PeerJ Reviewing Manuscript

Morphological Evidence supports Dryolestoid affinities for the living Australian Marsupial Mole *Notoryctes*

Federico Agnolin, Nicolas Roberto Chimento

Recent discoveries demonstrated that the southern continents were a cradle for the evolutionary radiation of dryolestoid mammals at the end of the Cretaceous. Moreover, it becomes evident that some of these early mammals surpassed the K/T boundary in South America, at least. *Notoryctes* is a poorly known living mammal, currently distributed in the deserts of central Australia. Due to its extreme modifications to fossoriality and peculiar anatomy, the phylogenetic relationships of this genus were debated in the past, but most recent authors agree in its marsupial affinities. A comparative survey of the anatomy of *Notoryctes* reveals the poorly sustained marsupial affinities for the genus and striking plesiomorphies for a living mammal. Surprisingly, *Notoryctes* exhibits similarities with dryolestoids. Dryolestoids were a diverse and mainly mesozoic mammalian group phylogenetically nested between the egg-lying monotremes and derived therians. In particular, *Notoryctes* share a number of shared features with the extinct dryolestoid *Necrolestes*, from the Miocene of Patagonia. Both taxa conform a clade of burrowing and animalivorous dryolestoids that survived other members of their lineage probably due to their peculiar habits. Accordingly, *Notoryctes* constitutes a “living-fossil” from the supposedly extinct dryolestoid radiation, extending the biochron of the group more than 20 million years to the present day. The intermediate phylogenetic position of *Notoryctes* has the pivotal potential to shed light on crucial anatomical, physiological, ecological, and evolutionary topics in the deep transformation from egg-lying to placental mammals. This finding, together with the Australian monotremes, constitutes the second example of early mammals that survived in Gondwana well after the KT boundary.

PeerJ PrePrints

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

Morphological evidence supports Dryolestoid affinities for the living Australian Marsupial Mole *Notoryctes*

Federico L. Agnolin[1,2] and Nicolás R. Chimento[2*]

[1] Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Av. Ángel Gallardo 470 (C1405BDB), Buenos Aires, Argentina. nicochimento@hotmail.com

[2] Fundación de Historia Natural "Félix de Azara", Departamento de Ciencias Naturales y Antropología, CEBBAD -Universidad Maimónides, Hidalgo 775 (C1405BDB), Buenos Aires, Argentina. fedeagnolin@yahoo.com.ar

*Corresponding author

Brief title. *Notoryctes*, a living Dryolestoidea

PeerJ PrePrints

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

INTRODUCTION

The "marsupial mole" genus *Notoryctes* is a genus that includes two species of aberrant mammals currently distributed in the deserts of inner Australia (Nowak, 1999). *Notoryctes* has long been considered as an example of a highly modified burrowing mammal (Stirling, 1891; Warburton, 2003; Archer et al. 2010); however, its behavior and biology are nearly unknown, as occurs with key characters of internal and external anatomy (Johnson and Walton, 1989). Due to its extreme modifications to fossoriality and peculiar anatomy, *Notoryctes* affinities were debated at past, but since the study of Gadow (1892) most authors considered it as an aberrant marsupial. Its divergent morphology, and absence of related fossils make the relationships of *Notoryctes* with other marsupials obscure, and its unique anatomy prompted the creation of its own marsupial Order Notoryctemorphia (Archer, 1984). Its affinities within marsupials have remained elusive, although authors include it among Australian marsupial clades, mainly by biogeographic reasons (Szalay, 1982; 1994; Woodburne & Case, 1996; Springer et al., 1998; Horovitz and Sanchez Villagra, 2003; Horovitz et al., 2009; Asher et al., 2004; Beck et al. 2008). As recognized by most authors, fossorial adaptations mask the phylogenetic relationships of *Notoryctes*. However, since Gadow (1982) article only some isolated voices (Cope, 1892; Turnbull, 1971) called attention about the plesiomorphic nature of *Notoryctes* anatomy. Interesting enough, *Notoryctes* was repeatedly compared and sometimes phylogenetically tied with the extinct mammal *Necrolestes*, from the Miocene of Patagonia (Cope, 1892; Turnbull, 1971; Asher and Sánchez-Villagra, 2005; Asher et al., 2007; Ladevèze et al., 2009). It is worth to mention that *Necrolestes*, long thought to be a marsupial (e.g., Patterson, 1952; Patterson and Pascual, 1972; Pascual and Ortíz Jaureguizar, 2007; Ladevèze et al., 2009) was recently reinterpreted as a non-therian dryolestoid mammal (Chimento et al., 2012; Rougier et al., 2012). Because of the

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

similarities shared by *Notoryctes* and *Necrolestes*, we ask wether the Australian Marsupial Mole *Notoryctes* is also a member of Dryolestoidea.

With the aim to test such hypothesis we review in the following pages the features previously employed to include *Notoryctes* within Marsupialia, as well as the gross osteological traits of this taxon. Moreover, for the first time, *Notoryctes* is included in a comprehensive cladistic morphological analysis published up to date, inclusing fossil and living mammals, in order to test the phylogenetic position of *Notoryctes* within Mammalia.

Previous ideas about phylogenetic affinities of *Notoryctes*. In the original description, and based on a poorly preserved specimen, Stirling (1888) described *Notoryctes* as a primitive mammal, probably related to monotremes, and showing interesting plesiomorphies in its dentition, shared with the Jurassic basal symmetrodontan *Amphitherium*. Later, Stirling (1891) described in detail *Notoryctes* and considered it as an aberrant marsupial. Ogilby (1892) indicated that *Notoryctes* shows several intermediate features between monotremes and marsupials, and suggested that it may occupy an intermediate condition between these two major taxa. Latter Gadow (1892), based on a detailed comparative analysis on the anatomy of *Notoryctes*, recognized that the existence of permanent marsupium and a medially tilted angular process of the mandible, both characters that definitely include this genus within marsupials. This criterion was followed by the vast majority of authors with some exceptions. Cope (1892) interpreted *Notoryctes* as closely related to the eutherian insectivores Chrysochloroidea, based on similarities of the dentition. He considered *Notoryctes* as a link uniting eutherians and metatherians, but only distantly related to monotremes. Cope (1892) stated that the tritubercular molars of *Notoryctes* points to its “primitive type”. More recently, Turnbull (1971) emphasized the peculiarities of the dentition in *Notoryctes* and related it to *Necrolestes*, as well as some zalambdodontan eutherian

PeerJ PrePrints

insectivores, creating the Order Zalambdadonta. *Necrolestes* is an enigmatic mammal from Miocene beds of Southern Patagonia that is the size of a shrew and exhibits fossorial adaptations in combination with cranial, postcranial, and dental features that are remarkably plesiomorphic for a therian mammal (Chimento et al., 2012). Since the XIX century, *Necrolestes* and *Notoryctes* were compared in detail by several authors, who noted the striking similarities between both genera (Cope, 1892; Scott, 1905; Leche, 1907; Abel, 1928; Patterson, 1958; Turnbull, 1971; Sánchez Villagra and Asher, 2005; Asher et al., 2007; Ladévèze et al., 2008). Recently, Chimento et al. (2012) and Rougier et al. (2012) tested the phylogenetic affinities of *Necrolestes*, and concluded that this mammal must be included within the extinct clade Dryolestoidea (but see Averianov et al., 2013).

Although the great majority of recent authors support metatherian affinities for *Notoryctes*, the position of *Notoryctes* within Metatheria lacks a consensus. Szalay (2006), in his detailed morphological studies about marsupial tarsus, included *Notoryctes* among derived australidelphians of the clade Diprotodontia, as the sister group of the Peramelidae, a criterion previously envisaged by Dollo (1899) and Bensley (1903). Similarly, Horovitz and Sánchez-Villagra (2003; Sánchez-Villagra et al., 2007; Asher et al., 2004) included *Notoryctes* as the sister-group of Peramelidae, and both conformed the sister clade to Diprotodontia. In a similar way, Sánchez-Villagra (2001) recovered *Notoryctes* as the sister group of the clade *Dromiciops* + Diprotodontia.

Gadow (1892) proposed dasyurid affinities for the marsupial mole on the basis of morphological grounds. Bensley (1903) indicate that *Notoryctes* present an interesting question on its molariform morphology: as to whether the modifications represent a more primitive phase or is the result of special development proceeding from the type represented the Dasyurida or Peramelidae. However, he was inclined to support peramelian affinities for the marsupial mole.

PeerJ PrePrints

Finally, Woodburne and Case (1996) proposed that *Notoryctes* was nearly related to the putative extinct marsupial clade Yalkapariodontidae, being both included within the clade Notoryctemorphia. However, Woodburne and Case (1996) do not include evidence supporting this taxonomic group.

Due to its unique characters, some authors indicated that affinities of the marsupial mole within metatherians cannot be stated with certainty. Archer (1976), on the basis of basicranial characters, concluded that *Notoryctes* was of uncertain position within marsupials, and on this basis, proposed its own marsupial order: Notorycterimorphia.

Regarding molecular data, several sources of information have concluded that *Notoryctes* was part of the crown Marsupialia, although most analyses have produced incongruent results concerning the placement of the marsupial mole within metatherians (Asher et al., 2004). Several studies have favored the association of *Notoryctes* with Dasyuromorphia (Springer et al., 1997; Amrine-Madsen et al., 2003; Nilsson et al., 2004; Phillips et al., 2006; Beck, 2008; Beck et al. 2008; Meredith et al., 2007, 2008, 2011), lending support nto an unresolved grouping of Dasyuromorphia, *Notoryctes*, and Peramelia (Amrine-Madsen et al., 2003). Analyses based on nuclear and mitochondrial genes found *Notoryctes* as the sister taxon to Dasyuromorphia, with Peramelemorphia the sister taxon to that clade (e.g., Amrine-Madsen et al., 2003; Nilsson et al., 2004, 2010; Phillips et al., 2006; Beck, 2008; Beck et al. 2008; Meredith et al., 2008). Other trees based on DNA (Springer et al., 1997; Asher et al., 2004) recovered the *Notoryctes* + Dasyuromorphia clade but not the Peramelemorphia. Some support for an association of Peramelemorphia, Dasyuromorphia, and Notoryctemorphia has emerged from previous analyses of nuclear genes (Amrine-Madsen et al., 2003; Meredith et al., 2008) and combined mitochondrial and nuclear DNA genes (Phillips et al., 2006; Beck, 2008; Phillips and Pratt, 2008), and morphological analysis (Archer et al., 2010), but only with marginal support.

Moreover, caryological evidence suggested that *Notoryctes* is related neither with Peramelidae nor Dasyuridae, but with Phalangeroidea (Calaby et al., 1974).

In a detailed analysis, Cardillo et al. (2004) indicated that the position of *Notoryctes* within australidelphians remains uncertain (Kirsch et al., 1997; Lapointe and Kirsch, 2001). Cardillo et al. (2004) pointed out that it is possible that the relationships among major groups of marsupials analyzed in their article have been blurred by additional stochastic error and conflicting signals associated with the inclusion of *Notoryctes*, which produces very low tree resolution. Nilsson et al. (2004), Phillips et al. (2006), and Meredith et al. (2008) in their respective analyses pointed out that the placement of *Notoryctes* within marsupials was inconstant and weakly supported. It is worth mentioning here that immunological studies by Baverstock et al. (1990) have confirmed the lack of special close relationship between *Notoryctes* and any other known marsupial.

The lack of consensus among different studies regarding the phylogenetic position of *Notoryctes* within marsupials is usually explained due to the deep adaptations shown by this mammal to burrowing mode of life. The same concept has been applied by several authors in order to understand the bizarre anatomy of *Notoryctes*; nevertheless, present analysis indicates that numerous features may be reinterpreted as plesiomorphies rather than adaptative responses to a specific lifestyle. A plausible possibility is that the unstable molecular phylogenetic results may indicate that *Notoryctes* does not belong to Marsupialia. In fact, the absence of molecular data in fossil taxa phylogenetically intermediate between Monotremata and Metatheria (e.g., Dryolestoidea, Symmetrodonta, Multituberculata) may be in part, responsible of the unstable position of *Notoryctes* in different cladograms. This topic, however, is not discussed here in depth, because is not the aim of the present paper, which mainly consists on a detailed morphological analysis.

PeerJ PrePrints

PeerJ PrePrints

In this regard, it is worth mentioning that most phylogenetic analysis in which *Notoryctes* was included were restricted to marsupial and stem-metatherian mammals, excluding more basal mammaliform taxa. *Notoryctes* is here included, for the first time, within a comprehensive cladistic analysis of living and fossil mammals in order to resolve its phylogenetic affinities.

MATERIALS AND METHODS

Nomenclature. We follow Sereno (2006) in the definition of main clades within mammaliamorphs, i.e. Mammaliaformes, Mammalia, Prototheria, Monotremata, Theriiformes, Theria, Metatheria, Marsupialia, Eutheria, Placentalia. Within Dryolestoidea we partially follow the systematic arrangement employed by Rougier et al. (2011). It is worth mentioning here that in Rougier et al. (2011) article they consistently misspell Meridiolestida under the name Meridiolestoidea. We consider that the later name is a typescript error, and thus, an invalid name.

Reviewed specimens. The following *Notoryctes typhlops* specimens were examined, and main bibliographic sources in which the specimens were previously mentioned are cited in parentheses.

-*Notoryctes typhlops*. ZMB (Zoologisches Museum Berlin, Germany) 35694, complete skeleton.

-*Notoryctes typhlops*. BMNH (The Natural History Museum of London, United Kingdom) 39.4210, left mandible.

-*Notoryctes typhlops*. ZIUT (Zoologisches Institut Universitat Tübingen, Germany) SZ10068, complete skull.

PeerJ PrePrints

SOME INTRODUCTORY COMMENTS ABOUT THE ANATOMY OF *NOTORYCTES*

Dental morphology and cusp homology in *Notoryctes*. Cusp homology and morphology is traditionally considered as the main source to distinguish different mammaliform clades, being cusp morphology a key diagnostic character for each mammalian group. As in other zalambdodont mammals, the homology of the cusps in *Notoryctes* molariforms is a matter difficult to assess (Asher and Sánchez Villagra, 2005; Archer et al., 2010). Recent authors considered the main labial cusp of the upper molariforms of *Notoryctes* as the metacone, mainly because this cusp is usually more developed than the paracone in marsupials (Archer et al. 2010). Probably the main argument in support of the later identification is based on the assumption that *Notoryctes* is a member of Metatheria, a group of therians in which the main central cusp is the metacone. Those authors also proposed the main lingual cusp of the teeth as the protocone, because *Notorcytes* was considered without any doubt as a therian mammal (Asher and Sánchez Villagra, 2005; Archer et al., 2010).

However, based on the position of cusps and wear facets a different arrangement can be proposed. At first sight in *Notoryctes*, contrasting with therian mammals, the upper molars have the principal lingual cusp of the molariforms unusually large, whereas in tribosphenic mammals the reverse condition occurs, being the labial cusp (i.e., the paracone in eutherians, and the metacone in metatherians) the largest of the upper teeth (Gelfo and Pascual, 2001). In tribosphenians the main lingual cusp is the protocone, which typically occludes in the talonid basin (see Averianov and Lopatin, 2008). In *Notoryctes* and meridiolestidans there is no talonid basin (Gelfo and Pascual, 2001; Chimento et al., 2012; Rougier et al., 2012). The lack of occlusion of the main cusp in a talonid basin in *Notoryctes* does not matches the indirect homology criterion of Butler (1978), and thus the main lingual cusp in upper molariforms of *Notoryctes* cannot be considered as a protocone.

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

Moreover, this cusp in *Notoryctes* and dryolestoids differs from the protocone (and also metacone/paracone) of therians in being located at nearly the same line than the main lingual cusp, in having two shearing surfaces (prevallid and postvallid facets), and especially differs from the metacone on its more central location on the teeth, occluding far from the paracristid (Clemens and Lillegraven, 1986). This combination of characters is present in the main cusp of non-therian mammals, which is commonly named as stylocone, a cusp that is secondarily reduced in therian mammals (Kielan Jaworowska et al. 2004). Thus, although the dentition of *Necrolestes* is zalambdodont, it is clear that it does not have the occlusal cusp relationships characterizing zalambdodont tribosphenidans (Patterson 1958; Asher and Sánchez-Villagra 2005; Asher et al. 2007) (see Figure 1).

