, the procumbency is not as relevant due to the orthodont conformation of the upper incisors. In fact, the 'Thomas's angle' (a usual measure of procumbency, see Becerra et al. 2012) is nearly 90° in *Telicomys giganteus*.

Another hypothesis is that low-quality food items such as twigs or branches were processed by incisors, probably also using head movements (see Cox et al. 2015).

Finally, tooth-digging in a substrate is another option, as observed in several living rodents. The large incisors of the rodents could be used for digging, and this behavior has been reported in several species (Lessa 1990; McIntosh and Cox 2016a, 2016b). The digging activity modifies the upper incisor, generating robust and procumbent teeth (e.g. *Lagostomus*, *Heterocephalus*, *Georychus*, *Fukomys*, and some species of the genus *Ctenomys*). *T. giganteus* does not show the expected procumbency in the upper incisors expected for a tooth-digging rodent. Nevertheless, there are some rodent taxa with digging activities that do not present upper incisors with strong procumbency (e.g. *Geomys* and some species of the genus *Ctenomys*). Taking this into account and due to the absence of mandibles in *Telicomys giganteus* (our reconstruction of the mandibles is not conclusive about the conformation of the lower incisors), we have been cautious to rule out the digging-activity hypothesis in this fossil rodent.

In any case, it is clear that *Telicomys giganteus* has remarkable skull adaptations in order to produce a large bite force. Besides, this taxon has very robust incisors, much more robust than necessary according to most reliable estimations of bite force based on muscles reconstruction and body mass.

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Cuarto artículo

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En este artículo estimamos la fuerza de mordida de *Josephoartigasia monesi* aplicando métodos computacionales, entre ellos el método de "Elementos finitos". Dicho método consiste en dividir una estructura en varios elementos teóricos, con el objetivo de que esta modelización permita describir el comportamiento de cada uno de estos elementos, en este caso frente a la aplicación de una fuerza, y, al conectar todos los elementos, mapear el comportamiento de toda la estructura frente a las fuerzas y tensiones involucradas. Gracias a la aplicación de dichos métodos se logró estimar la fuerza de mordida a nivel de los incisivos (dato que fue concordante con el obtenido en Blanco *et al.*, 2011 utilizando otros métodos), y a nivel de las serie prémolo- molar, mapeando las tensiones producidas en el cráneo de acuerdo a cado uno de los puntos de mordida. Es de destacar que la fuerza de mordida a nivel de los incisivos fue la esperable para un mamífero con el tamaño estimado de *Josephoartigasia monesi*, no siendo así a nivel de los molares, los cuales arrojaron altos valores de fuerza de mordida.

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Predicting bite force and cranial biomechanics in the largest fossil rodent using finite element analysis

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Abstract

Josephoartigasia monesi, from the Pliocene of Uruguay, is the largest known fossil rodent, with an estimated body mass of 1000 kg. In this study, finite element analysis was used to estimate the maximum bite force that *J. monesi* could generate at the incisors and the cheek teeth. Owing to uncertainty in the model inputs, a sensitivity study was conducted in which the muscle forces and orientations were sequentially altered. This enabled conclusions to be drawn on the function of some of the masticatory muscles. It was found that *J. monesi* had a bite of 1389 N at the incisors, rising to 4165 N at the third molar. Varying muscle forces by 20% and orientations by 10° around the medio-lateral aspect led to an error in bite force of under 35% at each tooth. Predicted stresses across the skull were only minimally affected by changes to muscle forces and orientations, but revealed a reasonable safety factor in the strength of the skull. These results, combined with previous work, lead us to speculate that *J. monesi* was behaving in an elephant-like manner, using its incisors like tusks, and processing tough vegetation with large bite forces at the cheek teeth.

Key words: bite force; cranial biomechanics; finite element analysis; *Josephoartigasia monesi*; rodent.

Introduction

The mammalian order Rodentia comprises well over 2000 extant species (Wilson & Reeder, 2005), the majority of which are small in size, i.e. under 1 kg in mass (Silva & Downing, 1995). The largest living rodent is the capybara, *Hydrochoerus hydrochaeris*, which has a body mass of around 60 kg (Mones & Ojasti, 1986). However, many extinct species of rodent, particularly those belonging to the South American families Dinomyidae and Neoepiblemidae, reached a much larger size. The largest known fossil rodent is *Josephoartigasia monesi*, a dinomyid species from the Pliocene of Uruguay (Rinderknecht & Blanco, 2008). The fossil is an almost complete skull measuring 53 cm in length, and its body mass has been estimated to be approximately 1000 kg (Rinderknecht & Blanco, 2008), although there is a degree of controversy about this figure (Blanco, 2008; Millien, 2008).

When studying fossil species, especially those of large size such as *J. monesi*, researchers are frequently interested in elucidating feeding ecology and potential bite force (e.g. McHenry et al. 2007; Bates & Falkingham, 2012).The bite force that *J. monesi* could generate at the incisors was estimated by three different methods in a previous study (Blanco et al. 2012). Using estimated muscle cross-sectional areas and measured muscle lever arms, the incisor bite force was calculated to be 959 N. Extrapolating from a measured bite force of 13 N in rats (Nies & Ro, 2004) and using estimated body mass of 1000 kg, the expected bite force of *J. monesi* was calculated as 991 N. However, using the relationship between incisor section modulus and bite force derived by Freeman & Lemen (2008), a much greater bite force of 3214 N was calculated. Blanco et al. (2012) explain this discrepancy by suggesting that the incisors of *J. monesi* may have been extremely procumbent, and thus would have experienced greater stresses during feeding, or that the incisors were used for activities other than feeding, such as digging or defence, in which other muscles, such as the neck musculature, would have been recruited. This second suggestion raises the possibility that *J. monesi* was using its incisors much as an elephant uses its tusks.

The large discrepancy in bite force estimates in Blanco et al. (2012) highlights the difficulty of determining such values in extinct organisms, in which a great deal of information, notably soft tissue data, is missing. The 'dry skull'

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method (Thomason, 1991) models the jaw as a simple lever and derives bite force from jaw-closing muscle cross-sectional areas and skull dimensions. This method has been frequently used in biomechanical research (Wroe et al. 2005; Christiansen & Wroe, 2007; Ellis et al. 2009; Grandal-d'Anglade, 2010), and rests on two major simplifications – the modelling of the skull as a beam, and the placement of each muscle force at the centroid of the area used to estimate cross-sectional area of the muscle (point load method). Although a significant correlation has been shown between measured bite forces and those calculated by the dry skull method, it has also been demonstrated that the point load method tends to miscalculate muscle cross-sectional areas (Davis et al. 2010).

Many recent studies have turned to finite element analysis (FEA) to predict bite forces in mammals (Wroe et al. 2007; Bourke et al. 2008; Dumont et al. 2011; Cox et al. 2012, 2013; Oldfield et al. 2012). FEA is an engineering technique that predicts stress, strain and deformation in an object subjected to a load (Rayfield, 2007). A virtual reconstruction of an object, such as a vertebrate skull, is created that is then converted to a mesh of many smaller and simpler elements, typically cubes or tetrahedra. The object is then constrained at a number of nodes, forces are applied, and an algorithm is used to calculate the stress and strain in each element. The advantage of FEA when calculating bite forces is that, rather than modelling the skull as a beam, its entire geometry is represented. In addition, the whole attachment area of each muscle can be loaded, instead of just a single point.

The aim of this study is to shed light on the palaeoecology of the largest fossil rodent, *J. monesi*. In particular, the feeding ecology of this unusual rodent species will be investigated using FEA to predict stress distributions across the skull during biting as well as the bite force that could be generated at each tooth. Based on previous work (Blanco et al. 2012), it is hypothesised that incisor bite force predicted by FEA will be well below that predicted by the incisor section modulus. Moreover, if *J. monesi* did indeed use its incisors in a tusk-like manner, it is predicted that peak von Mises stresses in the cranium will be considerably below the yield strength of bone. As many of the FEA input parameters, particularly muscle forces and directions of pull, will have to be estimated, a sensitivity analysis will be conducted to determine which parameters have the greatest influence on bite force predictions. Not only will this enable us to assess the accuracy of the bite force predictions, but, by varying muscle forces and orientations one by one, it will also allow us to make inferences of the specific function of the each masticatory muscle in this species. Overall, these results will help us to understand the ecology of a highly unusual fossil rodent, and will demonstrate how cranial morphology and masticatory muscle configuration can impact feeding performance.