Regarding the main lingual cusp of *Notoryctes*, if the upper molariform arcade is reconstructed to occlude with the lower dental arcade, the lingual cusp of the upper molars will result adjacent to the lower ectoflexid of the respective more posterior lower molars, and clearly not close to the paracristid. On the contrary, the metacones of therian mammals occlude closer to the paracristid of the more posterior lower molars (Clemens and Lillegraven, 1986; Asher et al. 2007). Because the main cusp of the upper molars of *Notoryctes* does not occlude near the paracristid, it must be concluded that it is not a metacone, even accepting a metatherian affiliation for *Notoryctes*. In this way, the main lingual cusp of upper molariforms of *Notoryctes* must be considered as the paracone following our interpretation. Identification of remaining cusps follows automatically upon the identification of these primary cusps. The general morphology of *Notoryctes* cusp morphology and disposition is similar to that of meridiolestidan dryolestoids, as for example *Cronopio* (Rougier et al., 2011), *Necrolestes* (Chimento et al., 2012; Rougier et al., 2012), and *Leonardus* (Bonaparte, 1990). Such resemblance concerns with the simplicity in crown morphology, conforming a simple triangle with three main cusps. In sum, the upper molar cusp

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

homologies of *Notoryctes* clearly matches the plesiomorphic mammaliform condition present in several extinct taxa, specially dryolestoids, rather than the derived and more complex morphology seen in tribosphenic therian mammals (Kielan Jaworowska et al. 2004) (Figure 2).

On the other hand, the lower dentition of *Notoryctes* also fits the plesiomorphic mammaliform pattern: the molariforms have a trigonid forming an obtuse angle with the protoconid at its apex. The paraconid is situated anterior to the protoconid, and the metaconid has a more lingual position. The paraconid is slightly higher than the metaconid, and both are lower than the protoconid (Clemens and Lillegraven, 1986).

Although several living zalambdodont mammals exhibit superficially similar tooth morphology and cusp disposition to that of *Notoryctes*, all the taxa show protocone-talonid occlusion. In the insectivore eutherian *Chrysochloris*, the talonid is reduced, resembling *Notoryctes* and the dryolestoid condition. However, in *Chrysochloris* the main upper cusp occludes between protocristids of adjacent molars, indicating that this cusp is, in fact, the protocone (Asher and Sánchez Villagra, 2005). Due to the absence of a protocone on upper molars, most dental characters that are usually employed to diagnose Theria are absent in *Notoryctes*, as for example the extent and development of pre- and post-protocristae, as well as molar cuspid and conule arrangement (Luo et al., 2002; Kielan Jaworowska et al., 2004) (Figure 3).

Our interpretation of tooth morphology and cusp homologies in *Notoryctes* has deep consequences regarding the recognition of dental synapomorphies of Theria and Metatheria.

Reinterpretation of the dental formula of *Notoryctes*. The dental formula and tooth number in *Notoryctes* shows a high intraspecific variation. In fact, its dental formula varies among i 3-4/3-2, c 1/1-0, pm 1-3/1-3, and m 4/4 (see Stirling, 1891; Gadow, 1892; Spencer, 1896; Thomas,

PeerJ PrePrints

1920; Turnbull, 1971). Traditionally, it has been regarded that metatherian dental formula typically is P3/3, M4/4 (Gadow, 1892), whereas in Eutheria this formula was plesiomorphically P5/5, M3/3 (McKenna, 1975; Novaceck, 1986). In consequence, following such reasoning, and assuming metatherian affinities for *Notoryctes*, most previous authors proposed a tooth count for the marsupial mole that matches the metatherian typical formula (e.g., Gadow, 1892; Thomas, 1920; Ashr and Sánchez Villagra, 2005; Archer et al., 2011). They considered that the last premolar was a tooth showing a linear cusp disposition, wereas the M1 was the first triangulated postcanine tooth. In fact, according with that interpretation, in all living and extinct metatherians there is no triangulated premolar (see Averianov et al. 2010). However, evidence of tooth replacement for *Notoryctes* is still wanting, and thus the identity of molariforms provided by previous authors may be regarded only as tentative.

On the other hand, if we adopt the phylogenetic hypothesis here proposed, the dental formula of *Notoryctes* may be reinterpreted in a different way. In the vast majority of therians, the metatherian P3 and eutherian P4 (homologous teeth *sensu* McKenna, 1975) are always placed below the infraorbital foramen (Averianov et al. 2010). In *Notoryctes* the infraorbital foramen is located above the molariform tooth that was identified by previous authors as the first upper molar. This may sustain the interpretation of such tooth as the last upper premolar.

In meridiolestidans, at least, the last premolar shows triangulated cusps (e.g. *Peligrotherium, Coloniatherium, Mesungulatum, Cronopio, Necrolestes*; Páez Arango, 2008; Rougier et al., 2011, 2012; Chimento et al., 2012), difficults distinction of last premolars from anterior molars. In this regard, in basal dryolestoids (e.g., *Guimarotodus, Krebsotherium, Dryolestes*; Martin, 1999) as well as meridiolestidans (e.g., *Cronopio*, *Peligrotherium*; Páez Arango, 2008; Rougier et al., 2011) the wider and taller of the molariforms in the upper tooth row is recognized as the P3. From M1 to through M3 the size decreases continuously, being all true molars smaller than the

PeerJ PrePrints

last premolar; in the same line, Martin (1997) indicated that the molars of dryolestids are mesiodistally shorter than the last two premolars. In addition, in both *Cronopio* and *Peligrotherium* the labial margin of the true molars are mesiodistally narrower than the last premolar (Páez Arango, 2008; Rougier et al., 2011), and the parastylar and metastylar areas are more expanded.

In *Notoryctes* the first molariform is wider and taller than other molariforms, and the last three teeth decreases in size continuously front to back. In addition, this tooth shows an extended mesiodistal labial margin and expanded parastylar and metastylar areas. This combination of characters suggests that this element may be considered as the P3 and not the M1 as advocated by previous authors. The triangulated condition of the crown in this dental piece does not contradict the condition of the last upper premolar of meridiolestidan dryolestoids (Figure 4).

On this basis we reinterpret here the basic dental formula of *Notoryctes* as i 4/3, c 1/1, pm 3/3, and m 3/3. This dental count is also congruent with dryolestoid dental formula.

Reinterpretation of the sternum in *Notoryctes*. The pectoral girdle and sternum of *Notoryctes* were regarded as unique among living mammals, a fact noted since its original description by Stirling (1891; Warburton, 2003). Peculiar characters include very robust and expanded first thoracic ribs (a feature shared with other fossorial taxa, such as dasypodid xenarthrans), thin and curved clavicle, and an enlarged additional mesoscapular segment, among other features (Warburton, 2003). In the present paper we include novel interpretations regarding the pectoral girdle of the marsupial mole. Warburton (2003) considered the sternum of *Notoryctes* as composed by a a manubrium, 6-5 sternebrae, and a cartilaginous xiphisternum. The first sternal piece, interpreted as the manubrium by Warburton (2003) shows some unique features allowing a different interpretation. In mammals the manubrium was defined as a sternal piece that has anteriorly two lateral processes called the manubrial wings, and behind them the

PeerJ PrePrints

articular surfaces for the costal cartilages of the first pair of thoracic ribs. Posteriorly, the second pair of ribs articulates with both the caudal margin of the manubrium and the first sternebra of the mesosternum (Campbell, 1939; Reed, 1951). In fact, the manubrium in most living and extinct taxa (e.g. *Pseudotribos, Ornithorhynchus, Tachyglossus, Zhangheotherium, Jeholodens, Akidolestes, Didelphis*; Hu et al., 1997; Luo et al. 2007; Chen and Luo, 2013) is connected on its anterior corner by the first thoracic rib. In *Notoryctes* the first sternal piece differs from the manubrium in having the articulation with the first thoracic rib on its posterior corner (Stirling, 1891), a feature that resembles in this aspect the interclavicle of basal taxa, such as monotremes, *Pseudotribos, Akidolestes* and *Jeholodens* (Ji et al., 1999, Luo et al. 2007; see discussion in Chen and Luo, 2013). In addition, is similar to non-therian interclavicle in being strongly keeled and in having a dorsoventrally flat and transversely expanded body. In this way, this element is here tentatively identified as a well-developed interclavicle, a plesiomorphic condition for mammals, absent in therians and reduced in multituberculates (Sereno, 2006; Luo et al. 2007). The gross morphology of this element is very similar to that described for the eutriconodont *Jeholodens* (Ji et al. 1999).

The second sternal element (considered as the first sternebra by most authors) is here reinterpreted as the manubrium. This bone resembles the manubrium of therian taxa, in being strongly keeled, in having a dorsoventrally low and expanded body, and in showing the articular surface for the first thoracic rib on its anteriormost corner (Reed, 1951).

If the present interpretation is followed, the morphology of the sternum in *Notoryctes* is strikingly plesiomorphic, looking very similar to that of basal non-therian mammals. This has profound implicances in the analysis and interpretation of *Notoryctes* skeletal morphology and phylogenetic relationships.

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

DISCUSSION

As noted by most previous authors, several adaptative features may mask some important traits of *Notoryctes* anatomy. In fact, *Notoryctes* shares with fossorial mammals, particularly chrysochloroids, features that may be regarded as related to fossoriality, including oblique scapular glenoid, reduced supraspinous fossa on scapula, enlarged epicondyles on distal humerus, large lesser tuberosity on proximal humerus, fused cervicals, double scapular spine, and ulna with large and medially oriented olecranon. Additional similarities with chrysochloroids include simple teeth, and especially lower molariforms without talonid. The unique morphology of *Notoryctes* led some authors to propose that most of its anatomy was modified in relation to its digging habits. However, *Notoryctes* is strongly different from other living fossorial mammals (including chrysochloroids, talpids, rodents, and xenarthrans) in skull and ear anatomy, as well as tarsal and carpal conformation. Since Gadow (1892) authors recognize several therian, metatherian and marsupialian synapomorphies in *Notoryctes* skeleton. As follows we review dental and osteological evidence employed to sustain metatherian affinities for *Notoryctes*.

Review of metatherian features mentioned for *Notoryctes*. Although *Notoryctes* has been usually considered a metatherian, it is devoid of several characters that are distinctive of metatherians and marsupials. In addition, several features present in *Notoryctes* that were frequently thought to diagnose Metatheria, have been also recently documented among South American dryolestoids (e.g., *Peligrotherium, Cronopio, Necrolestes*), and consequently, the condition of these features as unambiguous metatherian or marsupialian synapomorphies is not clear.

Recently, Vullo et al. (2009; see also Fox, 1975), listed a combination of characters that may be useful to diagnose stem-marsupialian teeth: 1) presence of similarly sized and well separated paracone and metacone, 2) wide stylar shelf, 3) occurrence of stylar cusps C and D, 4) well-

PeerJ PrePrints

developed protocone, 5) hypoconulid lingually approximated to the entoconid, 6) presence of cristid obliqua defining a shallow hypoflexid, 7) low protoconid, 8) weak ectocingulum and cusps C and D, 9) presence of a distinct, long and transversely oriented postmetacrista, 10) presence of a prominent mesiolingual flank of paraconid. In contrast with metatherians, *Notoryctes* lacks a well developed metacone on upper molars, lacks cusps C and D, protocone, hypoconulid, entoconid, and a cristid oblique. With regards to character 7, *Notoryctes* differs from the widespread metatherian condition in having very tall and broad protoconid, which represents the largest cusp of lower molariform crowns (Asher and Sánchez-Villagra, 2005). Finally, presence of a distinct, long and transversely oriented postmetacrista (character 9), and presence of a prominent mesiolingual flank of paraconid (character 10) are present in *Notoryctes*, but also in a large variety of dryolestoid meridiolestidans, including *Leonardus, Cronopio, Necrolestes, Mesungulatum,* and *Peligrotherium* (Bonaparte, 1986; Pascual and Gelfo, 2001; Chornogubsky, 2011; Rougier et al. 2011; Chimento et al., 2012). Moreover, a wide stylar shelf (character 2) is not only present in metatherians, but also dryolestoids, and the majority of basal mammalian taxa (Kielan Jaworowska et al., 2004) (see Figures 2-3).

In sum, details of tooth cusps in *Notoryctes* do not sustain marsupial or metatherian affinities for this genus.

Several cranial, dental, and postcranial features have been regarded in previous literature as shared between *Notoryctes* and Metatheria. The most complete morphological analysis that includes *Notoryctes* among metatherians is that proposed by Horovitz and Sánchez-Villagra (2003), in which they include all osteological characters nesting *Notoryctes* among marsupials cited by previous authors (see also Asher et al. 2004; Beck et al., 2008). The features employed to sustain the phylogenetic affinities of *Notoryctes* were detailed by Horovitz and Sánchez-Villagra (2003) and these traits (the same as Asher et al. 2004) are commented below.

PeerJ PrePrints

1) Dental formula composed by 7 postcanine tooth families, presence of 4 upper molars, and 3 upper premolars (see Rougier et al., 1998). These characters are related to the dental formula typical of metatherians, in which the dentition frequently shows P3/3, M4/4 (Gadow, 1892; although this formula is variable among marsupials, and the basalmost metatherian *Sinodelphys* has pm 4/4, m 4/4; Luo et al. 2003). In *Notoryctes* the formula is variable among different individuals of the same species, being: i 3-4/3-2, c 1/1-0, pm 1-3/1-3, and m 4/4 (see Stirling, 1891; Gadow, 1892; Spencer, 1896; Thomas, 1920; Turnbull, 1971). Moreover, our analysis suggests that *Notoryctes* has a minimal molariform formula of P3/3, M3/3, being different from that of metatherians, but similar to meridiolestidans (Rougier et al. 2008, 2009, 2011). In addition, in dryolestoids the dental formula is variable, including taxa with PM2 M4 (e.g., *Peligrotherium, Araeodon, Archaeotrigon*; Prothero, 1981; Páez Arango, 2008; Kielan-Jaworowska et al. 2004). In this way, characters regarding tooth formula are not usefull to sustain purported metatherian or marsupialian affinities for *Notoryctes*.

2) Procumbent first upper premolar separated by diastema (Rougier et al., 1998). Contrasting with most metatherians the first upper premolar of *Notoryctes* consist on a reduced, non-procumbent, and poorly developed peg-like tooth (see Stirling, 1891).

3) Lower i2 staggered (see detailed discussion in Hershkovitz, 1995; Horovitz and Sánchez-Villagra, 2003). This feature is clearly absent in *Notoryctes*, in which the i2 is highly reduced and non-staggered (Stirling, 1891).

4) “Marsupial” dental replacement. As explained above, due o the absence of collection specimens and published data, the dental replacement of *Notoryctes* is still totally unknown.

5) Medial inflection of angular process. A medially inflected angular process of the dentary was usually regarded as an unambiguous metatherian synapomorphy by most authors (see

PeerJ PrePrints

discussion in Sánchez-Villagra and Smith, 1997), and was one of the main arguments employed by Gadow (1892) in order to sustain marsupial affinities for *Notoryctes*. However, the distribution of such feature is not clear. In some Cretaceous therians, a medially inflected angular process has been reported (e.g., *Gypsonictops, Cimolestes, Asioryctes, Barunlestes*; Lillegraven, 1969; Kielan-Jaworowska, 1975). On this basis, Marshall (1979) proposes that the inflected angle was probably present in the therian ancestor of marsupials and placentals, and was latter lost in different lines of eutherians (see also Lillegraven, 1969). In addition, a medially inflected angular process on the dentary has been reported in the basal cladotherian *Vincelestes* (Bonaparte and Rougier, 1987; Bonaparte and Migale, 2010), and in some australosphenidans (e.g., *Asfaltomylos, Henosferus*; Martin and Rauhut, 2005; Rougier et al., 2007). Recently, Chimento et al. (2014) reported presence of inflected angular process in Gondwanatherian mammals. Regarding dryolestoids, a medially inflected angular process has been reported in the meridiolestidan genera *Cronopio* and *Peligrotherium* (Páez Arango, 2008; Rougier et al. 2011), and also in *Necrolestes* (Asher et al., 2007). Due to its distribution, this feature has been recently reinterpreted as plesiomorphic for mammals by some authors (Martin and Rauhut 2005; Chimento et al., 2014), and consequently it may not be considered as an unambiguous character sustaining the inclusion of *Notoryctes* within Metatheria.

6) Palatal process of premaxilla reaches canine alveolus or is immediately posterior to it; In *Notoryctes* the palatal process of the premaxilla does not reaches the canine alveolous, a condition shared with basal mammals, such as *Vincelestes* (Bonaparte and Rougier, 1987) and the dryolestoids *Henkelotherium, Drescheratherium,* and *Peligrotherium* (Krebs, 1993, 1998; Paéz Arango, 2008).

7) Absence of stapedial artery sulcus on petrosal. The absence of stapedial artery in adult individuals has been also reported for *Notoryctes* (Wible et al, 2001; Ladevèze, 2008). However,

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

Ladevèze et al. (2007) indicated the absence of such artery in the dryolestoid *Necrolestes*. In this way, this character may be variable considered as sustaining metatherian or dryolestoid affinities for *Notoryctes*.