Materials and methods

Model construction

The holotype cranium of *J. monesi*, housed in the Museo Nacional de Historia Natural, Montevideo (MNHN 921), was scanned using the Somaton Sensation CT scanner at the Hospital de Clínicas 'Dr. Manuel Quintela', Montevideo. Voxels were 0.58 × 0.58 mm and slice thickness was 0.6 mm. A 3D digital reconstruction of the skull was created from the CT scans using the segmentation function of AVIZO 8.0 (Visualization Sciences Group, Burlington, MA, USA). Internal anatomy of the bone was reconstructed as being solid, that is, trabecular bone was not separated from cortical bone, as the preservation of the specimen did not allow these to be distinguished. Recent work on macaque skulls (Fitton et al. 2015) indicates that solid models perform almost identically to models with trabecular bone, although small differences in strain will occur locally in areas where trabeculae are present. Damaged parts of cranial morphology, in particular the left zygomatic arch, were reconstructed by copying and reflecting the relevant structure from the opposite side of the skull. Missing molar teeth (right P4 and M1, and left M2) were reconstructed in the same way. The missing right incisor root was reconstructed by filling in the empty alveolus. The erupted portions of both incisors were reconstructed by eye with reference to the plastic reconstruction made for a previous study of this specimen (Blanco et al. 2012). Figure 1 shows the completed reconstruction of the *J. monesi* skull. Given the level of subjectivity in the reconstruction of the incisors beyond the alveolar margin, a second reconstruction was created with 50 mm added to the tips of both incisors (maintaining the same curvature), to assess the impact of incisor morphology on bite force and feeding biomechanics. The skull and teeth were segmented separately so that different mate-

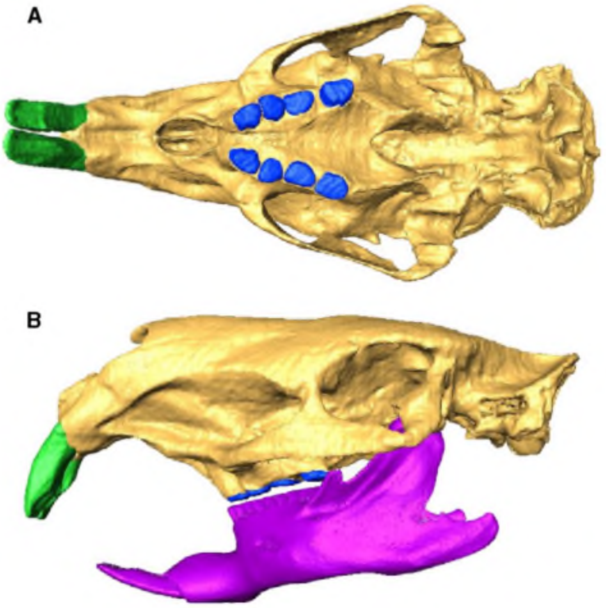

Fig. 1 Digital reconstruction of the skull of *Josephoartigasia monesi* in (A) ventral and (B) left lateral views, showing restored left zygomatic arch, incisors and molars. Scaled reconstruction of the mandible of *Lagostomus maximus* used to estimate masticatory muscle orientations also shown in lateral view.

rial properties could be applied to them. However, the component materials of the teeth (enamel, dentine and cement) could not be distinguished and so were not separately reconstructed. The reconstruction was downsampled to reduce processing time, generating an isometric voxel dimension of 1.16 mm. The downsampled reconstruction of *J. monesi* was then converted to a mesh of eight-noded cubic elements by direct voxel conversion using VOX-FE, in-house custom-built FEA software (Liu et al. 2012; available on request), resulting in a model of 1 526 906 elements. The model with elongated incisors had 1 549 885 elements. The surface reconstructions, with and without elongated incisors, and the finite element model are all available for free at http://figshare.com/authors/Philip_Cox/617885.

As no mandible exists for *J. monesi*, a scaled reconstruction of the mandible of an extant hystricognath rodent was created. The plains viscacha, *Lagostomus maximus*, was chosen as the representative hystricognath, as it was the nearest living relative of *J. monesi* for which image data was available (no mandible of *Dinomys branickii*, the sole extant dinomyid, was obtainable). The mandible of *L. maximus* is more elongate than that of *D. branickii*, and has a lower condyle; however, in these respects, it more closely resembles the mandible of *J. monesi* reconstructed in Blanco et al. (2012). The mandible of a specimen of *L. maximus* from the University Museum of Zoology, Cambridge (UMZC specimen E.3555) was imaged using the X-Tek microCT scanner at the Department of Engineering, University of Hull. Voxels were isometric and voxel dimensions were 0.069 mm. A 3D reconstruction of the mandible was created using the automatic thresholding function of AVIZO 8.0, and the resulting surface file was then scaled, rotated and translated to fit the cranial reconstruction of *J. monesi*. It can be seen from Fig. 1 that the posterior half of the *L. maximus* mandible is a good fit for *J. monesi* – the relative positions of the cheek teeth and the condyle are very similar. However, it is clear that much greater flexion would be needed in the anterior part of the mandible for incisor occlusion to occur. As all the muscle attachments are on the posterior part of the mandible, it was felt that, with appropriate sensitivity analyses (see below), the mandible of *L. maximus* could be used to estimate the masticatory muscle insertions of *J. monesi*. It should be noted that the mandibular reconstruction was not itself subjected to FEA.

Model inputs

The material properties assigned to the bone and teeth of the *J. monesi* model were based on previously published FE models of rodents (Cox et al. 2011, 2012, 2013). Bone was assigned a Young's modulus of 17 GPa and the teeth were given a Young's modulus of 30 GPa. Both materials were modelled as being linearly elastic and isotropic with a Poisson's ratio of 0.3 (Williams & Edmundson, 1984). The model was constrained in three areas: at the left and right jaw joints on the ventral surface of the zygomatic process of the squamosal; and at the biting tooth. The jaw joints were constrained in all three dimensions, but the bite point was only constrained in the direction of the bite, which was assumed to be perpendicular to the occlusal plane. The number of nodes constrained at each location varied between 140 and 521.

Loads were added to both sides of the model to represent the major muscles of mastication: superficial masseter; deep masseter; zygomaticomandibularis (ZM); infraorbital part of the zygomaticomandibularis (IOZM); temporalis; medial pterygoid; and lateral pterygoid. The layers of the masseter are here named superficial/deep/ZM following Turnbull (1970), Weijs (1973) and Cox & Jeffery (2011), as opposed to the superficial/lateral/medial nomenclature of other researchers (e.g. Wood, 1965; Woods, 1972). To facilitate comparisons with previous work, the cross-sectional areas (CSA) of the muscles were based on the estimates given in Blanco et al. (2012). In that study, bony proxies are used to determine the CSA of the '*masseter superficialis and masseter lateralis*' as a single unit, the '*masseter medialis*', and the '*temporalis*'. As the bony proxy used for the '*masseter medialis*' is the cross-section of the infraorbital foramen, it is clear that it is only the portion of this muscle attaching to the rostrum (i.e. the IOZM) that is being referred to here. In addition, the estimation of the CSA of the superficial and deep masseters, following the method of Thomason (1991), must also have included the parts of the ZM originating from the medial surface of the zygomatic arch (the anterior and posterior ZM). Thus the three muscle CSAs calculated in Blanco et al. (2012) refer to: the superficial masseter, deep masseter and ZM as a unit; the IOZM; and the temporalis. For the FE model in this study, the first of those CSAs was divided into its component muscles based on the muscle proportions measured in the capybara, *Hydrochoerus hydrochaeris* (Müller, 1933). Approximate relative CSA values for the capybara muscles were obtained by squaring the cube roots of the muscle masses. Although as absolute values these CSA values are of course highly inaccurate owing to the lack of data on fibre length, they will at least give an approximate indication of the relative sizes of the different muscle CSAs. Using the capybara CSA data as percentages, separate CSA values were obtained for the superficial masseter, deep masseter and ZM of *J. monesi* (Table 1). Similarly, CSA values for the medial and lateral pterygoid muscles were calculated for *J. monesi* based on their size relative to the other masticatory muscles in the capybara. Muscle forces (given in Table 1) were calculated by multiplying CSAs by an intrinsic muscle stress value of 0.3 N mm^{-2} (van Spronsen et al. 1989). For the accurate calculation of muscle force, CSA should be multiplied by the cosine of the pennation angle as well as intrinsic muscle stress. As pennation angles were unknown, it was not possible to include these in the force calculations. However, in most rodent masticatory muscles, the pennation angle is small, and thus the cosine is close to one (Druzinsky, 2010). The temporalis and medial pterygoid muscles have larger pennation angles and so their forces may have been overestimated, but the magnitudes of these two muscles were not found to have a large impact on bite force.

Muscle attachment sites were based on the descriptions given in Blanco et al. (2012) as well as descriptions of muscle origins and insertions in extant hystricomorph rodents (Müller, 1933; Turnbull,

Table 1 Muscle cross-sectional areas and loads applied to each side of the finite element model of *Josephoartigasia monesi*.

Muscle	CSA (cm^3)	Force (N)
Superficial masseter	22.83	685
Deep masseter	15.15	454
Zygomatico-mandibularis	12.02	360
IOZM	25.00	750
Temporalis	20.50	615
Medial pterygoid	15.85	476
Lateral pterygoid	6.57	197
Total	117.92	3537

1970; Woods & Howland, 1979; Woods & Hermanson, 1985; Hautier & Saksiri, 2009; Hautier, 2010; Cox & Jeffery, 2011). Both the IOZM and temporalis have clear fossae from which they originate on the rostrum and braincase, respectively. The deep masseter takes its origin along the length of the ventral margin of the zygomatic arch, and the origin of the superficial masseter is a small area located immediately anterior to deep masseter attachment. The ZM attaches to the medial surface of the zygomatic arch and the medial and lateral pterygoid muscles originate from the medial and lateral surfaces of the pterygoid flange, respectively. The directions of pull of the muscles were determined by placing landmarks at the centroids of the muscle insertion sites on the reconstructed mandible of *L. maximus*, which was aligned with the cranium with the teeth in occlusion (i.e. with the jaws closed; see Fig. 1). The landmarks were then uploaded to VOX-FE and used as the end points of the muscle vectors. The muscle attachment areas and vectors are shown on the FE model of *J. monesi* in Fig. 2.

Model solution and analysis

The loaded finite element model of *J. monesi* was solved for biting at each tooth, using VOX-FE. Owing to their close apposition, gnawing at the incisors was assumed always to be bilateral. Molar chewing, however, was modelled as unilateral biting on the right side. Bite force, von Mises stress patterns, and the maximum von Mises stress across the skull were recorded from each solved model. Given the approximate nature of the muscle loads, and in order to assess the influence of each muscle on bite force, the five largest muscle forces (IOZM, superficial masseter, temporalis, medial pterygoid and deep masseter) were increased and decreased by 20%, one at a time. Similarly, as muscle pull direction was based on the mandibular muscle attachment sites of a different species, the angle of the muscle vector relative to the direction of bite force was varied by 10° in both directions around the medio-lateral axis. The models with altered muscle force magnitudes and orientations were solved for biting at the incisors, premolar and third molar only (in order to represent bites at the most mesial and distal points on the cheek tooth row). In addition, a model was solved, for incisor gnawing only, with elongated incisors. Finally, based on the previous results, a model was created with all muscle forces increased by 20% and muscle vectors reoriented by 10° in the direction of increasing bite force, in order to maximise bite force, in addition to another model that minimised bite force, to produce a confidence interval for bite force estimates in *J. monesi*.

Fig. 2 Finite element model of the skull of *Josephoartigasia monesi* in left lateral view. Stippled red areas indicate muscle attachments, red arrows represent muscle vectors. DM, deep masseter; IOZM, infraorbital part of the zygomatico-mandibularis; LP, lateral pterygoid; MP, medial pterygoid; SM, superficial masseter; T, temporalis; ZM, zygomaticomandibularis.

Results

Bite force

Table 2 gives the bite force predicted by the FE model of *J. monesi* at each tooth. Bite force was calculated to be 1389 N at the incisors, rising to 2984 N at the premolar and 4165 N on the most distal tooth on the dental arcade, the third molar. The reaction forces at the working side temporo-mandibular joint are also given in Table 2. These show that, even when biting at the most distal tooth (M3), there are no distractive forces at the jaw joint that would tend to dislocate the jaw. The effect on bite force of changing the muscle force magnitudes by 20% is shown in Table 3. It can be seen that the muscles with the greatest influence on bite force are the superficial masseter, the IOZM and, to a slightly lesser degree, the deep masseter. A 20% change in the force applied by any of these three muscles will result in a 4–6% change in output bite force at either the incisors or the cheek teeth. The deep masseter appears to act equally on all teeth, whereas the superficial masseter and IOZM

Table 2 Bite force at each tooth predicted by the finite element model of *Josephoartigasia monesi.*

Biting tooth	Bite force (N)	Working side reaction force (N)	Peak von Mises stress (MPa)
I	1389	1689	24.85
PM	2984	991	23.36
M1	3298	718	27.43
M2	3625	516	31.18
M3	4165	113	39.09

I, incisor; PM, premolar; M1, first molar; M2, second molar; M3, third molar.

Table 3 Bite force at the incisor, premolar and third molar predicted by models with altered muscle load magnitudes. Percentage difference from bite force of original models (given in Table 1) calculated.

	Bite force (N)			% difference		
	I	PM	M3	I	PM	M3
SM +20%	1469	3150	4391	± 5.76	± 5.56	± 5.41
SM −20%	1309	2818	3940			
DM +20%	1447	3109	4339	± 4.16	± 4.19	± 4.17
DM −20%	1331	2859	3992			
IOZM +20%	1465	3147	4391	± 5.52	± 5.47	± 5.41
IOZM −20%	1312	2821	3940			
T + 20%	1391	2989	4171	± 0.18	± 0.15	± 0.14
T −20%	1386	2980	4160			
MP +20%	1413	3043	4256	± 1.77	± 1.97	± 2.16
MP −20%	1364	2925	4075			

I, incisor; PM, premolar; M3, third molar; SM, superficial masseter; DM, deep masseter; IOZM, infraorbital zygomaticomandibularis; T, temporalis; MP, medial pterygoid.

both have a slightly greater influence on incisor biting than on molar biting. Changes to the medial pterygoid load have much less of an effect on bite force – just a 2% difference resulting from a 20% change in muscle force. The medial pterygoid also differs from the other muscles in affecting molar bites more than incisor bites. The temporalis is unusual among the masticatory muscles in that varying its input force by 20% barely affects the output bite force at all, with just a 0.2% change being recorded.

The effect of changing muscle vector orientation on bite force shows a different pattern to that seen when changing force magnitudes (Table 4). Changing the pull direction of the IOZM has the greatest effect on bite force (7–9% difference), followed by the superficial masseter. Despite being relatively important with regard to its magnitude, the orientation of the deep masseter has minimal effect on bite force. Similarly, the orientation of the medial pterygoid appears to be largely unimportant with regard to bite force. The orientation of the temporalis was not varied in this way, as the position of the temporal fossa in relation to the jaw joint constrains its direction of pull to a narrow range of angles. The effect of superficial masseter orientation on bite force appears to be fairly consistent across all teeth, whereas the orientation of the IOZM has a greater effect on the force produced by the incisors than by the molars.

Changes to the length of the incisors had little effect on the predicted bite force. An addition of 50 mm to the tip of both incisors increased bite force from 1389 N to 1397 N – an increase of just < 1%.

Based on the above results, an estimate of the maximum error in bite force was calculated by increasing the load magnitude of the superficial masseter, deep masseter, IOZM and medial pterygoid by 20%, and reorienting the vector of the superficial masseter and IOZM by 10° towards the rostrum. A second model was constructed with the opposite loading conditions. The resulting bite forces are given in Table 5. It can be seen that, given an uncertainty of ± 20% in muscle force magnitude and ± 10° in muscle force vector, *J. monesi* would have been able to generate a bite force of between 967 and 1850 N at the incisors, between 2082 and 3970 N at the premolar, and between 2914 and 5534 N at the third molar. This represents a fairly consistent error across the teeth of ± 30–33% from the bite forces predicted by the original models.

Table 4 Bite force at the incisor, premolar and third molar predicted by models with altered muscle vector orientations. Positive angles represent rotations around the medio-lateral axis in an anterior direction. Percentage difference from bite force of original models (given in Table 1) calculated. Muscle orientations measured in the parasagittal plane.

	Bite force (N)			% difference		
	I	PM	M3	I	PM	M3
SM +10°	1467	3154	4401	5.63	5.68	5.66
SM −10°	1287	2766	3863	−7.31	−7.31	−7.26
DM +10°	1386	2980	4161	−0.21	−0.15	−0.11
DM −10°	1383	2970	4144	−0.42	−0.48	−0.52
IOZM +10°	1494	3205	4470	7.56	7.41	7.31
IOZM −10°	1264	2722	3804	−8.96	−8.79	−8.67
MP +10°	1378	2964	4140	−0.76	−0.67	−0.61
MP −10°	1397	2998	4181	0.58	0.46	0.37

I, incisor; PM, premolar; M3, third molar; SM, superficial masseter; DM, deep masseter; IOZM, infraorbital zygomaticomandibularis; MP, medial pterygoid.

Stress distribution

Figure 3 shows the distribution of von Mises stresses across the skull during biting at the different teeth. It can be seen that bites on all teeth produce high stresses on the zygomatic arch and the zygomatic process of the frontal bone. Incisor bites also generate a small region of high stress on the ventral rostrum around the incisive foramina, as well as a highly stressed area in the postero-dorsal part of the orbit. Moderate stresses are found across the rest of the orbital wall and along the dorsal part of the skull from the nares to the posterior orbital margin. Premolar bites produce lower stresses than incisor bites in the orbit and skull roof, but stress across the skull then increases as the bite point moves further along the molar tooth row towards the jaw joint. Bites on the third molar generate high stresses in the anterior orbital wall, the posterior part of the rostrum, the alisphenoid bone in the postero-ventral part of the orbit, and in a small zone on the skull roof dorsal to the posterior orbital margin. In unilateral molar bites, the von Mises stresses are generally lower on the balancing side, although still high in the zygomatic arch. Peak von Mises stresses in the cranium (excluding the teeth) are 24.8 MPa in incisor bites, 23.4 MPa in premolar bites, and between 27.4 and 39.1 MPa in molar bites (Table 2).

Despite notable effects on bite force, changing the length of the incisors or the magnitude of muscle force loaded on the model has no identifiable impact on the distribution of

Table 5 Minimum and maximum bite force at each tooth predicted by the finite element model of *Josephoartigasia monesi*.

Biting tooth	Minimum bite force (N)	Maximum bite force (N)
I	967	1850
PM	2082	3970
M1	2301	4389
M2	2533	4819
M3	2914	5534

I, incisor; PM, premolar; M1, first molar; M2, second molar; M3, third molar.

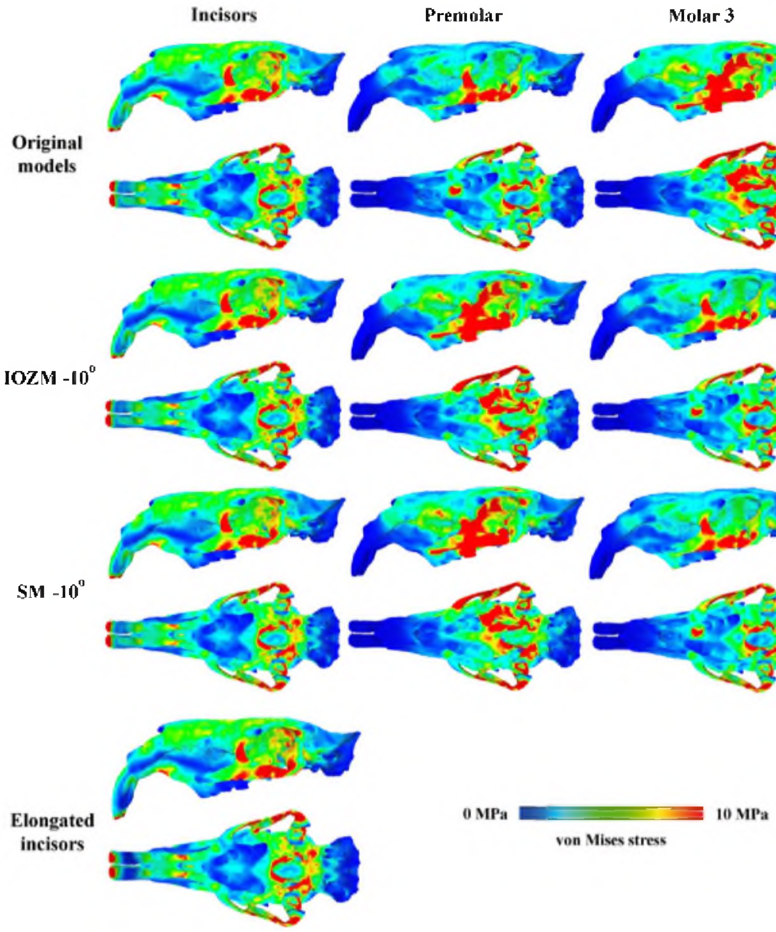

Fig. 3 Predicted distribution of von Mises stresses across the skull of *Josephoartigasia monesi* during bites at the incisors (first column), the left premolar (second column) and the left third molar (third column), shown in left lateral and ventral views. Lines 1 and 2, models with original orientation of muscle vectors; lines 3 and 4, IOZM vector rotated 10° posteriorly; lines 5 and 6, superficial masseter (SM) vector rotated 10° posteriorly; lines 7 and 8, model with incisors elongated by 50 mm.

von Mises stresses across the skull. Reorientation of the superficial masseter and IOZM vectors by 10° posteriorly slightly reduces the stresses around the incisive foramina during incisor biting, and reduces stresses on the rostrum immediately superior to the IOZM attachment area during biting at the third molar (Fig. 3). Otherwise, changing the orientation of the muscle vectors appears to have little impact on von Mises stress distributions.