Braincase features previously thought to diagnose Metatheria are present in *Notoryctes*, but also in meridiolestidans (e.g., *Peligrotherium, Reigitherium, Coloniatherium, Cronopio, Necrolestes*; Rougier et al., 2009; 2011; 2012; Chimento et al., 2012). These include petrosal sinus located between petrosal, basisphenoid, and basioccipital, extrabullar location of internal carotid artery, loss of stapedial artery, and presence of caudal tympanic recess (see Ladevèze, 2004; Ladevèze et al., 2008). In this way, presence of these characters cannot be considered as unambiguous evidence nesting *Notoryctes* within Metatheria (Figure 5).

There are several described synapomorphies present on distal tarsals that are shared by *Notoryctes* and metatherians. Among them, the medially expanded navicular facet of astragalus conforming a convex trochlea, with coalescense of astragalar and sustentacular facets of the calcaneum (Luo et al., 2003; Szalay, 2006), presence of expanded medial plantar tubercle on astragalus (Luo et al., 2003; Szalay, 2006), calcaneum with oblique and strengthened calcaneocuboid contact in a mobile transtarsal joint (Luo et al. 2003), calcaneal sustentacular facet with dorsal mesiolateral orientation (Horovitz and Sánchez-Villagra, 2003), and absence of tibial posterior shelf (Horovitz and Sánchez-Villagra, 2003). It must be mentioned that most of these characters are of problematic distribution and may be more widespread than previously thought, as was discussed in detail by Szalay and Sargis (2006). In spite of that, due to incomplete preservation, the absence or presence of these characters in dryolestoidean foot is still uncertain. In this way, tarsal morphology may not be usefull in order to sustain or reject metatherian apomorphies of *Notoryctes*, and may be regarded as uncertain until new dryolestoid material become available.

PeerJ PrePrints

PeerJ PrePrints

Review of marsupialian features mentioned for *Notoryctes*. In their detailed analysis, Horovitz and Sánchez Villagra (2003) listed the following cranial and postcranial apomorphies shared by Marsupialia and *Notoryctes*:

1) Transverse canal foramen anterior to carotid foramen (see also Rougier et al. 1998). Although this condition is seen in *Notoryctes* (Ladevèze et al., 2007), it is also present in the dryolestoid *Necrolestes* (Asher et al. 2007). In sum, this character may be variously considered as sustaining metatherian or dryolestoid affinities for *Notoryctes*.

2) Presence of a well developed tympanic wing of alisphenoid. *Notoryctes* shows a well-developed tympanic wing of alisphenoid, a well-known synapomorphy of Marsupialia (Springer et al., 1997; Rougier et al., 1998; Wroe et al., 2000; Luo et al., 2002; Horovitz and Sánchez-Villagra, 2003; Asher et al., 2004). This stands as the only derived unambiguous character shared by marsupials and *Notoryctes*.

3) Palatal vacuities present in both palatine and maxillary bones. This feature, frequently reported as diagnostic of Marsupialia, is absent in *Notoryctes*, in which the palate is solid and lacks any sign of vacuities (Stirtling, 1891) (see Figure 1).

4) Humerus with subequal proximal extension of capitulum and trochlea (see Chester et al. 2012). In contrast to other metatherians, in *Notoryctes* the capitulum plesiomorphically extends farther proximally than the trochlea (Warburton, 2003), a condition seen also in the dryolestoids *Henkelotherium* and *Necrolestes* (Vázquez-Molinero et al. 2001; Asher et al. 2007) (Figure 6).

5) Distal process of ulna spherical. A distal spherical styloid process on the ulna is also present in the dryolestoids *Henkelotherium* and *Necrolestes* (Krebs, 1991; Asher et al. 2007;

PeerJ PrePrints

Chimento et al., 2012), and was recently described for the spalacotheriid *Akidolestes* (Chen and Luo, 2012). It is worth mentioning here that a spherical styloid process on the ulna has also been illustrated for the basal eutherian *Eomaia* (Luo et al. 2003). Present analysis indicates that that styloid process on distal ulna (character 220-1) may be better considered as a synapomorphy nesting *Notoryctes* within Dryolestoidea (Figure 6).

Review of australidelphian features mentioned for *Notoryctes*. Many authors (Szalay, 1982; Springer et al., 1998; Beck et al., 2008) have agreed in the australidelphian affinities of *Notoryctes*. The recent studies of Horovitz and Sánchez-Villagra (2003) and Ladevèze et al. (2008) resulted in the recognition of several derived characters diagnostic for Australidelphia, the marsupial clade that purportedly includes *Notoryctes*. At following we analyze such characters in some detail.

1) Vertebral centrum of C5 shorter than T1 (Horovitz and Sánchez-Villagra, 2003). This trait cannot be checked in *Notoryctes*, due to its extreme modifications due to fusion seen in cervical vertebrae from the second to the sixth (Warburton, 2003).

2) Medial epicondyle of humerus small (Horovitz and Sánchez-Villagra, 2003). In contrast to australidelphian marsupials, as explained above, *Notoryctes* shows very well-developed and expanded ectepicondylar and entepicondylar processes on distal humerus (Warburton, 2003) (Figure 6).

3) Lateral extension of the capitulum of the humerus absent (Horovitz and Sánchez-Villagra, 2003). In *Notoryctes*, as occurs in the dryolestoid *Necrolestes* the capitulum (or radial condyle) is subcilindrical and well laterally extended (Asher et al. 2007), differing from the transverselly compressed condition seen in australidelphian marsupials (Horovitz and Sánchez-Villagra, 2003).

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

4) Prepollex absent (Horovitz and Sánchez-Villagra, 2003). As occurs in australidelphians, a prepollex is absent in *Notoryctes* (Character 4). However, this structure is also absent in *Ornithorhynchus* (Ji et al. 2002), eutriconodontans (e.g., *Jeholodens, Zhangheotherium*; Hu et al. 1998; Ji et al. 1999), and multituberculates (Kielan Jaworowska and Gambaryan, 1994). Regrettably, the detailed morphology of the hand is unknown in any dryolestoid, and as a consequence, the presence or absence of a prepollex cannot be corroborated in this mammalian clade.

5) Three lower incisors (Horovitz and Sánchez-Villagra, 2003). As indicated above, the number of incisive pieces is variable among individuals of *Notoryctes*, from 2 to 3. In *Coloniatherium* and an indeterminate lower jaw, the only known meridiolestidans for which the lower incisive number is known, there 3 elements (Forasiepi et al., 2012). In remaining dryolestoids, the lower incisive number is invariably 4, the plesiomorphic number for mammals (see Kielan Jaworowska et al. 2004). In this way, the number of lower incisives of asutralidelphians and *Notoryctes* also occurred in meridiolestidans, and thus, cannot be considered as an unambiguous australidelphian character for *Notoryctes*.

6) Maximum maxilla (palatal portion) length/width ratio less or equal to 1.5 (Horovitz and Sánchez-Villagra, 2003). Although a high maxillar ratio is present in some therians and *Vincelestes* (Horovitz and Sánchez-Villagra, 2003), Horovitz and Sánchez-Villagra (2003) considered this feature as diagnostic of Australidelphia, being also shared by *Notoryctes*. However, it must be pointed out that a similar ratio is present in the dryolestoids *Necrolestes* (Asher et al. 2007), and *Peligrotherium* (Páez Arango, 2008), being unknown in remaining members of the clade. In this way, the proportions of the palatal portion of the maxilla are not a unique apomorphy uniting australidelphians with *Notoryctes*.

PeerJ PrePrints

7) Ossicular axis 10-20° (Horovitz and Sánchez-Villagra, 2003). This characters is unknown in available *Notoryctes* specimens (Horovitz and Sánchez-Villagra, 2003).

8) Well-developed rostral and caudal tympanic processes fused in a petrosal plate (Ladevèze et al. 2008). In *Notoryctes* and australidelphians a protrudent and fused caudal and rostral tympanic processes conforming a petrosal plate are present (Ladevèze et al. 2008). In basal mammals, including dryolestoids, both processes are separated and do not conform a petrosal plate. In this way, this character may stand as a possible australidelphian apomorphy that is unambiguously shared with *Notoryctes*. However, present analysis suggests that the acquisition of such plate may be a convergent phenomenom between both taxa (Figure 5).

9) Presence of a stylomastoid foramen (Ladevèze et al. 2008). A stylomastoid foramen is not unique to *Notoryctes* and australidelphians, but is also present in the dryolestoids *Henkelotherium* (Ruf et al., 2009), *Necrolestes* (Ladèveze et al. 2008), and *Peligrotherium* (Páez Arango, 2008). In this way, existence of stylomastoid foramen appears to be more widespread than proposed by Horovitz and Sánchez-Villagra (2003).

Several characters proposed to unite Australidelphians and *Notoryctes* are unknown in all dryolestoids, including absence in the astragalus of an astragalonavicular facet connection with the sustentacular facet, calcaneum with merged calcaneal sustentacular facet and posterior calcaneoastragalar facets, calcaneum sustentacular facet does not reaches anterior end, and cuboid medial plantar process forms a groove (Horovitz and Sánchez-Villagra, 2003). These characters have not been preserved in any meridiolestidan and dryolestoid, and thus are difficult to interpret regarding the phylogenetic position of *Notoryctes*. However, absence of continuous atragalonavicular facet connection with the sustentacular facet, and calcaneus with merged sustentacular and astragalar facets have been observed in some basal mammals, such as

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

multituberculates and "symmetrodontans" (Luo and Yi, 2005; Yuan et al., 2013), suggesting that at least some of these tarsal features may be widespread basal mammal conditions.

In sum, *Notoryctes* exhibits sparse characters with metatherian clades. Among uniquely shared characters are: presence of a well developed tympanic wing of alisphenoid and alisphenoid bulla (synapomorphy of Marsupialia), and a well-developed rostral and caudal tympanic processes fused in a petrosal plate (synapomorphy of Australidelphia).

Plesiomorphies shared by *Notoryctes* and basal mammals. It is worth mentioning here that *Notoryctes* exhibits a set of plesiomorphic characters absent in living therians, but which are present in other basal mammals. Several plesiomorphic characters are related with the limb morphology of *Notoryctes*, and some authors propose that all these peculiarities may be explained as adaptations to the burrowing behaviour of *Notoryctes* (e.g., Warburton, 2003; Asher et al. 2007). However, most of these traits are lacking in other therian fossorial mammals (i.e. Xenarthra, Rodentia, Talpidae, Soricidae), or are only present in selected therian genera. Nevertheless, each of these characters is analyzed in detail below, and its potential significance are remarked.

1- Absence of the protocone in the upper molars (Character 100-0). Although the zalambdodont dentition of *Notoryctes* is difficult to interpret, the total absence of talonid basin in this genus indicates that the main lingual cusp of molariforms cannot be identified as the protocone. In tribosphenic mammals the main lingual cusp of upper molars is the protocone, which typically occludes on the talonid basin of lower molars, a derived condition diagnosing the clade Tribosphenida, that is even present in modified zalambdodont mammals (with the single exception of *Chrysochloris*; Patterson, 1956; Kielan Jaworowska et al. 2004; see also Fox, 1975;

PeerJ PrePrints

Butler, 1990; Cifelli, 1993; Sigogneau-Rusell, 2003; Luo et al., 2007). Thus, although the dentition of *Notoryctes* is zalambdodont, it does not have the cusp relationships characterizing zalambdodont tribosphenidans (Patterson 1958; Asher and Sánchez-Villagra 2005; Asher et al. 2007). On the other hand, as supported above, in *Notoryctes* the main lingual cusp is represented by the stylocone (= centrocone of Bonaparte, 2002), a condition that frequently occurs non-tribosphenic mammals, including dryolestoids (see Bonaparte, 1990) (Figures 1-2).

On the basis of the phylogenetic analysis here performed we interpret the absence of a protocone in *Notoryctes* as a truly plesiomorphic character, that excludes this genus from Tribosphenida.

2- Talonid absent (Character 85-0). The absence of talonid in *Notoryctes* was considered as a highly distinctive character since its original description (Stirling, 1891; see also Bensley, 1903), and its absence was early considered by Cope (1862) as indicating the plesiomorphic nature of *Notoryctes*. The talonid is a neoformation diagnostic of tribosphenic mammals (Patterson, 1956; Fox, 1975; Butler, 1990; Cifelli, 1993; Sigogneau-Russell 1998, 2003; Luo et al., 2002; Kielan-Jaworowska et al. 2004), although many authors have supported the presence of a “pseudotalonid” in the mesial margin of the teeth of different non-tribosphenic mammalian groups (Kermack et al. 1987; Luo et al. 2001a; Luo et al. 2007; Luo 2007). In these basal taxa a true talonid is totally absent, and its existence has been considered as a key character in the line towards living mammals (Kielan Jaworowska et al. 2004). In dryolestoids, the talonid is absent, and in basal taxa, only a small-sized shelf carrying a small cusp is present at the distal rear of the molariforms (e.g., *Henkelotherium*, *Foxraptor*, *Crusafontia*, *Dryolestes*; Schultz and Martin 2011). In more derived dryolestoids, including all meridiolestidans (e.g., *Leonardus*, *Cronopio, Necrolestes*; Bonaparte 1990; Asher and Sanchez-Villagra 2005; Chornogubsky 2011; Rougier et al. 2011) the talonid is totally absent, a condition interpreted as a derived feature of meridiolestidans (Rougier et al. 2011;

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

Chimento et al., 2012). It is worthy to mention that in mesungulatoids the distal margin of the molariforms develops a very large cingulum that appears to be not homologous with the therian talonid (Bonaparte, 1986, 1990, 2002). On the contrary, in basal therians a talonid is invariably present, including most zalambdodontan taxa (Asher and Sánchez Villagra, 2007), with the single exception of the genus *Chrysochloris* (Asher and Sánchez Villagra, 2007). Moreover, in metatherians there exists a tendence towards the broadening of the talonid basin (Cifelli, 1993).

Due to the basal position of *Notoryctes* in the present phylogenetic analysis, the absence of a talonid basin is here considered as a truly plesiomorphic character, and not as an apomorphic reversal, as opposed to Asher et al. (2007). (see Figures 1, 3).

3- Anterior lamina on the petrosal (Character 336-0). In *Notoryctes* there exists a relatively well-developed anterior lamina of bone in the anterolateral corner of the petrosal, being represented by a small flange of bone (see Ladevèze et al. 2008, fig. 4B).

In basal mammaliaforms, including morganucodontids, triconodonts, multituberculates, and *Vincelestes* a well-developed anterior lamina of the petrosal contributes to the side wall of the braincase (Wible 1990; Rougier, 1992; Wible and Hopson, 1993; Lucas and Luo, 1993; Hopson and Rougier, 1993). This lamina appears to be present in living monotremes, although its homology was doubted by some authors (Wible, 1990). In dryolestoids the middle and inner ear anatomy is only known in a bunch of taxa. The anterior lamina is well developed in the derived mesungulatoid *Peligrotherium* (Páez Arango, 2008) and possibly *Necrolestes* (Rougier et al., 2012), and *Cronopio* (Rougier et al. 2011), recalling the condition seen in basal mammaliaforms.

The strong reduction of this lamina has been considered as a synapomorphy exclusive of Theria, uniting eutherians and metataherians (Wible, 1990). However, selected basal eutherians (e.g., *Prokennalestes*; Wible et al., 2001) and metatherians (e.g., didelphids, peramelids,

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

Pucadelphys, Andinodelphys; Ladevèze, 2008) show the persistence, albeit reduced, of an anterior petrosal lamina. (see Figure 5).

Thus, on the basis of present analysis, the retention of an anterior lamina in *Notoryctes* represents a plesiomorphic condition absent in most (but not all) living and extinct therian mammals.

4- Lateral lamina on the petrosal (Character 337-0,1,2). In *Notoryctes* a lateral trough and small lateral flange are present along the lateral margin of the promontorium in the petrosal bone (see Ladevèze et al. 2008, fig. 4B). The lateral lamina is anteriorly extended and it is in near contact with the anterior lamina of the petrosal.

In non-mammaliaform cynodonts a very well-developed anterolateral osseous crest is present on the petrosal (Ladevèze, 2008). This crest is termed as the lateral trough, and it is usually further developed as a lateral flange, that partially protects the lateral head vein (Rougier et al. 1992). This lateral flange is well-developed in several basal mammals, including morganucodontids, multituberculates, triconodontans, and *Vincelestes* (Rougier et al. 1992; Wible and Hopson, 1993). In dryolestoids the distribution of the lateral flange is only known in sparse taxa. In *Peligrotherium* and *Cronopio* a large lateral flange lateral to the promontorium has been reported (Páez Arango, 2008; Rougier et al. 2011). In other taxa, including *Coloniatherium* and *Henkelotherium* the lateral flange is present but poorly preserved, and thus, the exact shape and extent cannot be determined (Rougier et al. 2009; Ruf et al. 2009). In the dryolestoid *Necrolestes* the lateral flange and its associated lateral trough are highly reduced (Ladevèze et al. 2008).