Discussion

Cranial biomechanics

The solved FE models presented here indicate that, based on previously estimated muscle forces (Blanco et al. 2012), *J. monesi* would have been able to generate a bite force of approximately 1389 N at the incisors, and between 2984 and 4165 N at the cheek teeth (Table 2). Although no explicit validation can be performed on these values, previous work has shown that bite forces predicted by FE models of rodent (rat and guinea pig) crania closely match forces measured by *in vivo* experiments (Cox et al. 2012). The incisor bite force is around 40% higher than the 959 N calculated by Blanco et al. (2012). This is partly due to the higher total muscle force in this study resulting from the addition of forces representing the (non-infraorbital) ZM and medial and lateral pterygoid muscles. However, the total muscle CSA is only 24% higher in the FE models in this study than in the Blanco et al. (2012) reconstruction, so other factors are likely to be contributing to the increased bite force as well, such as the orientation of the muscle vectors.

It should be noted that the incisor bite force estimated by this study is substantially lower than the 3214 N estimated from incisor cross-sectional area by Blanco et al. (2012). Even in light of the refined bite force estimations here, it still appears that the incisors of *J. monesi* were overengineered with respect to feeding; that is, they could resist much greater forces than could ever be generated by the masticatory muscles. Thus, it has been suggested that *J. monesi* may have regularly used its incisors for activities other than feeding, such as digging for food or defence against predators, both of which would generate higher forces at the incisors by using other muscles such as the neck musculature. The peak von Mises stresses predicted here certainly indicate that the skull could withstand activities generating greater forces than produced by feeding. The maximum stress calculated for incisor biting was 24.9 MPa, which is very much lower than both the compressive and tensile yield stresses of bone (180 and 130 MPa, respectively; Cezayirilioglu et al. 1985). Overall, the peak stresses experienced by the skull of *J. monesi* are quite high, exceeding those predicted for felids and canids (5.6–21.8 MPa; Thomason, 1991), and for the lion and *Smilodon* (< 20 MPa; McHenry et al. 2007). However, even the peak von Mises stress predicted for biting at the third molar (39.1 MPa) is exceeded by many small mammals during feeding, e.g. bats (Dumont et al. 2005) and callitrichid primates (Bourke et al. 2008). Unfortunately, data on cranial stress during feeding is lacking for large mammals, so it is not possible to ascertain whether *J. monesi* was unusual in this regard, but it is clear that there was a considerable margin of safety in the skull with respect to feeding behaviour.

The molar bite forces of *J. monesi* have not been estimated before and show an increase as the bite point moves closer to the jaw joint. Comparing the bite forces here with those predicted by previous FE studies on rodents (Cox et al. 2012, 2013), it can be seen that the ratio of premolar bite force to incisor bite force in *J. monesi* (2.15 : 1) is similar to that found in guinea pigs (2.10 : 1) but higher than most other rodents such as squirrels (1.86 : 1) and the Laotian rock rat (1.84 : 1). Beyond the premolar, the increase in bite force along the tooth row is relatively modest in *J. monesi*. The M3:PM bite force ratio is just 1.40 : 1, very similar to that seen in *Laonastes aenigmamus*, but lower than that found in *Sciurus carolinensis* and *Cavia porcellus* (1.80 : 1 and 1.72 : 1, respectively). These bite force ratios are reflective of the skull morphology of *J. monesi*: the extended rostrum and elongated diastema result in the disparity between premolar and incisor bite forces, whereas the relatively short molar tooth row leads to similar bite forces along all the cheek teeth.

It should be noted that the bite forces predicted here are based on maximal activation of all masticatory muscles on both sides of the jaw. Greaves (1978) proposed a model in which balancing side muscle forces are reduced at the distal molars to counteract distractive forces at the working side jaw joint, thus resulting in the generation of a similar bite force all along the molar tooth row. This is not the case in this model of *J. monesi*, in which the reaction force at the jaw joint on the working side is positive at all bites, including those on the third molar (Table 2). Furthermore, the reduced length of the tooth row means that the difference between bite force produced at the mesial and distal teeth is much less than it would be in the selenodont artiodactyls on which Greaves based his model. Nevertheless, it has been shown in guinea pigs that the balancing side muscle forces tend to be less than those of the working side during unilateral chewing (Byrd, 1981), so the results here should be interpreted as maximum possible bite forces rather than 'normal' chewing forces.

The lack of soft tissue data for *J. monesi* means, of course, that the bite forces predicted by the FE models are only estimates and have a degree of uncertainty surrounding them. The sensitivity analysis conducted here seeks to quantify that uncertainty. Taking all masticatory muscles into account, assuming an uncertainty of ± 20% in muscle force magnitude and ± 10° in muscle force vector, the bite forces reported in Table 2 have an error of ± 30–33%. This equates to a range of approximately 900 N for incisor bite forces, rising to 2600 N at the third molar. Although the ranges are large, they do give an indication of the magnitude of bite that *J. monesi* was able to deliver at each tooth. It is clear that the bite force of *J. monesi* was very large in absolute terms, at all teeth. Even with the assumptions that lead to the lowest bite forces (Table 5), the forces produced by *J. monesi* at the cheek teeth are still higher than all the canine bite forces estimated by Wroe et al. (2005) for some of the largest and most powerful carnivoran species. Indeed, the molar bite forces predicted for *J. monesi* are of similar magnitude to those measured at the molariform tooth of some of the largest crocodilian species (Erickson et al. 2012).

Blanco (2008) suggested that, owing to its short molar tooth row compared with its cranial length, *J. monesi* was not a good grazer and primarily only fed on soft plants. Isotopic analysis of fossil tooth enamel indicates that *J. monesi* and other large rodents fed almost exclusively on C_3 plants (Higgins et al. 2011). The very large molar bite forces predicted here indicate that *J. monesi* could feed on a wide variety of plant material, hard or soft. This prediction, combined with peak cranial stresses well below the yield stress of bone and the finding that the incisors were overengineered with respect to the bite forces generated by the masticatory muscles, indicates that *J. monesi* may have been behaving in a similar manner to an elephant. That is, it could process a broad selection of tough vegetation with the short molar tooth row, while using its unusually strong incisors like tusks for defence and digging for roots. Unfortunately, no *in vivo* bite force measurements exist for large herbivores, so direct comparisons with the bite force of elephants or other large herbivores are not possible.

Muscle function

The sensitivity analyses enable the determination of which muscles have the greatest impact on feeding biomechanics. In terms of the magnitude of muscle force, the superficial masseter has the greatest effect on bite force, followed by the IOZM and the deep masseter. This demonstrates that it is not simply the largest muscles that have the greatest influence. Indeed, the third largest muscle of mastication, the temporalis, has an almost negligible impact on bite force, which may be due to its largely horizontal direction of pull. Thus, the primary role of the temporalis in *J. monesi* may be something other than force generation. Electromyography studies on rats (Hiiemae, 1971) and hamsters (Gorniak, 1977) have suggested that the temporalis in rodents may principally act to retract the lower jaw. Alternatively, from work on the guinea pig, it has been proposed that the rodent temporalis functions as a counterbalance to lateral translation of the mandible (Byrd, 1981). It is likely that the fibres of the temporalis in *J. monesi* actually change direction from largely horizontal to a more vertical orientation, as they run over the zygomatic process of the squamosal. Such a morphology was also noted in *Hystrix* by Turnbull (1970), who suggested that it allowed the temporalis to position the mandible with great precision. This would compensate for the lack of precision supplied by the jaw joint owing to the open glenoid fossa, which is needed for the characteristic antero-posterior movements of the jaw found in rodents. In comparison, the size of the deep masseter, which is only the fifth largest muscle of mastication in *J. monesi*, has quite a considerable effect on bite force, probably owing to its strongly vertical mode of action. This is consistent with the calculations of Turnbull (1970), who found that the masseter of rodents contributed between 15 and 36% more to bite force than would be expected based on muscle mass alone. This supports the suggestion that the deep masseter is responsible for the power stroke of mastication in rodents (Hiiemae, 1971).