Among living mammals the only clades retaining the lateral flange are the monotremes (Hopson and Rougier, 1993), and some basal eutherians (e.g., *Prokennalestes*; Wible et al., 2001) and basal metatherians in which the lateral trough is still present, although highly reduced in

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.715v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

exposure (e.g., *Andinodelphys, Pucadelphys, Mayulestes*; Ladevèze, 2008; Ladevèze et al. 2008). The absence of a lateral flange and trough is diagnostic of therian mammals, being absent in most eutherians and metatherians (Wible, 1990; Wible and Hopson, 1993).

In this way, the retention in *Notoryctes* of a lateral lamina and trough are plesiomorphies shared by other basal mammals, including dryolestoids.

5-Petrosal with wide and well-raised stapedial fossa (Character 362-2). In *Notoryctes* the caudal tympanic process forms the posterolateral wall of the enormous stapedial fossa, which houses the stapedius muscle (Ladevèze et al. 2008). The stapedial fossa is deep, subcircular, and positioned posteromedial to the fenestra vestibule (Ladevèze et al. 2008). This fossa is absent in most cynodonts, trithelodontids, and monotremes (Fischer, 1978), being present in more derived mammaliaforms (Wible and Hopson, 1993). The existence of a very wide and deep stapedial fossa has been reported in several taxa, including *Vincelestes* (Rougier et al. 1992) and dryolestoids (e.g., *Necrolestes, Coloniatherium, Dryolestes*; Asher et al. 2007; Rougier et al. 2009; Luo et al., 2012), and has been regarded as a plesiomorphic character shared by most non-therian mammals (Rougier et al., 2009). Although in living taxa this fossa is usually small and poorly defined, it is enlarged in some basal eutherians (e.g., *Prokennalestes, Asioryctes,* leptictids; Wible et al., 2001).

The presence of both tensor tympanic muscle and stapedius muscle in Marsupialia seems to be universal (Mason, 2006; Ladevèze et al. 2008). However, the stapedial fossa in most marsupials is much smaller, shallower, and less defined than that exhibited by *Notoryctes* and basal mammaliaforms (see Ladevèze et al. 2008). In addition, this fossa is also small-sized in most eutherians, including fossorial forms (see Mason, 2003; 2006), and never reaches the large size exhibited by *Notoryctes* and.dryolestoids (see Ladevèze et al. 2008).

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

In this way, we interpret that the very deep and large size of the stapedial fossa of *Notoryctes* is a true primitive shared character with non-therian mammaliaforms.

6-Petrosal with large and deep epitympanic recess (Rougier et al., 2008). The epitympanic recess consists on the portion of the tympanic cavity dorsal to the incudo-malleolar articulation (Klaauw 1931). *Notoryctes* exhibits a relatively large and ovoidal epitympanic recess, despite the fact that the ear bones are reduced (Ladevèze et al. 2008). The epitympanic recess of *Notoryctes* shows very well-defined margins, in contrast with most extinct and living metatherians (see Ladevèze et al. 2008), but resembling the condition present in some dryolestoids, such as *Coloniatherium* (Rougier et al. 2009). It is worth mentioning that peramelids, among marsupials show a large and dep epitympanic fossa, similar to *Notoryctes* (Archer, 1976).

The presence of an epitympanic recess is found in multituberculates, dryolestoids, “symmetrodonts”, *Vincelestes*, and selected therians (Rougier et al. 1996; Hurum et al. 1996; Rougier et al. 2009; Ladevèze et al., 2010). More recently the existence of a large and deep epitympanic recess was proposed as a plesiomorphic mammaliaform character (Rougier et al. 2009). In sum, although we did not include this character in our numerical phylogenetic analysis, due to imposibilities to quantify it properly (Wible et al., 2001), we consider that the presence of a deep and wide epitympanic recess is a plesiomorphic mmamaliaform character, as proposed by previous authors (Wible, 1990; Rougier et al. 2009), and that its presence in *Notoryctes* may represents a truly primitive condition. (Figure 5).

7-Low stapedial ratio (Character 375-1). The stapedial ratio is calculated as length/width of oval window or footplate (Segall, 1970). In *Notoryctes* the stapedial ratio is low (approximately 1.57), a value that is similar to that of the dryolestoid *Necrolestes* and didelphid marsupials (Ladevèze et al. 2008). This value, indicating a nearly subcircular footplate was considered

PeerJ PrePrints

PeerJ PrePrints

plesiomorphic for mammals (Rougier et al. 1998; Wible et al. 2001). In most eutherians the footplate is elliptical, with a stapedial ratio higher than 1.8 (Segall, 1970; Wible et al. 2001; Ekdale et al., 2004; Ladevèze et al. 2008), although in "zhelestids" this ratio ranges from 1.6 through 1.8 (Ekdale et al., 2004). In metatherians and monotremes this condition is highly variable, but stapedial ratios range from 1.6 through 1.8 (Segall, 1970). The morphology of the distal end of the stapes is correlated with the contour of the fenestra vestibuli, which in life accommodates the footplate of the stapes. In correlation with footplate stapes contour, the existence of a subcircular fenestra vestibuli, is currently considered as a primitive morphology, present among basal mammals (e.g., *Vincelestes, Coloniatherium, Cronopio,* multituberculates; Wible, 1990; Rougier et al. 1992, 2009, 2011) and retained by a bunch of therians (Archibald 1979; Rougier et al. 2009). As a concluding remark, we concur with Rougier and collaborators (2009) in that the presence of a subcircular to oval footplate of stapes (and concomitantly a subcircular fenestra vestibule) are plesiomorphic characters shared by most non-therian mammals and *Notoryctes*.

8-Incus and malleus tightly contacted by a straight connection (Character 366-0). The morphology of the middle ear ossicles is known in a reduced sample of fossil mammals; thus, its evolution and character polarization is still problematic. As for example, ear ossicles are unknown for dryolestoids or symmetrodontans. Mason (2001) indicated that the middle ear ossicles of *Notoryctes* exhibit a peculiar morphology not matched by any living or extinct therian. Among these features, Mason (2001) pointed out the immobile straight connection between the incus and the malleus bones. This condition contrasts with that of therians, in which the incus and malleus meet in saddle-shaped groove-and-ridge facet, so that the malleus can push the incus (and stapes) inwards (Hurum et al. 1996; Kielan Jaworowska et al., 2004). In the monotremes (e.g., *Ornithorhynchus*, *Tachyglossus*) the incus and malleus are articulated by means of a nearly

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

flat and straight surface, a putative plesiomorphic condition for mammals (Zeller, 1993; Meng and Wyss, 1995; Rougier et al., 1996). Present analysis suggests that the straight connection between the incus and malleus is a plesiomorphic monotreme-like condition retained by *Notoryctes*.

9-Incus with reduced posterior process and lenticular apophysis (Character 369-0). In *Notoryctes* the incus bone is highly reduced (Mason, 2001). This ossicle shows a very short posterior process, and a strongly reduced lenticular apophysis.

In living therians the incus shows two well-developed processes: a ventral process (the lenticular apophysis), and a posterior process. In non-mammalian cynodonts, as well as morganucodontids, the posterior process is highly reduced or absent, whereas the lenticular apophysis is totally absent, and it is only present as a stalked portion of bone in morganucodontids (Luo and Crompton, 1994). Monotremes retain reduced processes, although in *Tachyglossus* a small-sized lenticular process is present (Allin and Hopson, 1992; Zeller, 1993). A similar condition to that of monotremes has been reported for some eutriconodontan taxa (Luo et al. 2007; Meng et al. 2011). In multituberculates (e.g., *Chulsanbaatar, Lambdopsalis*; Meng and Wyss, 1995; Hurum et al. 1996) the posterior process is well-developed, resembling the condition of living therians. However, the lenticular apophysis is strongly reduced, and in this aspect multituberculates resemble the plesiomorphic mammaliamorph condition. Regrettably, the incus is not preserved in dryolestoids and symmetrodontans, and thus, direct comparisons with *Notoryctes* are scarce.

Previously, a simple incus was considered as a character uniting monotremes with multituberculates (Meng and Wyss, 1995), although it was later reinterpreted as plesiomorphic for mammals (Rougier et al., 1996). In addition, the plesiomorphic nature of a reduced posterior process in the incus is supported by embryological studies, which found that in the first

PeerJ PrePrints

developmental stages of didelphids the posterior process is reduced and its length gradually increases with the age of the individual (Allin and Hopson, 1992; Rowe, 1996). In sum, a simple incus with a reduced lenticular process is a plesiomorphic morphology retained in *Notoryctes*.

10-Poorly coiled cochlea (Character 314-4). *Notoryctes* presents an extremely robust and stout cochlear canal, which exhibits a poorly coiled cochlea (1.6 spiral turns; Ladevèze et al. 2009). In basal mammaliamorphs, including morganucodontids, monotremes, symmetrodontans, and *Vincelestes* the cochlea is straight or coiled less than a turn (Rougier, 1992; Wible and Hopson, 1993; Kielan Jaworowska et al. 2004; Ruf et al. 2009; Luo et al. 2011). In dryolestoids the cochlea is partially (e.g., *Henkelotherium* and *Dryolestes* three fourths of a turn; Ruf et al. 2009; Luo et al. 2011) to fully (e.g., *Reigitherium*, *Cronopio, Peligrotherium*, *Coloniatherium*, more than 1 turn; *Necrolestes*, 1.1 turn; Ladevèze et al. 2007; Rougier et al. 2009) coiled. Most therians have strongly coiled cochlea, and no living therian has fewer than one and a half turns (Gray, 1908; Wible et al. 2001). Among them, low coiling values include sirenians, erinaceine insectivores, and vombatid marsupials, which approximate to the 1.5 cochlear turns (Ladevèze et al. 2009). In very basal extinct Cretaceous eutherians the cochlea coils only 1 turn (e.g. *Prokennalestes, Daulestes, Maelestes, Zalambdalestes,* zhelestids; Wible et al., 2001, 2009; Ekdale et al. 2004). In sum, *Notoryctes* retains of the plesiomorphic mammaliaform condition, as also shown by derived meridiolestidan dryolestoids, and sparse therian genera (Ladevèze et al. 2009). (Figure 7).

11-Presence of septomaxilla (Character 427-1). *Notoryctes* shows a septomaxillary ossification dorsal to the premaxilla, a remarkable feature not reported before for this mammal. In *Notoryctes*, although the septomaxilla is present at the dorsolateral corner of the snout, conforming part of the posteroventral rim of the external nares and exhibiting a very large lateral facial exposure, as typically occurs in basal mammalian taxa (e.g., dryolestoids, monotremates;

PeerJ PrePrints

Wible et al. 1990). In *Notoryctes* this bone interrumpts the premaxilla and reduces its contact with the nasals, resembling *Vincelestes*, *Cronopio*, and *Peligrotherium* among other non-therian mammals (Rougier, 1993; Páez Arango, 2008; Rougier et al, 2012) (Figure 8). The septomaxilla is totally absent in therians (Wible et al. 1990; Rowe, 1993; Archer et al., 1994), with the single exception of a reduced structure in the basal genus *Acristatherium* (Hu et al. 2010). Presence of septomaxilla has been reported for some living xenarthrans (see Wible et al. 1990); however, in these mammals the purported septomaxilla is a minute intranarial ossification without facial exposure (see Wible et al. 1990).

The presence of a large and laterally exposed septomaxilla constitutes a plesiomorphic trait of *Notoryctes* that is shared with basal taxa, including dryolestoids and *Vincelestes*. (Figure 9).

12-Reduced triquetrum, hamate, scaphoid, and trapezium (Characters 221-0, 222-0, 224-1, 223-1). In *Notoryctes* the carpus was analyzed in some detail by Stirling (1891) and Szalay (2006). This carpus is highly modified, and strong fusions between several bones have been reported. Close inspection on *Notoryctes* carpus is important, because recent analyses on fossil therians indicate that carpal bones are among the foremost anatomical section that allow phylogenetic distinction between marsupials and placentals (Luo et al. 2003; 2011). In the basalmost metatherian *Sinodelphys*, the hamate is hypertrophied (being much larger than the triquetrum), the triquetrum is twice the size of the lunate, and the scaphoid is enlarged (more than one and a half the size of lunate), a combination of apomorphies diagnostic of Metatheria (Ji et al. 2002; Luo et al. 2003). On the other hand, in eutherians the hammate, triquetrum, and scaphoid are plesiomorphically small (Ji et al., 2002; Luo et al. 2011), whereas the trapezium is apomorphically elongate, being taller than wide (Ji et al. 2002). Carpal morphology of *Notoryctes* does not fit neither the metatherian nor the eutherian molds. In *Notoryctes* the hamate is dorsoventrally compressed and disc-like (Szalay, 2006), contrasting with the dorsoventrally

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

expanded and transversely compressed condition diagnostic of metatherians (Luo et al., 2003; Szalay, 2006; Character 222-1). In *Notoryctes* the triquetrum is beam-shaped and reduced in size, being different from the enlarged condition interpreted as synapomorphic for Metatheria by Luo and collaborators (Luo et al., 2003; but see Szalay, 2003 for a different view). The scaphoid, in *Notoryctes* is strongly fused with the triquetrum, and its morphology is difficult to discern (Szalay, 2006). However, as was noted previously (Stirling, 1891) the scaphoid in *Notoryctes* is relatively reduced in total size, and does not duplicate the size of the lunate.

On the other hand, in most eutherians including the basal form *Eomaia*, the carpus is derived in having a very enlarged, dorsoventrally extended and transversely compressed trapezium (Kielan Jaworowska, 1977; Ji et al., 2002; Luo et al. 2003; Character 223-0). On the contrary, in basal mammals (e.g., monotremes, triconodontans; Ji et al., 2002), most metatherians (Ji et al., 2002; Szalay, 2006), as well as in *Notoryctes* (Szalay, 2006), the trapezium is plesiomorphically small and beam-shaped (Character 223-1).

It is worth to mention that in several extinct mammals the arrangement of the carpals is not well known, and its morphology is totally unknown among dryolestoids. However, the reduced size of the triquetrum, hamate, scaphoid, and trapezium in *Notoryctes* matches the plesiomorphic pattern seen in basal mammals, including monotremes, triconodontans, and symmetrodontans (Figure 10).

13-Cuboid dorsoventrally low and subtriangular in contour (Ji et al., 2002). In *Notoryctes* the cuboid is subequal to the navicular (Character 278-0) and is subtriangular in shape (Szalay, 2006). In contrast, therian mammals the cuboid is dorsoventrally extended, and subrectangular in shape (Ji et al. 2002). In metatherians, including *Sinodelphys*, the cuboid is relatively large, but is narrower than the navicular, which is transversely expanded (Luo et al., 2003; Character 278-1). In non-therian mammals, as for example in monotremes,

PeerJ PrePrints

multituberculates and *Jeholodens*, the cuboid is irregular or subtriangular in contour, and this condition has been regarded as plesiomorphic for mammals (Ji et al., 2002; Luo et al., 2003). The small, subtriangular cuboid of *Notoryctes* resembles the condition of basal mammals and contrasts with tha of therians.

14-Metatarsal V in wide contact with the calcaneum (Character 282-1, 283-0). *Notoryctes* is metatarsal V exhibits an enlarged projection that contacts along the lateral surface of the calcaneum (Stirling, 1891; Szalay, 2006). In contrast, in therian mammals the cuboid is dorsoventrally extended (Luo et al., 2003). The enlargement of the enlarged cuboid precludes a contact between metatarsal V and calcaneum, a condition that is considered as synapomorphic of therian mammals (Ji et al. 2002).

In basal mammals, such as multituberculates (Kielan Jaworowska and Gambaryan, 1994), the eutriconodont *Jeholodens* (Ji et al., 1999), the symmetrodont *Akidolestes* (Li and Luo, 2006), and monotremes (Szalay, 2006), the condition is similar to *Notoryctes* in that the metatarsal V exhibits a wide contact with the distal portion of the calcaneus (see Szalay and Sargis, 2006). (Figure 11).

15-Sternal ribs (Horovitz and Sánchez-Villagra, 2003). In therian mammals each sternal rib articulates with two subsequent sternebrae of the sternum (Character 35-1 in Horovitz and Sánchez Villagra, 2003). However, in monotremes (Horivitz and Sánchez Villagra, 2003) and in multituberculates (Kielan Jaworowska and Gambaryan, 1994) each sternal rib articulates with a single sternebra, a condition clearly different from that of therians.

In *Notoryctes* the articulation of sternum with the sternal ribs is similar to that of monotremes, constituting a possible plesiomorphic feature for this mammal. (Figure 12).

PeerJ PrePrints

16-Scapular glenoid oblique and facing posteriorly (Character 205-1). In *Notoryctes* the glenoid of the scapula is oblique and posteriorly oriented (Warburton, 2003). In the monotremes, as well as non-mammaliaform cynodonts, the scapular glenoid is subparallel to the scapular main axis (Sereno and McKenna, 1995; Martinelli et al. 2007), a condition related with sprawling posture (Kielan Jaworowska et al. 2004). In dryolestoids (i.e., *Henkelotherium, Necrolestes*; Krebbs, 1991; Asher et al. 2007), and other basal taxa, sucha as multituberculates, symmetrodontans, and triconodonts (Sereno and McKenna, 1995; Gambaryan and Kielan Jaworowska, 1997; Hu et al., 1997; Luo and Wible, 2006; Hu et al., 2005; Li and Luo, 2006; Chen and Luo, 2013) the glenoid is not subparallel, but oblique and posteriorly oriented (Luo et al. 2007). In therian mammals the glenoidal portion of the scapula is located perpendicular to the main axis of the scapula which precludes a transverse movement of the forelimbs (Sereno and McKenna, 1995; Gambaryan and Kielan Jaworowska, 1997; Sereno, 2006). This condition is present in most therians, including fossorial forms such as *Talpa* and *Scapanus* (Reed, 1951; Warburton, 2003). The conformation of the scapular glenoid in therians is related to an apomorphic parasagittal gate, which is derived with respect to the sprawling locomotion in non-therian mammaliaforms (see Sereno and McKenna, 1995; Gambaryan and Kielan Jaworowska, 1997; Sereno, 2006).

The orientation of the glenoid, together with other limb characters, are related to a semi-parasagittal condition seen in *Notoryctes* which osteologically possess an intermediate limb posture between monotremes and therians, a condition that has been advocated previously for the dryolestoid *Henkelotherium* (Vázquez-Molinero et al. 2001).

17-Scapula with supraspinous fossa weakly developed (Character 195-1) and narrower than the infraspinous fossa (Character 196-0). In *Notoryctes* the supraspinous fossa is restricted to a small flattened area near the dorsal margin of the scapula, because the scapular

PeerJ PrePrints

spine originates closer to the cranial border of the scapula, a feature shared with basal mammals (e.g., monotremes, multituberculates, *Fruitafossor*; McKenna, 1961; Luo and Wible, 2005), *Necrolestes*, and some fossorial soricoid (e.g., *Sorex*, *Nesotrichus*; Reed, 1951) and chrysochlorid therians (Asher et al., 2007; Asher and Avery, 2010). On the other hand, the existence of an expanded supraspinous fossa that extends along the anterior margin of the scapular blade, that is much wider than the infraspinous fossa, is a conformation considered as related to the parasagittal gait acquired by therian mammals, including most fossorial forms, such as xenarthrans and diverse hystricomorphs (Sereno, 2006).

In the development and conformation of scapular fossae *Notoryctes* resembles basal mammals and some fossorial forms rather than strictly parasagittal therians. In spite that under the present phylogenetic analysis, the scapular conformation of *Notoryctes* may be regarded as plesiomorphic, remarkable similarities with some fossorial taxa may indicate that such morphology may be better representing adaptative response for fossoriality rather than a truly plesiomorphic character.

18-Distal end of humerus with enlarged distal epicondyles (Character 217-0). *Notoryctes* shows a very robust and expanded distal humeral end, with enlarged and transversely protrudent distal epicondyles (Warburton, 2003). This morphology is also present in some fossorial therians (e.g., *Chrysochloris*, *Talpa*; Asher and Avery, 2010). In a large array of basal eucynodonts, as well as morganucodontids (e.g., *Morganucodon*; Jenkins and Parrington, 1976) and “triconodonts” (e.g., *Yanoconodon, Volaticotherium*; Luo et al., 2007; Meng et al. 2011) the distal entepicondyle and ectepicondyle of the humerus are dorsoventraly and transversely expanded (Martinelli et al. 2007). In monotremes the distal end of the humerus is also transversely expanded (Pridmore et al., 2005), and this condition is also present in several basal mammals, including docodonts,

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

Fruitafossor, *Pseudotribos* and dryolestoids (e.g., *Necrolestes, Henkelotherium*; Vázquez-Molinero et al., 2001; Asher et al., 2007)(Luo and Wible, 2006; Ji et al., 1999; Luo et al. 2007).

On the other hand, in more derived taxa, including multituberculates and therian mammals the distal end of the humerus is transversely compressed and the epicondyles are weakly developed and reduced in size (Sereno and McKenna, 1995; Sereno, 2006). In most living burrowing and fossorial mammals (e.g., *Scapanus, Neurotrichus*; Reed, 1951) the epicondyles are enlarged but in a dorsoventral sense, being transverselly compressed as seen in other therians.

Under the present phylogenetic analysis, the condition of the distal end of the humerus in *Notoryctes* may be possible considered as plesiomorphic. However, its occurrence in selected living therians with burrowing adaptations suggest that such morphology may be better represent an adaptative response for fossoriality rather than a truly plesiomorphic character. (Figure 6).

19-Proximal end of humerus with large lesser tuberosity (Character 211-0). In *Notoryctes*, the proximal end of the humerus is strongly similar to that of the dryolestoid *Necrolestes*; in both genera the lesser trochanter is plesiomorphically large and rounded, subequal in size to the greater trochanter (Warburton, 2003; Asher et al. 2007).

In terrestrial tetrapods with sprawling posture the lesser trochanter on the proximal end of humerus is enlarged and medially expanded (Gambaryan and Kielan Jaworowska, 1997). In basal eucynodonts, monotremes and morganucodontids the lesser trochanter is subequal or larger than the major trochanter (Gambaryan and Kielan Jaworowska, 1997; Hu et al. 1997; Pridmore et al. 2005; Martinelli et al. 2007; but see Sereno, 2006). This morphology is also present in some living burrowing mammals, including *Chrysochloris*, *Scapanus*, and *Nerotrichus* (Reed, 1951; Gambaryan and Kielan Jaworowska, 1997; Asher and Avery, 2010). On the contrary, in multituberculates (Sereno, 2006), *Vincelestes* (Rougier, 1993), and most therians, the greater

PeerJ PrePrints

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

tubercle is much larger and more expanded than the lesser trochanter (Gambaryan and Kielan Jaworowska, 1997).

The large size of the lesser trochanter in *Notoryctes* may possible represent a plesiomorphic condition, however, its occurrence in living fossorial therians suggest that such morphology may also represent an adaptative response for their mode of life. (Figure 6).

20-Distal end of humerus without a cylindrical trochlea for ulnar articulation (Character 215-0). In *Notoryctes* the distal condyles are well-separated each other by a deep and narrow intercondylar groove and do not conform a continuous articular surface (see Warburton, 2003, Figure 6). In *Notoryctes* the ulnar condyle is bulbous, and is far from the radial condyle, the latter being transversely expanded and dorsoventrally flattened (Warburton, 2003).

In basal mammals, such as monotremes, morganucodontids, and triconodontans the condyles are bulbous and separated each other by a wide and deep intercondylar notch (Gambaryan and Kielan Jaworowska, 1997; Hu et al. 1997; Luo and Wible, 2005). In multituberculates (Gambaryan and Kielan Jaworowska, 1997; Chester et al., 2010) and basal dryolestoids (e.g., *Henkelotherium*; Vázquez-Molinero et al., 2001) the distal condyles of humerus are still bulbous and well-differentiated, but they are placed close each other, approaching a hinge-like condition (see Sereno, 2006). In the burrowing dryolestoid *Necrolestes* a cylindrical trochlear-like condition is present, being convergently acquired with that seen in therian taxa (Asher et al., 2007; Chimento et al., 2012).

In living therians, as well as multituberculates, the humerus and elbow joint are positioned close to the body wall, resulting in a parasagittal gait (Sereno and McKenna, 1995; Luo et al., 2002; Sereno 2006). This condition is indicated among other features by the presence of a hinge-like morphology of the elbow joint at the distal end of the humerus, that is further developed in

PeerJ PrePrints

PeerJ PrePrints

therians conforming a trochlear joint with enhanced flexion-extension capabilities (Jenkins, 1973; Sereno, 2006). Such trochlea posteriorly ends in a deep olecranal fossa (Reed, 1951). This horizontally oriented cylindrical trochlea is formed due to the joining of distal condyles (Sereno and McKenna, 1995; Gambaryan and Kielan Jaworowska, 1997).

As a concluding remark, the distal humeral condyles of *Notoryctes* look truly plesiomorphic when compared with that of therian mammals.

21-Proximal end of femur with low greater trochanter (Li and Luo, 2006). In *Notoryctes* the proximal end of the femur is transversely expanded and anteroposteriorly compressed, and shows a short and robust femoral neck and a robust and low greater trochanter (Warburton, 2003; Figure 6).

In monotremes, the basal symmetrodont *Akidolestes* and "triconodonts" (e.g., *Yanoconodon, Jeholodens, Repenomamus*; Ji et al., 1999; Hu et al., 2005; Luo et al., 2007; Chen and Luo, 2013) the proximal end of the femur exhibits the following combination of plesiomorphies: reduced femoral neck, low and broad femoral trochanter, and lesser trochanter distally located and well-separated from the femoral head (Li and Luo, 2006; see also Worthy et al., 2006). The proximal end of the femur in these taxa is transversely expanded, and conforms a typical "winged" aspect (Vázquez-Molinero et al., 2001). This combination of characters is related with a sprawling mode of locomotion (Chester et al., 2012) and is present in the vast majority of eucynodont taxa, as well as morganucodontids, triconodontans, symmetrodontans, docodontans, and *Vincelestes* (Gambaryan and Averianov, 2001; Meng et al., 2006; Ji et al., 1999; Li and Luo, 2006; Martinelli et al., 2007; Chester et al. 2012). On the contrary, in therians the femur has a high and vertically oriented greater trochanter, a distinctive neck offset from the shaft, and lesser trochanter near the femoral head, a combination of traits related to parasagittal gait (Li and Luo, 2006). This conformation is present in most therians, including fossorial forms, such as *Scapanus* and *Neurotrichus* (Reed, 1951).

In dryolestoids (e.g., *Necrolestes, Henkelotherium*; Krebbs, 1991; Asher et al. 2007) the proximal end of the femur is anteroposteriorly compressed and transversely expanded, showing a winged appearance, a condition similar to basal mammals. In these taxa the greater trochanter is low and robust, showing a transversely expanded base. In addition, in dryolestoids the lower trochanter is located near the femoral head (Character 241-1) a condition shared with therian mammals (Li and Luo, 2006).

In sum, the conformation of the proximal end of the femur of *Notoryctes* matches the plesiomorphic morphology present in basal mammals.

22-Hypertrophied parafibular process in the fibula (Character 249-1). The parafibula is a plesiomorphic mammalian trait consisting of a large independent ossification located near the fibular diaphysis, that extensively fuses to the shaft in adult multituberculates, monotremes, the spalacotheroid *Akidolestes* (Luo and Ji, 2005) and the basal multituberculate *Rugosodon* (Yuan et al., 2013). Such hypertrophied parafibular process is correlated with the sprawling posture, because it constrains the knee to be permanently flexed (Pridmore, 1985). In extinct dryolestoids the fibula is only known in the genera *Necrolestes* and *Henkelotherium* (Krebbs, 1991; Asher et al., 2007). In both taxa the parafibular process is highly expanded and laminar, and in the case of *Necrolestes* is proyected well beyond the proximal margin of the fibula (Asher et al., 2007). The absence or reduction of such parafibular process has been regarded as a derived feature for therians (Li and Luo, 2006).

In *Notoryctes*, as occurs in dryolestoids and other basal mammals the parafibular process is laminar, strongly developed and proximally projected, departing from the condition seen in

PeerJ PrePrints

PeerJ PrePrints

eutherians and metatherians (Warburton, 2003; see details in Barnett and Napier, 1953). (Figure 6).

The combination of a femur with a low femoral head, short and robust neck, distally positioned lower trochanter, asymmetrical distal femur, and hypertrophied parafibular process of tibia are correlated with a sprawling posture, suggesting a strongly flexed knee for *Notoryctes* (Jenkins and Parrington, 1975; Li and Luo, 2006; Chen and Luo, 2013).

23-Fully ossified patella (Character 288-1). In *Notoryctes* an enlarged patella with a keel showing well-developed muscle site attachments is present, a feature that constrasts with metatherians (Warburton, 2003). As noted by Reese (2001) a cartilaginous disc-like patella is diagnostic of metatherians (Kielan Jaworowska et al. 2004). In fact, in all known fossil and living metatherians the patella is unossified, with the single exception of peramelids, in which a reduced and flattened sesamoid structure is present (Warburton, 2003; Kielan Jaworowska et al. 2004). In basal mammals, including monotremes, multituberculates, the zhangheotheriid *Zhangheotherium*, and *Vincelestes* a patella is well developed and ossified (Rougier, 1993; Luo and Ji, 2005), whereas in others (e.g., triconodontans, most symmetrodontans) a patella is absent. Regrettably, most dryolestoids not preserved a patella, and thus, its presence is still mater of debate. However, as pointed out by Asher et al. (2007) the presence of a small patellar surface on the distal femur of *Necrolestes* may suggest the existence of an ossified patella in this dryolestoid. In spite of its patchy distribution, a well-ossified patella appears to be the plesiomorphic condition for mammals (Kielan-Jaworowska et al., 2004).

In sum, presence of a well-developed patella in *Notoryctes* possibly represents a plesiomorphy shared with basal mammals.

PeerJ PrePrints

PHYLOGENETIC RESULTS

Phylogenetic analysis. We present here a cladistic analysis of mammaliaform higher-level relationships mostly based on the studies published by Luo et al. (2007) with the modifications made by Chimento et al. (2012). The data set was compiled including most characters traditionally used to diagnose Dryolestoidea, Metatheria, Marsupialia, and Australidelphia. The data matrix is composed of 458 characters distributed among 114 taxa (Appendix 1,2). Characters 1-445 follow Luo et al. (2007) and characters 446-458 were added in the present analysis from different data sources (i.e., Bonaparte, 1990; Chornogubsky, 2011; Rougier et al., 2011; Chimento et al., 2012). Codification of characters for *Necrolestes* follows mostly Chimento et al. (2012) and Rougier et al. (2012). Most features regarding braincase characters of *Reigitherium*, *Peligrotherium* and *Cronopio* follows the codifications of Páez Arango (2008) and Rougier et al. (2011). Postcranial characters of *Peligrotherium tropicalis* follow the codifications of Rougier et al. (2011). Additional postcranial osteological data for *Notoryctes* was extracted from Warburton (2003). The metatherian (29) and eutherian (26) taxa included in the analysis represent the major radiations with which *Notoryctes* was compared by previous authors, in order to test its phylogenetic position within a clear phylogenetic context.

The phylogenetic analysis was performed using TNT 1.1 (Goloboff et al., 2008). All characters were equally weighted and treated as unordered. Heuristic searches were performed after 1,000 pseudoreplicates of WAG+TBR search strategy, with 10 random addition sequences after each search and 100 trees were saved at each replicate. The phylogenetic analysis resulted in the recovery of 20 Most Parsimonious Trees (MPTs), of 2443 steps, with a consistency index of 0.31, and a retention index of 0.77. (Figure 13)

The strict consensus tree recovered *Notoryctes* as the sister-group of the dryolestoid *Leonardus* and *Necrolestes*. The inclusion of *Notoryctes* as a Metatheria was found in suboptimal

PeerJ PrePrints

trees of 2479 length, being 37 extra-steps. Inclusion within Marsupialia is 57 steps longer. This clearly indicates a more robust position of *Notoryctes* among dryolestoids, rather than Marsupialia. Additional analyses have yielded different tree lengths for dissimilar position of *Notoryctes*: *Notoryctes* + Prototribosphenida tree of 2455 length; *Notoryctes* + Eutheria tree of 2499 length; *Notoryctes* + Insectivora tree of 2501 length; *Notoryctes* + Australidelphia tree of 2492 length; *Notoryctes* + Dasyuromorpha tree of 2490 length; and *Notoryctes* + Peramelimorphia tree of 2486 in length.

With the aim to test the robusticity of tree topology, we calculated the Templeton test and Bremer support for each node. Nesting of *Notoryctes* within Dryolestoidea is very strongly supported (Bremer support =6), and its position within Meridiolestida is well supported (Bremer support =6), thus conforming a robust phylogenetic signal (Fig. 3).