In terms of the orientation of muscle pull, the muscles with the greatest influence on bite force were (in order) the IOZM, superficial masseter and the temporalis. In contrast, a change of 10° in the orientation of the medial pterygoid and deep masseter muscle had very little effect; the bite force was altered by $< 1\%$. It seems that bite force is most sensitive to changes in the vectors of those muscles which form the greatest angle with the bite force vector, such as the superficial masseter and IOZM. A change of 10° in the orientation of these muscles can cause a large change in the dorsal component of pull and thus can have a large impact on the force generated at the teeth, compared with the negligible change in bite force generated by re-orienting the deep masseter or medial pterygoid, both of which are almost parallel to the direction of bite force. However, it should be noted that the superficial masseter and IOZM are also the largest masticatory muscles and so would be expected to have a greater effect on bite force based on load magnitudes alone. This notwithstanding, the IOZM is clearly an important muscle of mastication in *J. monesi*, with changes to its direction of pull leading to differences in bite force of between 7 and 9%. A similar result was found in a study of the Laotian rock rat (Cox et al. 2013) in which the position of IOZM, and by extension its force orientation, was found to affect bite force by around 10% at all teeth. The results from this study indicate that the IOZM may affect incisor biting slightly more than molar biting in *J. monesi*.

Overall, when estimating bite force in *J. monesi*, and probably most caviomorph rodents, the accuracy of the estimate is most dependent on the accuracy of the orientation of the IOZM, and superficial masseter. In addition, the accuracy of the muscle force data for the masseter complex (superficial masseter, deep masseter and IOZM) is also important. The size of the temporalis and medial pterygoid, and the orientation of the deep masseter and medial pterygoid have little effect on the results. Surprisingly, the reconstructed length of the incisors had very little effect on the estimation of bite force, which is encouraging for researchers wishing to study feeding biomechanics of extinct taxa only known from damaged specimens. Despite the large variation in bite force with muscle input parameters, few differences were noticed in the von Mises stress distributions across the skull among the models solved as part of the sensitivity analysis (Fig. 3). It appears that the major driver of stress pattern is the geometry of the skull itself, rather than the relative magnitudes of the muscle forces or the orientation of the muscle force vectors.

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Author contributions

P.G.C. designed and carried out the study. A.R. and R.E.B. arranged CT scanning of the specimen. All authors analysed the results and contributed to the writing and editing of the manuscript.

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Quinto artículo

RINDERKNECHT, A., UBILLA, M.,MANZUETTI, A., PEREA, D. & P. TORIÑO, 2019. First record of *Tetrastylus* Ameghino, 1886 (Riodentia; Dinomyidae) from the upper Miocene of Uruguay. *Revista Brasileira de Paleontología*, 22(1): 30-37, figs. 1-5, 1 tabla.

Reportamos la presencia del género *Tetrastylus* por primera vez para Uruguay y realizamos consideraciones sobre el desarrollo ontogenético en este taxón. El material en estudio consiste en una rama mandibular derecha en excelente estado de preservación identificado como perteneciente a un individuo juvenil y proveniente del Departamento de San José.

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FIRST RECORD OF *TETRASTYLUS* AMEGHINO, 1886 (RODENTIA; DINOMYIDAE) FROM THE UPPER MIOCENE OF URUGUAY

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ABSTRACT – The first record for Uruguay of the dinomyid rodent *Tetrastylus* Ameghino, an almost complete right mandible from the upper Miocene Camacho Formation, is described. According to the p4 and m3 morphology it is inferred a juvenile- subadult ontogenetic stage for this specimen.

Keywords: Rodentia, Dinomyidae, upper Miocene, Uruguay.

RESUMO – O primeiro registro para o Uruguai do roedor dinomiideo *Tetrastylus* Ameghino, baseado em uma mandíbula direita quase completa do Mioceno superior da Formação Camacho, é descrito. O material provém de sedimentos do Mioceno superior do Uruguai (Formação Camacho). Tendo em conta a morfologia do p4 e m3 é inferido um estágio ontogenético juvenil- subadulto para este espécime.

Palavras-chave: Rodentia, Dinomyidae, Mioceno superior, Uruguai.

INTRODUCTION

Dinomyidae is one of the three families of 'giant' rodents known from South America (Bondesio, 1978 and references therein). Nowadays the family includes only the "pacarana" (*Dinomys branickii* Peters, 1873), which is a peculiar "long headed" cursorial Amazonian caviomorph considered among the largest living rodents, with a body mass of approximately 15 kg (Collins & Eisenberg, 1972; Peters, 1873; Pocock, 1926; Sanborn, 1931; White & Alberico, 1992). Contrary to this impoverished current record, the past diversity of the group was notable, with a large number of fossil genera and species reaching body sizes even larger than that of the pacarana. The most extreme example is the giant *Josephoartigasia monesi* Rinderknecht & Blanco, 2008, the largest rodent ever recorded with an estimated mean body mass close to a ton (Rinderknecht & Blanco, 2008; but see Blanco, 2008; Millien, 2008). The fossil record of the Dinomyidae undoubtedly begins during the middle Miocene (Friasian?/Laventan SALMA), but the genus *Branisamys* Hoffstetter & Lavocat, 1970 from the Salla beds in Bolivia (Deseadan SALMA, late Oligocene) has been placed in the family by some authors (see Vucetich *et al.*, 1999; Nasif, 2009; Nasif & Abdala, 2015). Fossil members of the Dinomyidae have been described from almost every South American country (Figure 1), being the collections from Argentina, Colombia, Venezuela, Brazil and Uruguay the most important.

While the first described fossils of the family date back to the late 19th century (Ameghino, 1883, 1885, 1886, 1891a, 1981b, 1889; Burmeister, 1885), only in recent years the phylogeny of Dinomyidae has been addressed using a modern cladistic approach (see Nasif, 2009; Kramarz, 2013; Kerber *et al.*, 2016a,b; 2018). The revision made by Kraglievich (1926, 1932) remains as the current systematic arrangement for the entire family (but see Rinderknecht *et al.*, 2018). Following Kraglievich´s main framework complemented and corrected by Fields (1957), Pascual (1967), and Mones (1981), the family is subdivided into four to five subfamilies: Potamarchinae (including the oldest known representatives of the family, extending from the late Oligocene? to the early? Pliocene); Gyriabrinae (late Miocene–late? Pliocene), Dinomyinae (including only the extant *Dinomys branickii*); Eumegamyinae (late Miocene–late Pliocene? including the largest representatives of the family), and Tetrastylinae (late Miocene–Pleistocene), considered by many authors as a subgroup of the Eumegamyinae or Dinomyinae (see Fields, 1957; Mones, 1981). According to the latest systematic revisions (Rinderknecht *et al.*, 2011; 2018; Rinderknecht & Blanco, 2015; Kerber *et al.*, 2018), the family is composed only by the subfamilies Eumegamyinae, Tetrastylinae and

Figure 1. Map of South America showing the approximate current distribution of *Dinomys branickii* (black) and the locations (points) with a fossil record of the Dinomyidae. Modified from Rinderknecht *et al.* (2011, fig. 1).

Potamarchinae. Although this systematic scheme gives some stability to the more than 60 fossil species described (Kraglievich, 1926, 1930; Mones, 1986), knowledge of the morphology of these animals is far from been satisfactory due to the lack of associated cranial and postcranial remains. In fact, most specimens are known only by isolated teeth and/ or small fragments of skulls or mandibles (Mones, 1986), preventing any possibility of developing a comprehensive comparative analysis of the different lineages in Dinomyidae.

In Uruguay, in comparison with other groups of mammals, the fossil record of the family is poor and restricted to the southwest portion of the country (Figure 1). The study of these animals began during the first half of the 20th century with the discovery and description of a partial palate without clear stratigraphic provenance assigned to one new species: *Gyriabrus teisseirei* Kraglievich (1930). Later, Francis & Mones (1966) described *Artigasia magna* (see Mones, 2007) based on a reworked jaw fragment bearing part of the dental series and an isolated incisor of presumed late Pliocene age, and tentatively ascribed to the San José Formation (currently Raigón Formation, see Tofalo *et al.*, 2009, or San José Member of Raigón Formation, Bossi *et al.*, 2009). Calcaterra (1972) proposed the presence of *Eumegamys* sp. based on a reworked incisor fragment recovered from the coast of El Real de San Carlos, Colonia Department. The new species *Isostylomys intermedius* Mones & Castiglioni, 1979 was based on a single premolar collected in the upper Miocene sediments of the Camacho Formation, San José Department. This last taxon was synonymized with *Isostylomys laurillardi* by Rinderkencht el at. (2018). Recent revisions of the materials deposited in the collection of the Museo Nacional de Historia Natural de Montevideo, Uruguay (MNHN), have contributed to the knowledge of the morphology of the group. Rinderknecht (2007) reported the first known articulated postcranial remains of an eumegamyine; Rinderknecht and Blanco (2008) described the well preserved skull of *Josephoartigasia monesi*; Rinderknecht *et al.* (2011) described a new genus (*Arazamys*) based on remains coming from Miocene deposits of the Camacho Formation. Finally, Rinderknecht *et al.* (2018) presented the first associated craniomandibular remains of the genus *Isostylomys* Kraglievich, 1926 and the first juvenile remains know for the subfamily Eumegamyinae, addressing some aspects of dental development in eumegamyines.

In this work we reported for first time in Uruguay the presence of the dinomyid rodent *Tetrastylus* Ameghino, 1886, based on an almost complete right mandible ramus. The material comes from sediments of the upper Miocene.

MATERIAL AND METHODS

The studied specimen is housed in the Vertebrate Paleontological Collection of the Facultad de Ciencias, Departamento de Paleontología, Uruguay (**FC-DPV**). As a comparative framework oriented towards analysing the ontogenetic development of the Tetrastylinae, we studied specimens in different ontogenetic stages of the genus *Dinomys*, and followed the recent study of Nasif & Abdala (2015) about the craniodental ontogeny of this genus. The present study considers four stages of ontogenetic development: the neonate, juvenile (specimens with some unerupted tooth, or some tooth with minimal worn, including the stages juvenile II-V in Nasif & Abdala, 2015), subadult (specimens with all erupted and functional tooth, but less worn than in full-growth adult, subadult VI in Nasif & Abdala, 2015) and adult stage (adult VII in Nasif & Abdala, 2015).