Bootstrap analysis under parsimony was performed in order to test nodal support (see Xu and Pol, 2013). Analysis here conducted resulted in a relatively high support for dryolestoidean (54 %) and very robust support for meridiolestidan (76 %) affinities for *Notoryctes*.

The presence of several dryolestoid-like features, and plesiomorphic traits along the skull and postcranial skeleton, together with poorly documented synapomorphies uniting *Notoryctes* with Metatheria or even Theria, suggest that the phylogenetic position of *Notoryctes* is far from being well understood. Based on the analysis here performed, we conclude that *Notoryctes* is part of a dryolestoid radiation and constitutes the sister-group of the genera *Leonardus* and *Necrolestes*. At following we discuss in detail the dryolestoid and meridiolestidan synapomorphies that are present in *Notoryctes* and that allow its referral to this mammalian clade.

PeerJ PrePrints

Synapomorphies nesting *Notoryctes* within Dryolestoidea and Meridiolestida. Present analysis prompted to recognize three different diagnostic features that constitute synapomorphies uniting *Notoryctes* and Dryolestoidea.

136(1)-Distal metacristid absent on lower molariforms (Figure 14). The talonid (or pseudotalonid) of lower molars in mammals usually exhibits a ridge uniting the entoconid with the metaconid cusp of the trigonid (Fox 1975; Kielan-Jaworowska et al. 2004). This ridge is termed as the distal metacristid (Kielan-Jaworowska et al. 2004). In *Notoryctes* a talonid is totally absent in molariforms, and consequently, a distal metacristid cannot be recognized (see Asher and Sánchez-Villagra, 2005).

Basal mammaliaforms, including australosphenidans lack a true talonid and metacristid, and this conformation is currently considered as plesiomorphic for the entire clade (Kielan Jaworowska et al., 2004). On the other hand this ridge is present in several basal mammals, including "peramurids", *Kielantherium*, and Deltatheridia, and is usually considered as a diagnostic trait of the entire clade Zatheria (Sigogneau-Russell, 1999, Kielan-Jaworowska et al., 2004; Lopatin and Averianov, 2007). In all known therian mammals, including most zalambdodont ones the lower molars show a well-developed talonid, usually with a well developed distal metacristid (Kielan-Jaworowska et al. 2004). The only living therian in which a metacristid is absent is the zalambdodont insectivoran *Chrysochloris* (Asher and Sánchez-Villagra, 2005). Within cladotherians a metacristid is usually present in most taxa, but in basal Dryolestoidea a well developed talonid (or pseudotalonid) and a distal metacristid are apomorphically absent, and the molariforms are considered as zalambodont-like (Bonaparte, 2002; Kielan-Jaworowska et al., 2004; Rougier et al., 2011). In fact, absence of distal metacristid was considered as synapomorphic of Dryolestoidea by Chimento et al. (2012).

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.715v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

In this way, the absence of distal metacristid is here recovered as a synapomorphy shared by *Notoryctes* and Dryolestoidea.

79(2)-Nearly transverse orientation of the paracristid relative to longitudinal axis of the molar (Figure 14). In *Notoryctes* the paracristid of lower molariforms consists on an acute ridge that develops along the anterior rear of the teeth (Stirling, 1894). This crest is nearly transversely oriented with respect to the main mesiodistal axis of the teeth.

In dryolestoids the paracristid of lower molars exhibits a nearly transverse orientation when compared with the longitudinal (=mesiodistal) molar length (see Bonaparte, 1990). This morphology is clearly related to the transverse expansion and mesiodistal compression of each dental element, a condition typical of dryolestoids (Bonaparte, 1986; 1990; Kielan Jaworowska et al., 2004). This morphology also occurs in most meridiolestidan dryolestoids, including *Necrolestes, Leonardus,* and *Mesungulatum*, among others (Bonaparte, 1986, 1990, 2002; Asher et al., 2007; Chornogubsky, 2011; Chimento et al., 2012). Presence of dryolestoid-like disposition of paracristid on lower molars is a feature that was convergently acquired by some zalambdodont taxa (Asher and Sánchez-Villagra, 2005).

In our analysis, presence of transverse paracristid is considered as a possible synapomorphy nesting *Notoryctes* within Meridiolestida.

104(3)- Upper molariforms lacking metacone (Figure 2). As analyzed above, in *Notoryctes* the occlusal surface of the upper molariforms is constituted by the stylocone, paracone and metastyle, with the total absence of a metacone.

The metacone is currently considered as a neoformation in the upper molars of "eupantotherian" mammals (Crompton 1971; Kielan-Jaworowska et al. 2004). In most dryolestoids (e.g. *Dryolestes*, *Laolestes*, *Tathiodon*, *Henkelotherium*; Krebs 1991; Martin 1999;

PeerJ PrePrints

Kielan-Jaworowska et al. 2004) the metacone is highly reduced, being represented by a small cusp located near cusp "C", both being connected through a metacrista (Krebs 1991; Martin 1999; Schultz and Martin 2011). In Meridiolestida, the metacone is totally absent, as observed in all known mesungulatids, *Cronopio* and *Necrolestes* (Gelfo and Pascual 2001; Bonaparte 2002), and was considered as a synapomorphy of Meridiolestida Chimento et al., 2012; Rougier et al., 2012).

As a result of our analysis, the absence of this cusp in *Notoryctes* is hypothesized as a synapomorphy that unites *Notoryctes* with Meridiolestida.

152(2)- Three upper premolars. In *Notoryctes* the dental formula is highly variable among individuals of the same species. As discussed above, a maximum number of three upper premolars has been reported for *Notoryctes*.

Most basal zatherian mammals show a plesiomorphic premolar number of five (McKenna, 1975; Kielan Jaworowska et al. 2004). On the other hand, metatherians show a derived dental formula composed by three upper premolars, with the possible single exception of the retention of five premolars in the basal taxon *Sinodelphis* (Luo et al. 2003). In eutherian (Kielan Jaworowska et al. 2004) as well as dryolestoid mammals, such as *Krebsotherium, Henkelotherium*, and *Dryolestes* (Krebs, 1991; Martin, 1999; Kielan Jaworowska et al. 2004), and the basal meridiolestidan *Cronopio* (Rougier et al. 2011) there are four upper premolars, representing a possible plesiomorphic condition. On the other hand, in remaining meridiolestidan dryolestoids only three upper premolars are exhibited, as exemplified by *Coloniatherium, Peligrotherium,* and *Necrolestes* (Asher et al. 2007; Páez Arango, 2008; Rougier et al. 2009; Chimento et al., 2012). The same number is also reported for the possible paurodontid dryolestoid *Drescheratherium* (Krebs, 1998).

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

In the present analysis, presence of three premolars is recovered as a possible synapomorphy of the Meridiolestida including *Notoryctes*, which was convergently acquired by metatherians. (Figure 4).

244(1)-Shallow and weakly developed patellar groove on distal femur (Figure 6).

In *Notoryctes* the distal end of the femur shows on its anterior surface a poorly developed patellar groove represented by an incipient concavity with ill-defined margins (Warburton, 2003).

In basal mammaliaforms, such as monotremes, triconodonts, didelphids, *Dromiciops*, and the extinct therian *Asiatherium* the distal end of femur is anteriorly flat and lacks any sign of patellar groove (Jenkins and Parrington 1976; Ji et al. 1999; Forasiepi and Martinelli 2003; Chester et al. 2012). On the other hand, in multituberculates and most therians the patellar groove is deeply excavated and shows well-defined and sharply ridged longitudinal edges (see Forasiepi and Martinelli 2003). This condition that is also present in fossorial eutherians (e.g., *Scapanus*, *Sorex*, *Neurotrichus*; Reed, 1951). Among dryolestoids the femur is only known in *Necrolestes* and *Henkelotherium*, and both taxa lack a well-developed and defined patellar groove on its anterior surface. In both taxa the patellar groove of the femur is only developed by an incipient concavity with ill-defined margins (Krebs 1991; Asher et al. 2007). This feature was considered by Chimento et al. (2012) as a synapomorphy of Dryolestoidea (Figure 6).

In the context of the available evidence, a poorly marked patellar groove on distal femur is considered as a possible derived feature diagnostic of Dryolestoidea, including *Notoryctes*.

458(1)-Second crus commune on semicircular canals of the middle ear (Figure 7). The secondary crus commune constitutes a point of the inner ear at which the posterior semicircular canal cross-over the lateral one (Ladevèze et al. 2008). Gray (1908) described for the inner ear of *Notoryctes* a peculiar junction between the lateral and posterior semicircular canals at the point in

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

which the later passes under the former, thus constituting a secondary crus commune. This condition is only present in a bunch of therian mammals, including the derived marsupials *Monodelphys* and *Didelphis* as well as in sparse eutherian genera (Schmelzle et al. 2007; Ladevèze et al. 2008; Ekdale, 2009; Luo et al. 2011). Moreover, its presence has also been reported for the dryolestoids *Dryolestes* and *Henkelotherium* (also Ruf et al. 2009; Luo et al., 2011), and *Necrolestes* (Ladevèze et al. 2008). Thus, on the basis of a comprehensive phylogenetic analysis Chimento et al. (2012) conclude that presence of secondary crus commune was a synapomorphy of Dryolestoidea.

In concordance, present analysis indicates that the existence of a secondary crus commune may constitute a synapomorphy uniting *Notoryctes* with dryolestoids. (Figure 4).

Furthermore, *Notoryctes* exhibits the following six synapomorphic characters with the dryolestoid clade Meridiolestida:

4(2)- Meckel´s sulcus absent (Figure 14). In basal mammaliaforms, including australosphenidans, multituberculates, and basal Jurassic dryolestoids, a well-developed meckelian sulcus is present on the medial surface of dentary (Krebs 1969; 1971; Martin 1995; 1999; Kielan-Jaworowska et al. 2004; Rich et al. 2005). This condition is also retained in selected basal Mesozoic therians (e.g., *Kokopellia*, *Prokennalestes*, *Eomaia, Kielantherium*; Dashzeveg and Kielan-Jaworowska 1984; Kielan-Jaworowska and Dashzeveg 1989; Ji et al. 2002; Kielan-Jaworowska et al. 2004). On the contrary, this sulcus is absent in Cretaceous dryolestoids, including *Crusafontia* and all Meridiolestida (e.g., *Cronopio*, *Coloniatherium, Necrolestes*; Rougier et al. 2009; Rougier et al. 2011; Chimento et al., 2012). The absence of a meckelian groove is also reported in most living and extinct metatherian and eutherian mammals (Kielan-

PeerJ PrePrints

Jaworowska et al. 2004). In the present analysis, the absence of meckelian sulcus is recovered as a synapomorphy of the Meridiolestida, and *Notoryctes*.

31(1)- Gracile and elongate dentary peduncle. In *Notoryctes* the peduncle for the mandibular condyle is extremely gracile and elongate, it is dorsally oriented, and ends in a small articular surface for the skull. (Figure 14)

In basal mammaliamorphs, such as *Morganucodon* and docodontans the peduncle of the articular condyle of the dentary is slightly developed and is relatively short and strong (see Kielan Jaworowska et al., 2004). In the same way, in basal australosphenidans, such as *Bishops* (Rich et al., 2001) the dentary condyle shows a highly reduced peduncle. Basal dryolestoids show a robust and poorly developed dentary peduncle (e.g., *Krebsotherium, Dryolestes, Crusafontia*; Krebs, 1993; Martin, 1999), a morphology widespread in basal therians, including the metatherians *Mayulestes, Alphadon,* and *Didelphodon* (Fox and Taylor, 1986; Cifelli et al., 1996; Muizon, 1998), and the eutherians *Barunlestes, Zalambdalestes, Kennalestes,* and *Maelestes* (Kielan Jaworowska, 1975; Wible et al. 2009). The condition of the condylar peduncle is variable among living therians, and a gracile and elongate peduncle is present, as for example, in *Chrysochloris* (Asher et al., 2007).

In the meridiolestidan dryolestoid *Cronopio* the dentary peduncle is elongated and very well developed, being also well dorsally extended (Rougier et al. 2011), a condition also present in *Necrolestes* (Asher et al., 2007).

In our analysis, presence of an elongate condylar peduncle results as a synapomorphy of Meridiolestida, including *Notoryctes*.

220(1)- Strong styloid process on distal ulna (Figure 6). The distal ulna of marsupials shows a poorly developed and distally oriented process on the caudal surface of the bone, that is

PeerJ PrePrints

frequently termed as the styloid process, and that is currently considered as a possible synapomorphy for Marsupialia (Ahser et al. 2007). However, this ball-like distal process is also present in known dryolestoids, including *Necrolestes* and *Henkelotherium* (Krebs, 1991; Asher et al. 2007), as well as the spalacotherioid *Akidolestes* (Chen and Luo, 2013). In the same way, in *Notoryctes* a ball-like styloid process is also present on the distal ulna.

The analysis here performed indicates that presence of large styloid process on ulna may be considered as a Meridiolestida synapomorphy, convergently acquired by marsupials.

Similarities shared by *Notoryctes* and dryolestoids. In addition to the synapomorphies described above, there are several additional similarities between *Notoryctes* and meridiolestidan dryolestoids that do not results as synapomorphic in our analysis due to its complex distribution or low support. In spite of that, some of them appears to be important and we anayze them as follows.

Chimento et al. (2012) considered the presence in lower molars of protoconid and metaconid subequal in height as a synapomorphy of the Dryolestoidea. This contrasts with the reduced metaconid seen in most Metatheria, in which this cusp is at least 30% smaller than the protoconid (Asher et al., 2007). In *Notoryctes*, both the metaconid and protoconid are similar sized, recalling the dryolestoid condition.

Bensley (1903) indicated that in *Notoryctes* molariforms the large internal cusp (paracone herein) is crescentic in shape when viewed from the crown, and its tip is placed at much lower level than the external cusp (stylocone herein). The talonid is absent or present only by a minute tubercle attached to the postero-internal angle of the trigonid in the first and second molariforms. This combination of characters is widespread in dryolestoids, including *Groebertherium* and

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

Casamiquelia (Bonaparte, 1990), and the absence of talonid was regarded as diagnostic of meridiolestidan dryolestoids by Chimento et al. (2012). Moreover, *Notoryctes* also resembles meridiolestidans in having a metastylar lobe much larger than the parastylar lobe, a condition regarded as synapomorphic of such clade (Rougier et al., 2011; Chimento et al., 2012). In addition, *Notoryctes*, such as mesungulatids (e.g., *Mesungulatum, Coloniatherium*, *Peligrotherium*; Páez Arango, 2008; Rougier et al. 2009), *Leonardus*, and *Groebertherium* (Bonaparte, 1990) show a very distinctive, proportionately large, and centrally located stylocone. As in these genera, in *Notoryctes* the lower molariforms exhibit a nearly straight paracristid, and a transverse metacristid. *Notoryctes* resembles meridiolestidans, such as *Leonardus, Cronopio* and *Necrolestes* in having non-imbricate upper molariforms which are well separated each other (Chornogubsky, 2011; Rougier et al., 2011; Chimento et al., 2012). This condition contrasts with the imbricate condition shared by Laurasian dryolestoids (e.g., *Dryolestes, Henkelotherium, Krebsotherium*; Martin, 1999).

In contrast with paurodontids and mesungulatoids, *Notoryctes* has a shallower and gracile dentary bone with a subhorizontal symphysis, a condition reminiscent to that of the basal meridiolestidans *Cronopio* and *Necrolestes* (Martin, 1999; Páez Arango, 2008; Rougier et al., 2011; Chimento et al., 2012). Moreover, *Notoryctes* shares with *Leonardus, Necrolestes*, and *Cronopio* hypsodont-like molariforms, mesiodistally compressed upper molariforms, and presence of a parastylar hook in upper premolars (Bonaparte, 1990; Chimento et al., 2012). Finally, *Notoryctes* and *Necrolestes* share posteriorly situated mandibular glenoid fossa lateral to the pars cochlearis of the petrosal (Asher et al., 2007), as well as absence of prootic canal and a small-sized lateral lamina and through (Ladevèze et al., 2009; Rougier et al., 2012). The later two characters are different from basal dryolestoids, but similar to plesiomorphic eutherian mammals (Wible et al., 2009), a condition that was probably convergently acquired. Moreover, both

Notoryctes and *Necrolestes* show a large amount of postcranial features probably related with fossoriality (e.g., fused cervicals, double scapular spine, ulna with very large olecranon which is medially infected; Asher et al., 2007), since these traits are also present in digging eutherian insectivores (e.g., chrysochloroids).

In this way, several similarities shared by *Notoryctes* and *Necrolestes* suggest that both genera may be closely related, and is it is probable that the traits common to these genera may reflect close phylogenetic relationships rather than adaptative paralellisms responding to similar modes of life.

Another important source of iformation regarding phylogenetic analysis is the disposition and composition of enamel microstructure. The schmelzmuster of *Notoryctes* is asymmetrical. In longitudinal section shows radial enamel and steeply apically oriented prisms in the inner zone and antapical prisms in the outer region (Asher et al., 2007). In cross section the prisms are obliquely oriented in the inner zone and longitudinal in the outer zone (Asher et al., 2007). This kind of enamel is present in small marsupials and "insectivoran" placentals (Koeningswald and Goin, 2000), but also in meridiolestidan dryolestoids (e.g., *Necrolestes, Reigitherium*; Wood and Rougier, 2005; Asher et al., 2007), and was previously regarded as the plesiomorphic condition for Theria. Although far from conclusive, the enamel morphology and disposition of *Notoryctes* does not substantially differs from that of basal cladotherian and basal therians, and thus, do not contradict the basal position for *Notoryctes*, as here proposed.

The phylogenetic position of *Naraboryctes philcreaseri* Archer et al. 2010. Archer et al. (2010) described the new genus and species *Naraboryctes philcreaseri* from the Early Miocene of Queensland, Australia. *Naraboryctes* was considered as nearly related to *Notoryctes* and was consequently included by Archer et al. (2010) within Notoryctidae. They allied *Notoryctes* and *Naraboryctes* on the basis of the tendency of zalambdodonty in upper molars, with paracone smaller (or absent) than metacone, large protocone, and lower molars with reduced (to absent) talonids (see main text for a different arrangement of cusp homologies).

However, *Naraboryctes* dentition and skull clearly differ from *Notoryctes* in retaining features recalling typical metatherian condition, as for example the presence of I5 (only I4 in *Notoryctes*), distinct paracone on upper molars and three cusped talonids on the lower molars, talonid only slightly smaller than the trigonid, anterior cingulid evident, and dentary with a very large coronoid process. Moreover, as can be deduced from the list of characters diagnosing Notoryctidae, Archer et al. (2010) do not report a single unique apomorphy uniting *Notoryctes* and *Naraboryctes*, and most characters point to a “tendence” towards zalambdodonty, rather than discrete apomorphic characters. On this basis, we consider that cranial material *Naraboryctes* cannot be confidently included within Notoryctidae or Notorycteomorphia, and we consider it as Metatheria *incertae sedis*, pending new detailed studies.

Archer et al. (2010) described *Naraboryctes* based on dissociated cranial and postcranial material. Archer et al. (2010) referred to *Naraboryctes* an ulna and humerus that show all the diagnostic features of these bones seen in *Notoryctes*. These bones were not found in association with any element unambiguously referable to *Naraboryctes* and are here considered as Notoryctidae indet., representing the only probable fossil record for the clade.

As a concluding remark, we exclude *Naraboryctes* from the *Notoryctes* lineage, and we consider that the only possible fossil record of notoryctids consist on a Miocene isolated ulna and humerus described by Archer et al. (2010).

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

Mammalian plesiomorphies present in the soft anatomy of *Notoryctes*. Since the end of the XIX century, the soft anatomy of *Notoryctes* was considered as unique among mammals, and regarded as highly modified for burrowing habits (Stirling, 1891; Gadow, 1892; Ogilby, 1892; Thompson, 1905; Sweet, 1906). In spite of such strong modifications, the soft anatomy of *Notoryctes* allow to recognize some interesting topics. At following we summarize some highly plesiomorphic features present on internal organs of the marsupial mole.

The brain of *Notoryctes* presents a combination of characters that distinguishes it from both monotreme and eutherian mammals, showing an intermediate morphology between both clades (Figure 15). For example, the olfactory bulbs in *Notoryctes* are plesiomorphic in being placed entirely in front of the cerebrum, with a size smaller than in any living therian, but more developed than in monotremes (Smith, 1895; Benshemesh and Johnson, 2003; Ashwell, 2010; Vaughan et al., 2010). In therians the olfactory bulbs are ventro-laterally displaced from midline, a condition that has been traditionally regarded as synapomorphic of the group (Ashwell, 2010). In *Notoryctes*, the neopallium is smaller than in other mammals; the inrolling and folding of the hippocampus (arquipalium) are less well developed than in therians and the cerebellum is very small and exhibits an extreme degree of simplicity, a unique plesiomorphic combination of traits absent in therian mammals (Smith, 1895; Vaughan et al., 2010). The neopallium forms merely a dorsal cap lying on the pyriform lobe, and is not separated by any fissure, a condition reminiscent to that of monotremes, but different from that exhibited by tribosphenic mammals (Ashwell, 2010; see also Rowe et al., 2011). The pyriform lobe is very large, and not only constitutes the ventral part, but also much of the lateral walls of the brain, a plesiomorphic condition for mammals (Smith, 1895; Benshemesh and Johnson, 2003; Ashwell, 2010). In the same way, the cerebellum is small, and shows an extreme degree of simplicity (Smith, 1895). As a result, the

PeerJ reviewing PDF | (v2014:12:3598:1:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

small and simple brain of *Notoryctes* is very similar in several features to that of monotremes, lacking a large amount of derived traits present in therian mammals.

In addition to its brain anatomy, in *Notoryctes* the reproductive system shows a strikingly plesiomorphic morphology. Since its original description *Notoryctes* was considered as peculiar among metatherians in having a single exit for both urinal and reproductive ducts (Gadow, 1892). In fact, in *Notoryctes,* the uterus/deferent sperm-ducts pass into a common urogenital canal together with the ureters, ending in a common cloaca (Renfree, 1993; Presley, 1997). This constitutes the plesiomorphic condition for mammals (Renfree, 1993; Presley, 1997). Monotremes also exhibit a single cloacal opening, but these mammals present a wide urogenital sinus, much wider than the urogenital canal of *Notoryctes* (Stirling, 1891; Gadow, 1892; Renfree, 1993). In *Notoryctes* this single duct becomes narrower and longer than that of monotremes, approaching in this aspect the derived therian condition. However, in most therians this duct is divided among most of its length (Stirling, 1891; Renfree, 1993; Presley, 1997). Among living mammals, only egglaying monotremes, and possibly tenrecid eutherians, retains as adults an undoubted typical cloaca (Temple-Smith and Grant, 2001; Riedelsheimer et al., 2007). The presence of a true cloaca has been denied in most placental and marsupial mammals, in which the small common “pseudo-cloaca” outlet is composed only by a skin fold, with the fold´s epithelium keratinized and endowed by epidermal appendages (Sweet, 1907; Djakiev and Jones, 1982; Frey, 1991; Shoshani and McKenna, 1998; Mess and Carter, 2006; Riedelsheimer et al., 2007). On the contrary, in monotremes, as well as *Notoryctes* (Temple-Smith and Grant, 2001) the true cloaca is devoid of classical skin glands and associated ducts, and the epithelium is not keratinized (Sweet, 1907). (Figure 16).

The male reproductive system of *Notoryctes* exhibits striking plesiomorphic morphology, being reminiscent to that of egg-laying mammals. In *Notoryctes* the penis is located inside the

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

internal wall of the cloaca, as occurs in monotremes, whereas in therians the penis is placed external to it (Gadow, 1892; Stirling, 1891; Temple-Smith and Grant, 2001; Riedelsheimer et al., 2007). The testicles in *Notoryctes* are internal to the body, located between the pubis and the abdominal wall, a morphology that represents an intermediate condition between the intra-abdominal testicles of monotremes and the external one of most therian testicles (Gadow, 1892; Stirling, 1891; Werdelin and Nilssone, 1999; Temple-Smith and Grant, 2001; Riedelsheimer et al., 2007; Kleisner et al., 2010). *Notoryctes* lacks of scrotum, a condition also shared with monotremes, whereas in therians the scrotum is present and well-developed (Waddle et al., 1999; Temple-Smith and Grant, 2001; Riedelsheimer et al., 2007; Kleisner et al., 2010). In *Notoryctes* (as in monotremes) only a single pair of additional bulbo-uretral glandulae are present, whereas in therians exists several additional structures, including prostate and uretral glandules, and in derived eutherians a seminal vesicle is present. (Figure 17).

As a whole, the reproductive organ anatomy and brain morphology of *Notoryctes* are also indicative of the exclusion of this mammal from Theria. (Figure 18).

BIOGEOGRAPHICAL IMPLICANCES

***Notoryctes* and meridiolestidan radiation.** Present analysis results in that *Notoryctes* is very different from Laurasian dryolestoids, and appears to be well-nested within the meridiolestidan South American radiation. Strong similarities with the Cretaceous genus *Leonardus* and the Miocene *Necrolestes* indicating that the lineage has an extremely long evolutionary history, and that its fossil record appears to be patched during the last 70 my.

Meridiolestidan radiation includes a large amount of ecologically divergent taxa. Among them, there are small sized and acute cusped taxa, such as *Groebertherium* and *Brandonia*

PeerJ PrePrints

(Bonaparte, 1991). Mesungulatids, including *Mesungulatum, Coloniatherium, Peligrotherium, Reigitherium* and *Paraungulatum* (Bonaparte, 1986; 1990, 2002; Gelfo and Pascual, 2001; Rougier et al., 2009) share extensive tooth to tooth occlusion with expanded cingula and bulbous bonodontan cusps. This later morphology was linked to herbivorous habits, and the great radiation of these taxa was related to the high angiosperm diversification (Rougier et al., 2009). On the other hand, there also existed a bunch of taxa including small-sized and fossorial taxa, showing acute cusped and hypsodont-like teeth, such as *Necrolestes, Notoryctes,* and probably *Cronopio* and *Leonardus* (Bensley, 1903; Bonaparte, 1991; Rougier et al., 2011; Chimento et al., 2012). This suggests that dryolestoids underwent a very large evolutive radiation, including still unexpected forms, as previously advocated by Bonaparte (1994).

Survival of ancient mammals in the Cenozoic of southern continents. In South America, contrasting with other landmasses the fossil record indicates a Late Cenozoic survival of several Mesozoic lineages. Well-documented provincialism of mammals in the Mesozoic of South America, includes highly distinctive taxa related to Jurassic forms of the northern continents (Bonaparte, 1990). In contrast to the Northern Hemisphere, several mesozoic mammals survive the K/T boundary. In fact, by Eocene and Oligocene times several multituberculate gondwanatheres were recovered from Patagonia and Perú (Goin et al., 2006, 2012; Antoine et al., 2011). In addition, dryolestoids were also found in Paleocene and Miocene beds of Patagonia (Bonaparte et al., 1993; Gelfo and Pascual, 2001; Chimento et al., 2012; Rougier et al. 2012). In addition, a monotreme was also recoverd in the early Paleocene beds of Patagonia (Pascual et al., 1992). The existence of such atavisms, coexisting with derived placental mammals during the Cenozoic was considered as a "mixture fauna", a pattern different from that seen in Northern Continents (Rougier et al., 2012). The increasing number of Mesozoic lineages now known to survive in the Cenozoic of South America demonstrates the integration of these basal mammals into the eutherian and metatherian faunas of the Cenozoic.

In Antarctica, together with placental and marsupial mammals remains of multituberculate gondwanatherians were also reported (Goin et al. 2006), suggesting a similar pattern to that seen in South America.

A similar history appears to be also evident in Australia, New Zealand and adjacent islands (see Fooden, 1972). In fact, living monotremes constitute a surviving mesozoic australosphenidan lineage, and are known since the Late Mesozoic to Recent times in Australasia (Luo et al. 2001), coexisting with marsupial and possibly placental mammals. In addition, recent finding of a Mesozoic ghost lineage on New Zealand is in agreement with the general pattern envisaged here (Worthy et al. 2006). Moreover, the addition of dryolestoids to Cenozoic (i.e. *Yalkaparidon*) and Recent (i.e. *Notoryctes*) australasian biota, suggest that the composition of mammalian faunas in this continent show similarities to South America.

It is striking that the animalivorous and fossorial habits of *Notoryctes*, perhaps akin of African golden moles, have no close analog among living or extinct Australian mammals (Warburton, 2003). The same may be applied to the mammalian woodpecker *Yalkaparidon* (Beck, 2003). This suggests that these forms exploitted marginal niches outside the ecological diversity of Australian therians. This is reminiscent to the equally relictual modern monotremes, which occupy a highly specialized ecological nicha (Phillips et al. 2009). In this way, the survival of *Notoryctes* may be also considered the result of the absence of usefull competitors of its niche.

CONCLUSIONS

PeerJ PrePrints

PeerJ PrePrints

Extant mammalian faunas around the world are mostly composed by marsupials and placentals. They conform the 99% of living species and are rather abundant. The only exception is the monotremes, currently restricted to five species geographically restricted to Australia and New Guinea. Survival in recent times of another archaic mammal lineage (i.e. Dryolestoidea) that took origin in Jurassic times seems improbable. But recent discoveries and research made in South America revealed that dryolestoids were highly diverse during Late Cretaceos, and most surprising, that survived well into Cenozoic times (Figure 19). Thus, although improbable, the survival of a dryolestoid in recent times, as here proposed for *Notoryctes*, it may not be as extraordinary as can be think.

Early authors doubted and debated about the phylogenetic relationships of the “marsupial mole” *Notoryctes*. However, recent analyses agreed in considering it as one of the most aberrant marsupials, due to the extreme peculiarities of its skeleton and soft anatomy. It is probable that the referral of *Notoryctes* to the Metatheria was based mainly by biogeographic grounds. A Dryolestoid affinity for Notoryctes constitutes the most parsimonious phylogenetic proposal and is congruent with the Late Cenozoic survival of the clade on southern landmasses. Present phylogeny indicates that dryolestoids underwent an unexpected post-Mesozoic radiation in some Gondwanan landmasses, and most of this evolutionary history remains obscure.

Notoryctes join monotremes as examples of ancient and formerly widespread mammalian taxa that are currently living with relictual distributions in Australasia. The early isolation of such landmass probably allowed the survival of several archaic endemic taxa that became extinct in remaining continents. In fact, the mammalian faunas of such territories are dominated by plesiomorphic clades, including egg-lying monotremes and australidelphian marsupials (Jones et al., 2009), to which we add here the new “living fossil” *Notoryctes*.

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

From a paleontological and phylogenetic perspective, efforts to conserve *Notoryctes*, the sole surviving member of an ancient mammalian clade with deep evolutionary roots in Gondwana, should be given the highest priority. If it can be preserved, the Mesozoic zoo that survives today in Australia can offer invaluable insights regarding past and present biodiversity.

ACKNOWLEDGEMENTS

To F. Novas and M. Ezcurra for their critical reading of the manuscript. Special thanks to T. Rich and M. Archer because of their detailed review of an advanced version of the manuscript. To D. Flores for his help during the revision of the comparative material under his care. To S. Lucero, G. Lio, F. Brisson Egli, M.R. Derguy, R. Lucero, A. Scanferla, and E. Guerrero for their useful comments and discussions. Finally to J.F. Bonaparte for his comments and sharing several unpublished data.

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

REFERENCES

Allin E.F., Hopson J.A. 1992. Evolution of the auditory system in Synapsida (‘mammal-like reptiles’ and primitive mammals) as seen in the fossil record. In: Webster DB, Fay RR, Popper AN, eds. The evolutionary biology of hearing. New York: Springer-Verlag, 587–614.

Amrine-Madsen, H., Scally, M., Westerman, M., Stanhope, M. J., Krajewski, C. W. & Springer, M. S. 2003 Nuclear gene sequences provide evidence for the monophyly of australidelphian marsupials. Mol. Phylogenet. Evol. 28, 186-196.

Antoine, P.-O., Marivaux, L., Croft, D.A., Billet, G., Ganerød, M., Jaramillo, C., Martin, T., Orliac, M.J., Tejada, J., Altamirano, A.J., Duranthon, F., Fanjat, G., Rousse, S., Gismondi, R.S. 2012. Middle Eocene rodents from Peruvian Amazonia reveal the pattern and timing of caviomorph origins and biogeography. Proceedings of the Royal Society B, 279(1732): 1319-1326.

Archer, M. 1976. The basicranial region of marsupicarnivores (Marsupialia), interrelationships of carnivorous marsupials, and affinities of the insectivorous marsupial peramelids. Zoological Journal of the Linnean Society, 59: 217-322.

Archer, M. in *Vertebrate Zoogeography & Evolution in Australasia* (eds M. Archer & G. Clayton) 633–808 (Animals in Space & Time, Hesperian Press, Carlisle, 1984).

Archer, M., Hand, S. J. & Godthelp, H. 1988. A new order of Tertiary zalambdodont marsupials. *Science* **239**, 1528-1531.

Archer, M., Hand, S. & Godthelp, H. 1994. Riversleigh – the story of animals in ancient rainforests of inland Australia. Reed Books, Sydney.