The morphological terminology used in this paper follows Nasif & Abdala (2015), Rinderknecht *et al.* (2018), and Patterson & Wood (1982). The examined specimens that were used as comparison and their institutional abbreviations are listed in the Appendix 1. The fossil material was measured with a digital Vernier caliper (0.1mm accuracy).

GEOLOGICAL SETTING

The fossil-bearing strata are located in southwestern Uruguay (San José Department; 34°34'S, 56°58'W) in exposures located on the coastal cliffs and littoral platform of the Río de La Plata (Figure 2). There, the lithostratigraphic units recognized from base to top are the Camacho (upper Miocene), Raigón (Pliocene and Pleistocene) and Libertad (Pleistocene) Formations (Bossi & Navarro, 1991; Tófalo *et al.*, 2009). The first two units yield many vertebrate fossils, including a variety of cingulates, ground sloths, rodents and notoungulates (Vizcaíno *et al.*, 2003; Rinderknecht *et al.*, 2011; 2018; Perea *et al.*, 2013). The remains described here were found in sediments of the Camacho Formation. This Formation is the representation in Uruguay of an extended, late Miocene, eustatic event regionally known as the *Paranean transgression* or *Paranean Sea* (Sprechmann *et al.*, 2000). In the San José Department, the facies are related to the regressive phase characterized as estuarine and/or paralic environments. Terrestrial and marine vertebrates in association with marine invertebrates and ichnofossils comprise the fossil assemblage of the unit (Ubilla *et al.*, 1990; Perea *et al.*, 1996; Sprechmann *et al.*, 2000; Perea, 2005; Perea *et al.*, 2013). The sediments of the Camacho Formation are composed by greenish-grey friable and medium compacted pelite that becomes greenish-brownish towards the top of the formation. The mammalian fossil assemblage includes marsupial carnivores, xenarthrans, notoungulates, litopterns, hystricognath rodents, and cetaceans, showing affinities with the upper Miocene Chasicoan and Huayquerian Ages/Stages of Argentina, especially with the one informally known as the *"Mesopotamiense"* (formerly considered as a Huayquerian local fossil fauna), of the Entre Ríos Province (Bostelmann & Rinderknecht, 2010; Brandoni, 2013; Mones & Rinderknecht, 2004; Perea *et al.*, 1994; Perea, 2005; Perea *et al.*, 2013; Rinderknecht *et al.*, 2011; Vizcaíno *et al.*, 2003). ^{40}Sr/^{39}Sr dated levels of the Paraná Formation and its southern correlative, the Puerto Madryn Formation (Scasso *et al.*, 2001), renders a late Miocene 9.5 Ma–10 Ma (Tortonian) age for the top of the *Paranean Sea* in Argentina. Recently, the Camacho Formation was dated in 7.5–6 Ma, using Sr-isotope stratigraphy (del Río *et al.*, 2018) or 11–9 Ma, (Soibelzon *et al.*, 2019).

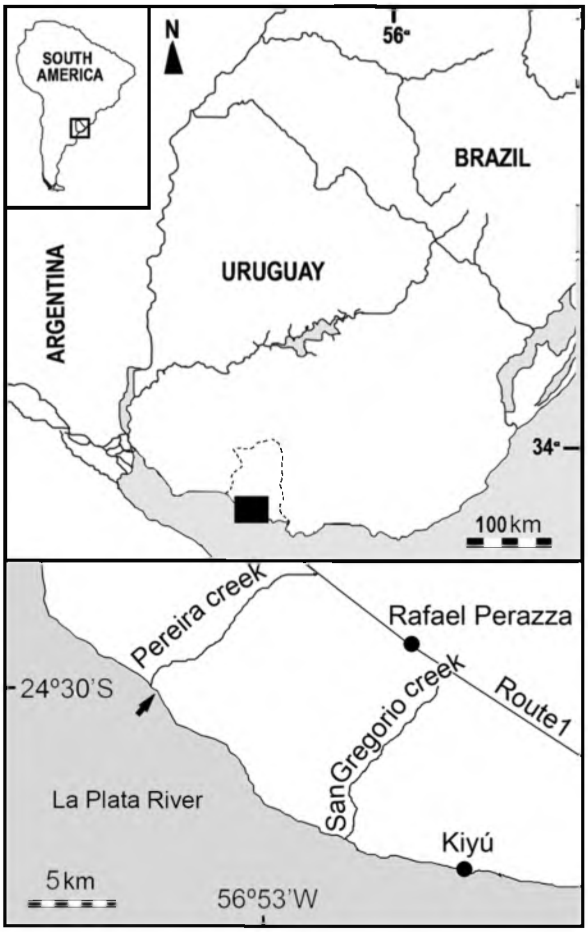

Figure 2. Geographic location of *Tetrastylus* sp. (FC-DPV 2891) in Departament of San José (dotted line). The arrow shows the approximate site of collection.

SYSTEMATIC PALEONTOLOGY

Family DINOMYIDAE Alston, 1876
Subfamily TETRASTYLINAE Kraglievich, 1931

Tetrastylus Ameghino, 1886

Tetrastylus sp.
(Figures 3–5; Table 1)

Material. FC-DPV 2891: An almost complete right mandible with incisor and p4–m3 (Figures 3–5 and Table 1).

Geographic and Stratigraphic provenance. Uruguay, Departamento de San José, Puerto Arazatí, Camacho Formation (upper Miocene, Huayquerian SALMA).

DESCRIPTION

The mandible is almost complete, lacking most of the angular process, the ascending ramus, and the extralveolar portion of the incisive. The masseteric fossa is not well defined and is located below the m1. Like all Dinomyidae (especially Eumegamyinae and Tetrastylinae) the coronoid process is reduced, forming a small uneven surface on the posterolabial side at the m3 level. The incisor is robust and the enamel surface does not have the tiny longitudinal ridges commonly observed in Eumegamyinae (see Rindeknecht *et al.* 2018). The alveolar portion of the incisor shows a slight curvature starting below the m3. The grinding teeth are constituted by four lophids of dentine recovered by enamel, which is thicker in the posterior face than in the anterior one (Figures 3–4). A thin layer of cementum separates the lophids. The two-anterior lophids are labially joined in m1-m2 and completely free in p4 and m3. Three poorly defined columns of enamel form the anterior lophid of the p4. The cheek teeth of Dinomyidae usually have these columns before complete the ontogenetic process (see Kraglievich, 1932; Mones, 1997; Nasif & Abdala, 2015; Rinderknecht *et al.*, 2018). In fact, these are cusps that meanwhile the specimen is growing become fused to form a complete lophid (see Marivaux *et al.*, 2004; Nasif & Abdala, 2015). Similar structures can be seen in the M3 of many giant dinomyids, but these structures can remain in the adult stage (Rinderknecht *et al.*, 2018). The specimen FC-DPV 2891 present the last two lophids of the p4 free and a small enamel column located between the lingual borders of both lophids can be identified. This structure is also considered characterizing juvenile and subadult stages and probably disappears in the adult stage (see Figure 5, and Nasif & Abdala, 2015, fig. 11a). The m1 and m2 are similar in morphology with the two first lophids joined in the labial face and free in the lingual ones. The two posterior most lophids of m1 and m2 are completely free and only are connected each other by a thin layer of interprismatic cementum. The m3 has the four lophids free and is the smallest tooth of the check teeth due it is in phase of eruption; it has a cone configuration observed in juvenile and subadult hypselodont mammals (Kraglievich, 1930). The first lophid is the smallest and has a mesial projection in the medial portion of the anterior border (see Figures 3–4). This structure is the remnant of an enamel column recently fused to the lophid. The last lophid of m3 is the smallest and lacks the projections or columns of enamel. All the aforementioned features indicate that FC-DPV 2891 was a juvenil (state V *sensu* Nasif & Abdala, 2015) - subadult specimen.

Figure 3. Right mandible of *Tetrastylus* sp. (FC-DPV 2891) in occlusal (**A**), external (**B**), and internal (**C**) views. Scale bar = 50 mm.

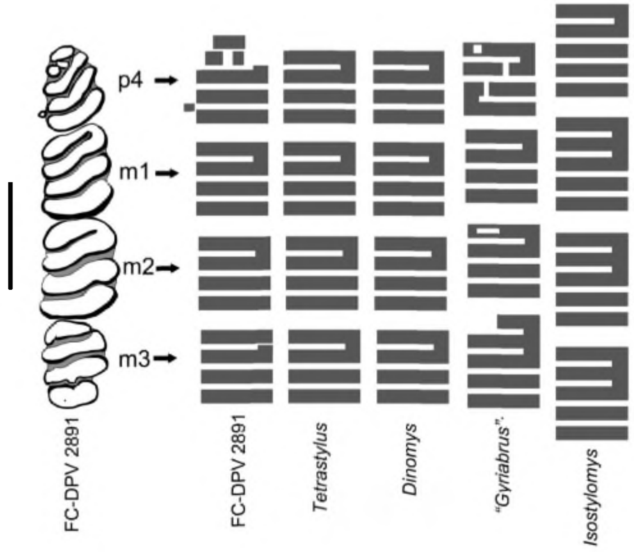

Figure 4. Right p4-m3 of *Tetrastylus* sp. (FC-DPV 2891), in occlusal view, and schemes (not at scale) of lower cheek-tooth in different Dinomyidae genera. Scale bar = 10 mm.

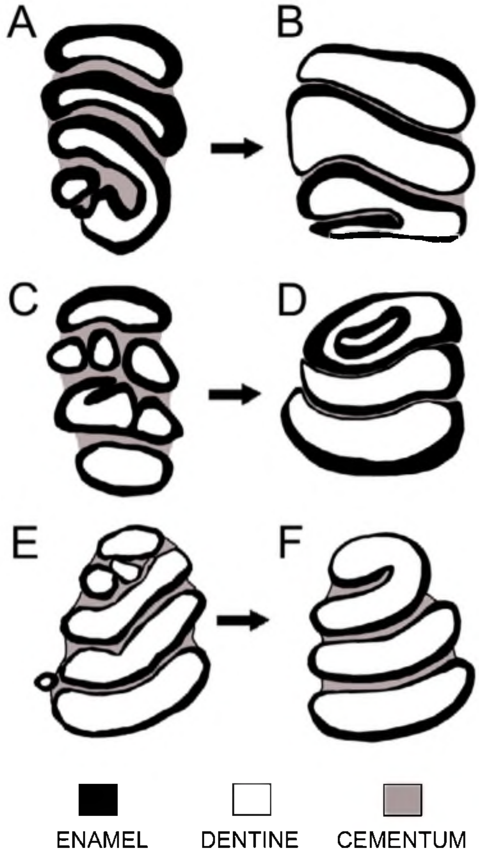

Figure 5. Occlusal view of Dinomyidae adult and juvenile teeth (not to scale). **A**, right upper first molar of *Dinomys branickii* juvenile (NHMUK 12.1.15.14). **B**, right upper first molar of *D. branickii* adult (NHMUK 3796). **C**, left first lower molar of *D. branickii* juvenile (MACN 12962). **D**, left first lower molar of *D. branickii* subadult (NHMUK 34.9.10.191). **E**, lower premolar of *Tetrastylus* sp. (FC-DPV 2891). **F**, lower premolar of *Tetrastylus laevigatus* (Ameghino, 1885) adult (MLP52-X-1-59). Modified from Rinderknecht *et al.* (2018, fig. 11), and Kraglievich (1932, fig. 5).

Table 1. Dental measurements (in mm) of *Tetrastylus* sp. (FC-DPV 2891).

	Mesiodistal length	Buccolingual width
Right p4	7.9	6.2
Right m1	8.7	6.9
Right m2	10.0	7.5
Right m3	8.2	6.1
Right i	6.5	7.0

DISCUSSION AND CONCLUSIONS

Tetrastylus is the best-represented dinomyid in the fossil record. This genus has at least eight species described (see Mones, 1986), ranging from Miocene to late Pliocene (or even Late Pleistocene, see Paula Couto, 1951), and mainly recovered in the fossil record of Argentina, Venezuela, Brazil and Peru. Some of these species were described based on well-preserved specimens (like *T. intermedius* Rovereto, 1914) but others on scarce and fragmentary materials. Nasif *et al.* (2013) indicate a non-monophyletic condition for this group of species mainly based on an unpublished work (Nasif, 2009).

Due to the high overall similarity among the species described and included into the subfamily Tetrastylinae, is extremely difficult to identify species based on mandibles not associated to skulls. Nevertheless, the material here described yields useful characters, enough to confidently assign it to this genus according to the present state of knowledge.

FC-DPV 2891 is assigned to the subfamily Tetrastylinae based on hypselodont teeth and tetralophodont grinding teeth condition, differing from Eumegamyinae because this last subfamily has lower grinding teeth (except the m1 of some taxa) with five lophids. The teeth of FC-DPV 2891 has all the lophids free in the lingual face, differing from the members of the subfamily Gyriabrinae that exhibit joined lophids in this face. However, it should be highlighted that the validity of Gyriabrine was questioned because its included taxa could be in fact juvenile specimens of other subfamilies of Dinomyidae (Rinderknecht *et al.*, 2018). The possession in FC-DPV 2891 of joined lophids only in the labial face of lower teeth, and rudimentary coronoid process, also allows to dismiss the subfamily Potamarchinae (see Kerber *et al.*, 2016a,b). The differentiation of the studied material of Uruguay with regard to the giant tetrastylines *Telicomys* and *Carlesia* (this last genus sometimes equivocally assigned to Eumegamyinae, see Bondesio, 1978), is based on the relation between the incisor size and grinding teeth. *Telicomys* and *Carlesia* yield extremely large incisors even for the entire family, meanwhile the material here studied follow the pattern showed by *Dinomys* and *Tetrastylus*. The smaller size of our material (Table 1) compared with *Telicomys* and *Carlesia* could be an additional difference. However, caution should be taken with size when having only mandibular remains, since some members of fossil Dinomyidae could reach the complete configuration of the mandible early in the ontogeny, still being smaller compared with adults (see Nasif & Abdala, 2015; Rinderknecht *et al.*, 2018).

The genus *Tetrastylopsis* Kraglievich, 1931 has lower teeth with lophids lingually joined (p4); lophids joined in the labial face (last two lophids of m1) and in the lingual face (two anterior lophids of m1). This pattern clearly differentiates it from the Uruguayan specimen.

Tetrastylomys Kraglievich, 1926 was described on an isolated tooth with four free lophids. Even though there is no assignation to a specific tooth (grinding teeth, premolar, lower or upper) it could belong to the subfamily Tetrastylinae based on the morphology of the lophids and because its small size. Nevertheless, Kraglievich (1926) hesitantly refer it to some antillean giant rodents and not to Dinomyidae. Unfortunately, the fragmentary information available precludes any comparison with the Uruguayan material. In addition, due to the fragmentary condition of *Tetrastylomys* it should be considered as a "nomen inquirendum".

The FC-DPV 2891 specimen differs from *Dinomys* in having a larger size, relatively larger teeth and by a lesser curvature radius of the incisor. This last feature turn the FC-DPV 2891 incisor more proodont than *Dinomys*. In addition, the masseteric mandibular fossa is more anteriorly located in *Dinomys* than in the Uruguayan specimen. It is important to note that this last characteristic changes during the ontogenetic development in *Dinomys*, since the juvenile individuals present the masseteric mandibular fossa in a more anterior position than the adults (see Nasif & Abdala, 2015). However, in FC-DPV 2891 this structure is in a more posterior location even than the adults of *Dinomys*.

Despite having a characteristic morphology, in particular the p4 and m3, FC-DPV 2891 is interpreted as having a juvenil-subadult condition. Juvenile specimens of *Dinomys* show similar morphology in the erupting teeth, maintaining enamel column not yet joined forming a lophid (NHMUK 12.1.15.4, UDCA-UIFS 032, UDCA-UIFS 098, UDCA-UIFS 136, and see Nasif & Abdala, pp.11, 13). This last condition also can see in the p4 of subadult specimens (NHMUK 34.9.10.191) but with a somewhat higher degree of fusion of columns than in the FC-DPV 2891. Our studies on ontogeny of *Dinomys* and previous works (Ray, 1964; Mones, 1997; Nasif & Abdala, 2015; Rinderknecht *et al.*, 2018) show that the last two teeth in eruption are the p4 and m3. This is the reason of the peculiar morphology of these teeth of FC-DPV 2891. Due to the late eruption stage of the p4 and m3, it is expected to have less wear than the remaining teeth, and reach later the definitive configuration than the m1 and m2. Far from considering this morphology as having taxonomic value, we conclude that caution should be taken about any specific taxonomic decision about this material.

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Appendix 1. Examined specimens that were used as comparison and their institutional abbreviations.

Specimens of *Dinomys branickii* utilized in our analysis belong to the following institutions: **MACN**, Colección Mastozoológica del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MNHN**, Museo Nacional de Historia Natural, Montevideo, Uruguay; **NHMUK**, The Natural History Museum, London, United Kingdom; **UDCA-UIFS**, Unidad de Investigación en Fauna Silvestre de la Universidad de Ciencias Aplicadas y Ambientales, Bogotá, Colombia; **UNMSM-MUSM**, Colección de Mastozooología del Museo de Historia Natural de la Universidad Nacional de San Marcos, Lima, Perú.

List of specimens (*Dinomys branickii*): nearly complete skeleton (MNHN 3795, adult); skull and mandibles: (MNHN 3796, adult); (NHMUK 34.9.10.191, subadult); (NHMUK 12.1.15.4, juvenile); (MACN 12961, adult); (MACN-M 12962, neonate); (UNMSM-MUSM 2217); (UNMSM-MUSM 5048); (UNMSM-MUSM 7887); (UNMSM-MUSM 11231); (UNMSM-MUSM 19855); (UNMSM-MUSM 23153); (UNMSM-MUSM 25759); (UDCA - UIFS 032, juvenile); (UDCA-UIFS 098, juvenile); (UDCA - UIFS 094, neonate); (UDCA - UIFS 136, juvenile).

Sexto artículo

RINDERKNECHT, A. & S. SOLER. 2015. Gigantes Bajo Tierra: animales misteriosos de nuestro pasado. *Ediciones Banda Oriental/Más Cerca*. Montevideo, 72 pp.

Aprovechando la gran difusión mediática que han tenido alguno de los descubrimientos paleontológicos de dinómidos, aprovechamos para realizar un libro de divulgación para niños y niñas de Uruguay. Se trata de una obra que comprende la temática de la paleontología en general, y utilizando como hilo conductor del relato, a estos carismáticos mamíferos fósiles. Es de destacar que el presente libro obtuvo una mención en el Premio Anual de Literatura del MEC.

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GIGANTES BAJO TIERRA

ANIMALES MISTERIOSOS DE NUESTRO PASADO

Andrés Rinderknecht · **Silvia Soler** · Ilustraciones: **Pantana**

+cerca BANDA ORIENTAL


SOFÍA


LUCAS

¿Sabías que en Uruguay vivió el roedor más grande del mundo?

Existen seres vivos en la Tierra desde al menos 3 500 millones de años. Hay muchos rastros de esos seres que vivieron en el pasado lejano: huesos, caparazones, hojas petrificadas... Esas huellas se llaman fósiles, una palabra de la que Sofía y Lucas no tenían la menor idea hasta que algo ocurrió y decidieron salir a investigar.

En las páginas siguientes te contamos por qué salieron a investigar y qué fue lo que encontraron. ¡Los seguimos!

Conclusiones finales y perspectivas

Nuestros estudios permitieron analizar el desarrollo ontogenético dental en Eumegamyinae, al menos en una parte importante del ciclo de vida de estos animales. Inesperadamente los fósiles de *Isostylomys* analizados no corroboraron ninguna de las anteriores hipótesis planteadas para el grupo, las cuales sostenían que los dinómidos presentaban grandes cambios en la morfología dental durante su crecimiento. Y esto sería especialmente notable en relación a la disminución gradual del número de lofos, lo cual ocasionaría que los adultos tuvieran dientes compuestos por menos lofos que los juveniles. Los fósiles analizados en esta tesis no corroboran dichas propuestas ya que se describe un juvenil y un adulto de la misma especie, con una diferencia de tamaño muy notable entre ambos materiales, y sin embargo las morfologías dentales de los dos ejemplares son virtualmente idénticas.

También se pone en duda la validez de la subfamilia Gyriabrinae la cual podría estar representando un grupo artificial en donde tradicionalmente se habrían incluido ejemplares juveniles de diferentes subfamilas.

El estudio de la fuerza de mordida en el género *Telicomys*, corrobora que algunas de las notables particularidades anatómicas en el cráneo de este taxón son adaptaciones para incrementar la fuerza de mordida. Con una masa estimada en el entorno de los 100 kg, la fuerza de mordida (estimada en base a la reconstrucción muscular) a nivel de los incisivos resultó muchos más elevada que lo esperado para un mamífero de su tamaño, arrojando un muy interesante dato para su interpretación paleobiológica. Este último taxón también posee unos incisivos desproporcionadamente grandes en relación al tamaño del cráneo y con una disposición opistodonta (a diferencia de *Josephoartigasia* en donde los incisivos son proodontes). De hecho, los incisivos son incluso muy grandes para la gran fuerza de mordida de la especie. Estos factores combinados nos hacen suponer que dicho taxón utilizaba los incisivos para una actividad específica diferente a la relacionada con la alimentación, como ser defenderse de depredadores o cavar.

El análisis de la fuerza de mordida de la especie *Josephoartigasia monesi* sugiere que dicho taxón presenta incisivos desproporcionadamente grandes y una fuerza de mordida en el entorno de los 1400 Newtons, una fuerza esperable para un mamífero del tamaño estimado para este roedor. Sin embargo, las fuerzas estimadas para los molares (de hasta 4165 Newtons) indican que *Josephoartigasia monesi* poseía una fuerza de mordida muy poderosa en lo que respecta a esta parte del cráneo.

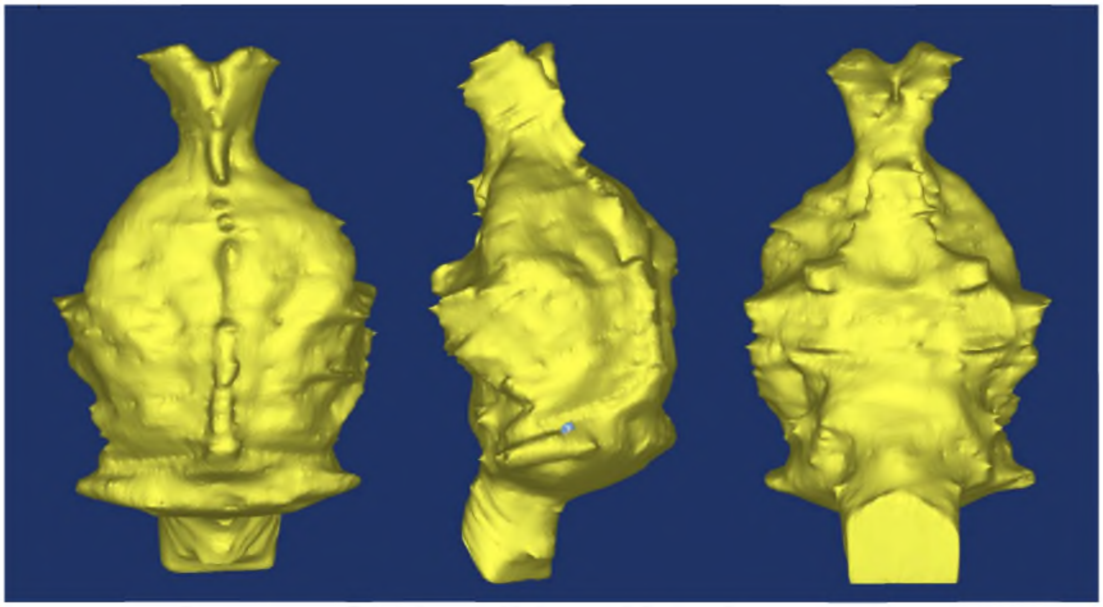
Somos conscientes que al no haber estudios filogenéticos con metodologías cladistas para la familia Dinomyidae la principal perspectiva de trabajo que deja planteada esta tesis es la de poder avanzar en este aspecto. También es cierto que nuestros propios estudios (especialmente los referidos a la región auditiva) muestran que un abordaje de estas características resulta por el momento muy difícil de realizar. De todos modos creemos que con nuevos hallazgos y con la localización de materiales actualmente extraviados se podrían resolver algunos puntos que aclararían notablemente el panorama sistemático de estos roedores. Estos puntos son:

A) Corroborar si los Gyriabrinae son un grupo artificial.

B) Verificar las relaciones de parentesco entre los Tetrastylinae y los Eumegamyinae.

C) Analizar la posibilidad de que el género *Dinomys* quede incluido dentro de los Tetrastylinae.

Por otra parte el excelente estado de preservación de algunos de los restos aquí estudiados permitirá realizar estudios de la dieta mediante el análisis isotópico dental. Si bien este tipo de estudios son muy poco comunes en Sudamérica la colaboración con especialistas de EE.UU. (Case Western Reserve University y University of Rochester) nos ha permitido comenzar a realizar dichas investigaciones. También tenemos en preparación el análisis de la tomografía realizada sobre el cráneo de *Josephoartigasia monesi* el cual nos permitirá realizar un estudio de la paleoneurología de dicho taxón (en colaboración con especialistas del Museo de La Plata) y un análisis de la resistencia mecánica del cráneo utilizando la técnica computacional de elementos finitos (en conjunto con investigadores de la Facultad de Ingeniería de Mar del Plata).


Reconstrucción digital de la cavidad cerebral de *Josephoartigasia monesi*.

Todos estos estudios así como los ya publicados esperamos puedan contribuir a mejorar sustancialmente al conocimiento de esta familia de mamíferos sudamericanos.

Materiales

Ofrecemos un listado de los materiales utilizados para esta tesis. Los acrónimos de las instituciones repositorios son los siguientes BMNH, British Museum of Natural History, Londres, Inglaterra; MNHN, Museo Nacional de Historia Natural, Montevideo, Uruguay; MLP, Museo de La Plata, La Plata, Argentina; MACN, colección paleontológica del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MACN-A, Colección Florentino Ameghino-Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina. MACN-M, Colección de Mastozoología del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina. UDCA-UIFS: Unidad de Investigación en Fauna Silvestre de la Universidad de Ciencias Aplicadas y Ambientales, Bogotá, Colombia; UNMSM-MUSM: Colección de Mastozoología del Museo de Historia Natural de la Universidad Nacional de San Marcos, Lima, Perú.

Josephoartigasia monesi — Complete skull (holotypo) (MNHN 921).

Arazamys castiglionii — Incomplete skull (holotypo) (MNHN 2521).

Eumegamysops praependens — Cráneo imcompleto (MLP 41XII–13–237); caja craneana asignada a *E. praependens* (MACN 4007) ver Fernández de Alvarez (1958).

Eumegamys paranensis — Caja craneana asignada a *E. paranensis* by Kraglievich (1926) (MACN 4006).

Isostylomys laurillardi — Porción anterior de mandíbula (holotypo) (MACN-A 5823*);* mandíbula derecha incompleta (topotypo) (MLP 15-247); mandíbula derecha incompleta (topotypo) (MACN 3963).

Isostylomys intermedius — p4 izquierdo (holotypo) (MNHN 614).

Isostylomys ameghinoi —Rama mandibular izquierda (holotypo) (MACN 8935); paladar (MACN-A 5879).

Isostylomys magnus — p4 izquierdo (calcotypo) (MACN 1508).

Telicomys giganteus — Cráneo casi completo (holotypo) (MACN 8011).

Tetrastylus intermedius — Cráneo casi completo y mandíbulas (holotypo) (MACN 8323).

Gyriabrus glutinatus — Diente aislado (holotypo) (MACN-A5881).

Gyriabrus holmbergi — Paladar (MACN-A5879); rama mandibular derecha (MACN 3956); (MLP 4).

Gyriabrus rebagliattii — Rama mandibular izquierda (holotypo) (MACN 4728)

Gyriabrus teisseirei — Paladar (MNHN 1342).

Dinomys branickii — Esqueleto casi completo (MNHN 3795); cráneo y mandíbulas: (MNHN 3796); (BMNH 34.9.10.191); (BMNH 12.1.15.4); (MACN-M 12961); (MACN-M 12962); (UNMSM-MUSM 2217); (UNMSM-MUSM 5048); (UNMSM-MUSM 7887); (UNMSM-MUSM 11231); (UNMSM-MUSM 19855); (UNMSM-MUSM 23153); (UNMSM-MUSM 25759); (UDCA – UIFS 032); (UDCA-UIFS 098); (UDCA – UIFS 094); (UDCA – UIFS 136).

Hydrochoerus hydrochaeris — Cráneo y mandíbulas: (MNHN 250); (MNHN 252); (MNHN 322); (MNHN 1224); (MNHN 1230); (MNHN 2551); (MNHN 2558); (MNHN 2577); (MNHN 2579); (MNHN 2583); (MNHN 2583); (MNHN 2606); (MNHN 2609); (MNHN 2667); (MNHN 2850); (MNHN 2929); (MNHN 3265).

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