PeerJ PrePrints

Archer M, Beck R, Gott M, Hand S, Godthelp H, Black K (2011) Australia’s first fossil marsupial mole (Notoryctemorphia) resolves controversies about their evolution and palaeoenvironmental origins. Proc R Soc B 278: 1498-1506.

Archibald, J.D. 1979. Oldest known eutherian stapes and a marsupial petrosal bone from the Late Cretaceous of North America.Nature 281: 669–670.

Asher RJ, Horovitz I, Martin T, Sánchez-Villagra MR (2007) Neither a Rodent nor a Platypus: a Reexamination of *Necrolestes patagonensis* Ameghino. Amer Mus Novit 3546:1-40

Asher RJ, Sánchez-Villagra MR (2005) Locking yourself out: diversity among dentally zalambdodont therian mammals. J Mammal Evol 12:265-282

Asher, R. J., Horovitz, I. & Sánchez-Villagra, M. R. 2004. First combined cladistic analysis of marsupial mammal interrelationships. Mol. Phylogenet. Evol. 33, 240-250.

Ashwell, K.W.S. *The Neurobiology of Australian Marsupials. Brain evolution in the other mammalian radiation*. Cambridge University Press, New York, USA (2010)

Averianov AO, Archibald JD, Ekdale EG (2010a) New material of the Late Cretaceous deltatheroidan mammal Sulestes from Uzbekistan and phylogenetic reassessment of the metatherian–eutherian dichotomy. J Syst Palaeontol 8: 301–330.

Averianov, A.O., Martin, T. and Lopatin, A.V. (2013). A new phylogeny for basal Trechnotheria and Cladotheria and affinities of South American endemic Late Cretaceous mammals. Naturwissenschaften 100(4): 311-326.

Barnett, C.H. and Napier, J.R. 1953. The form and mobility of the fibula in metatherian mammals. Journal of Anatomy 87(2): 207-213.

Beck, R.M.D. 2009. Was the Oligo-Miocene Australian metatherian Yalkaparidon a ‘mammalian woodpecker’? Biological Journal of the Linnean Society, 2009, 97, 1–17.

Beck, R.M.D. 2008. 'A dated phylogeny of marsupials using a molecular supermatrix and multiple fossil constraints: comparison with the fossil record.' Journal of Mammalogy 89: 175-189.

Beck, R.M.D., Godthelp, H., Weisbecker, V., Archer, M., Hand, S.J. 2008. 'Australia's oldest marsupial fossils and their biogeographical implications.' PLoS ONE 3: e1858.

Benshemesh, J. & K. Johnson (2003). Biology and conservation of marsupial moles (Notoryctes). In: Jones M., C.R. Dickman & M. Archer, eds. Predators with Pouches: the biology of carnivorous marsupials. Page(s) 464-474. Melbourne, CSIRO Publishing.

Bensley, B.A. 1903. On the evolution of the Australian Marsupialia: With remarks on the relationships of the marsupials in general. Trans. Linnean Soc. Lond., Ser. 2, Zool. 9: 83-217.

Bonaparte JF (1986) Sobre *Mesungulatum houssayi* y nuevos mamíferos cretácicos de Patagonia. IV Congr Arg Paleont Bioestr Actas 2:48-61

Bonaparte JF (1990) New Late Cretaceous mammals from the Los Alamitos Formation, northern Patagonia. Nat Geogr Res 6:63-93

Bonaparte, J. F. Approach to the significance of the Late Cretaceous mammals of South America. *Berl. Geow Ab. E* **13**, 31–44 (1994).

Bonaparte, J. F. New Dryolestida (Theria) from the Late Cretaceous of Los Alamitos, Argentina, and paleogeographical comments. *N. Jahrb. Geol. Palaont., Ab*. **224**, 339-371 (2002).

PeerJ PrePrints

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.715v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

Bonaparte, J.F. & Migale, L.A. *Protomamíferos y mamíferos mesozoicos de América del Sur*. Municipalidad de Mercedes, Museo Municipal de Ciencias Naturales “Carlos Ameghino”. 441 pp. (2010).

Bonaparte JF, Rougier GW. 1987. Mamíferos del Cretácico Inferior de Patagonia. IV Congr Latinoamer Paleont. 1:343–359.

Bonaparte, J.F., Van Valen, L.M. & Kramarz, A. La Fauna local de Punta peligro, Paleoceno inferior, de la provincia del Chubut, Patagonia, Argentina. *Evol. Mon.* **14**, 1–61 (1993).

Butler PM. 1990. Early trends in the evolution of tribosphenic molars. Biol Rev. 65:529–552.

Calaby, H.J., Corbett, L.K., Sharman, G.B. & Johnston, P.G. (1974). The chromosomes and systematic position of the marsupial mole, *Notoryctes typhlops*. Australian Journal of Biological Science 27: 529–532.

Cardillo M, Bininda-Emonds ORP, Boakes E, Purvis A. 2004. A species-level phylogenetic supertree of marsupials. Journal of Zoology 264: 11–31.

Cifelli, R. L. 1993 Theria of metatherian-eutherian grade and the origin of marsupials. In Mammal phylogeny: Mesozoic differentiation, multituberculates, monotremes, early therians, and marsupials (eds F. S. Szalay, M. J. Novacek & M. C. McKenna), pp. 205–215. New York, NY: Springer.

Cifelli RL, Rowe T, Luckett WP, Banta J, Reyes R, et al. (1996) Fossil evidence for the origin of the marsupial pattern of tooth replacement. Nature 379: 715–718.

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

Chester, S.G.B., E.J. Sargis, F.S. Szalay, J.D. Archibald & A.O. Averianov. 2010. Mammalian distal humeri from the Late Cretaceous of Uzbekistan. Acta Palaeontol. Pol. 55: 199-211.

Chester SGB, Sargis EJ, Szalay FS, Archibald DJ, Averianov AO (2012) Therian femora from the Late Cretaceous of Uzbekistan. Acta Paleontol Pol 57:53-64

Chester SGB, Sargis EJ, Szalay FS, Archibald JD, Averianov AO (2010) Mammalian distal humeri from the Late Cretaceous of Uzbekistan. Acta Palaeontol Pol 55:199-211.

Chimento NR, Agnolin FL, Novas FE. 2012. The Patagonian fossil mammal Necrolestes: a Neogene survivor of Dryolestoidea. Rev Mus Argentino Cienc Nat ns. 14(2):261–306.

Chimento NR, Agnolin FL, Novas FE. 2014. The bizarre 'metatherians' *Groeberia* and *Patagonia*, late surviving members of gondwanatherian mammals. Historical Biology, DOI: 10.1080/08912963.2014.903945.

Chornogubsky L (2011). New remains of the dryolestoid mammal *Leonardus cuspidatus* from the Los Alamitos Formation (Late Cretaceous, Argentina). Palaontol Z 85:343-350

Clemens WA, Lillegraven JA (1986) New late Cretaceous, North American advanced therian mammals that fit neither the marsupial nor eutherian molds. In: Flanagan KM, Lillegraven JA (eds) Vertebrates, Phylogeny and Philosophy. Contributions to Geology, University of Wyoming 3: 55-86.

Cope, E. D. On the habits and affinities of the new Australian mammal, *Notoryctes typhlops*. *Amer. Nat.* **26**, 121–128 (1892).

Crompton AW (1971) The origin of the tribosphenic molar. In Kermack DM, Kermack KA, (eds) Early Mammals. Zool J Linn Soc 50, supplement 1:65-87

PeerJ PrePrints

Dashzeveg D, Kielan-Jaworowska Z (1984) The lower jaw of an aegialodontid mammal from the Early Cretaceous of Mongolia. Zool J Linn Soc 82:217-227

Djakiew, D. and Jones, R.C. 1981. Structural differentiation of the male genital ducts of the echidna (Tachyglossus aculeatus). J. Anat. 132, 2: 187-202.

Dollo, Les ancêtres des Marsupiaux étaient-ils arbicoles ? in: Miscellanées biologiques dédiées au Professeur Alfred Gtiard à l'occasion du 25. anniversaire de la fondation de la station zoologique de Wimereux, Paris 1899. Ekdale, 2009

Ekdale, E.G., J.D. Archibald, and A.O. Averianov. 2004. Petrosal bones of placental mammals from the Late Cretaceous of Uzbekistan. Acta Palaeontologica Polonica 49: 161–176.

Fleischer, G. 1978. Evolutionary principles of the mammalian middle ear. Adv. Anat. Embryol. Cell Biol. 55, 1–70.

Fooden J. 1972. Breakup of Pangaea and isolation of relict mammals in Australia, South America, and Madagascar. Science. 175 (4024):894–898.

Forasiepi AM, Martinelli AG (2003) A femur of a monotreme (Mammalia, Monotremata) from the Early Paleocene Salamanca Formation of Patagonia, Argentina. Ameghiniana 40:625-630

Forasiepi, A.M., Coria, R.A., Hurum, J. and Currie, P.J. 2013. First dryolestoid (Mammalia, Dryolestoidea, Meridiolestida) from the Coniacian of Patagonia and new evidence on their early radiation in South America. Ameghiniana 49(4): 497-504.

Fox RC (1975) Molar structure and function in the Early Cretaceous mammal *Pappotherium*: Evolutionary implications for Mesozoic Theria. Can J Earth Sc 12:412-442

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014
PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)

PeerJ PrePrints

Fox, R.C. & Naylor, B.G. (1986). A new species of Didelphodon Marsh (Marsupialia) from the Upper Cretaceous of Alberta, Canada: Paleobiology and Phylogeny. Neues Jahrbuch für Geologie und Paläontologie. Stuttgart. Abhandlungen 172: 357–380

Frey, V.R. Zur Ursache des Hodenabstiegs (*Descensus testiculorum*) bei Säugetieren. *J. Zool. Syst. Evol. Res.* **29**, 40-65 (1991).

Gadow, H. On the systematic position of *Notoryctes typhlops*. *Proc. Zool. Soc. London* **1892**, 361–370 (1892).

Gambaryan, P.P. and Kielan−Jaworowska, Z. 1997. Sprawling versus parasagittal stance in multituberculate mammals. Acta Palaeontologica Polonica 42: 13–44.

Gelfo JN, Pascual R (2001) *Peligrotherium tropicalis* (Mammalia, Dryolestida) from the early Paleocene of Patagonia, a survival from a Mesozoic Gondwanan radiation. Geodiversitas 23:369-379

Goin, F.J., Carlini, A.A., and Pascual, R. 1986. Un probable marsupial del Cretácico Tardío del norte de Patagonia, Argentina. IV Congreso Argentino e Paleontología y Bioestratigrafía, Actas 2: 401–410.

Goin FJ, Reguero MA, Pascual R, von KoenigswaldW, Woodburne MO, Case JA, Marenssi SA, Vieytes EC, Vizcaíno SF. 2006. First gondwanatherian mammal from Antarctica. In: Francis JE, Pirrie D, Crame JA, editors. Cretaceous–Tertiary high-latitude paleoenvironments, James Ross Basin, Antarctica. London: Spec Publ Geol Soc; p. 145–161.

Goin FJ, Tejedor MF, Chornogubsky L, López GM, Gelfo JN, Bond M, Woodburne MO, Gurovich Y, Reguero M. 2012. Persistence of a Mesozoic, non-therian mammalian lineage (Gondwanatheria) in the mid-Paleogene of Patagonia. Naturwissenschaften. 99:449–463.

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

Goloboff PJ, Farris J, Nixon K (2008) A free program for phylogenetic analysis. Cladistics 24:774-786

Gray, A. A. *The labyrinth of animals*. Vol. 2. (J. & A. Churchill, London, 1908).

Hopson, J. A. & G. W. Rougier. 1993. Braincase structure in the oldest known skull of a therian mammal: Implications for mammalian systematics and cranial evolution. American Journal of Science, 293-A: 268-299.

Horovitz, I. & Sánchez-Villagra, M. R. A morphological analysis of marsupial mammal higher-level phylogenetic relationships. *Cladistics* **19**, 181–212 (2003).

Horovitz, I. & Sánchez-Villagra, M. R. 2003 A morphological analysis of marsupial mammal higher-level phylogenetic relationships. Cladistics 19, 181-212.

Horovitz, I., Martin, T., Bloch, J., Ladevèze, S., Kurz, C. & Sánchez-Villagra, M.R. Cranial Anatomy of the Earliest Marsupials and the Origin of Opossums. *PLoS ONE* **4**, e8278. doi:10.1371/journal.pone.0008278 (2009).

Hu Y-M, Wang Y-Q, Luo Z-X, Li C-K (1997) A new symmetrodont mammal from China and its implications for mammalian evolution. Nature 390:137-142

Hu Y-M, Fox RC, Wang Y-Q, Li C-K (2005) A new spalacotheriid symmetrodont from the Early Cretaceous of Northeastern China. Am Mus Nov 3475: 1–20.

Hu, Y., J. Meng, C. Li, and Y. Wang. 2010. New basal eutherian mammal from the Early Cretaceous Jehol biota, Liaoning, China. Proceedings of the Royal Society of London B Biological Sciences 277: 229–236.

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

Hurum, J.H., Presley, R., and Kielan−Jaworowska, Z. 1996. The middle ear in multituberculate mammals. Acta Palaeontologica Polonica 41: 253–275.

Jenkins, F. A., Jr. (1973). The functional anatomy and evolution of the mammalian humero-ulnar articulation. Am. J. Anat. 137: 281–298.

Jenkins FA Jr, Parrington FR (1976) The postcranial skeletons of the Triassic mammals *Eozostrodon*, *Megazostrodon* and *Erythrotherium*. Philos Trans Royal Soc London 273:387-431

Ji Q, Luo Z-X, Ji S-A (1999) A Chinese triconodont mammal and mosaic evolution of the mammalian skeleton. Nature 398:326-330.

Ji Q, Luo Z-X, Yuan C-X, Wible JR, Zhang J-P, Georgi JA (2002) The earliest known eutherian mammal. Nature 416:816-822

Johnson, K. A. & Walton, D. W. in *Fauna of Australia. Mammalia*. (eds D.W. Walton & B.J. Richardson) 1B: 591-602 (Australian Government Publishing Service, Camberra, 1989).

Jones, M. E. H. *et al.* A sphenodontine (Rhynchocephalia) from the Miocene of New Zealand and palaeobiogeography of the tuatara (*Sphenodon*). *Proc. R. Soc. B* **276**, 1385–1390 (2009).

Kermack KA, Lee AJ, Lees PM, Mussett F (1987) A new docodont from the Forest Marble. Zool J Linn Soc 89:1-39

Kielan-Jaworowska Z. 1975. Preliminary description of two new eutherian genera from the Late Cretaceous of Mongolia. Palaeontol Pol. 33:5–16.

PeerJ PrePrints

Kielan−Jaworowska, Z. 1977. Evolution of the therian mammals in the Late Cretaceous of Asia. Part II. Postcranial skeleton in Kennalestes and Asioryctes. In: Z. Kielan−Jaworowska (ed.), Results of the Polish−Mongolian Palaeontological Expeditions, Part VII. Palaeontologia Polonica 37: 65–83.

Kielan-Jaworowska Z, Cifelli RL, Luo Z-X (2004) Mammals from the age of dinosaurs: origins, evolution, and structure. Columbia Univ. Press, New York

Kielan-Jaworowska Z, Dashzeveg D (1989) Eutherian mammals from the Early Cretaceous of Mongolia. Zool Scrip 18:347-355

Kielan-Jaworowska, Z., and Gambaryan, P. P. (1994). Postcranial anatomy and habits of Asian multituberculate mammals. Fossils Strata 36: 1–92.

Kielan−Jaworowska, Z. & Hurum, J. H. Limb posture in early mammals: Sprawling or parasagittal. *Acta Palaeontol. Pol.* **51**, 393–406 (2006).

Kirsch, J.A.W., F.J. Lapointe & M.S. Springer (1997). DNA-hybridisation Studies of Marsupials and their Implications for Metatherian Classification. Australian Journal of Zoology. 45:211-280.

Klaauw, C.J. van der 1931. The auditory bulla in some fossil mammals, with a general introduction to this region of the skull. Bulletin of the American Museum of Natural History 62: 1–352.

Kleisner, K., Ivell, R., Flegr, J. 2010. The evolutionary history of testicular externalization and the origin of the scrotum. Journal of Biosciences 35(1): 27-37.

Krebs B (1969) Nachweis eines rudimentären Coronoids im Unterkiefer der Pantotheria (Mammalia). Paläontol Z 43:57-63.

PeerJ PrePrints

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

Krebs B (1971) Evolution of the mandible and lower dentition in dryolestoids (Pantotheria, Mammalia). In Kermack DM, Kermack KA (eds) Early Mammals. Zool J Linn Soc 50, supplement 1:89-102

Krebs B (1991) Das Skelett von *Henkelotherium guimarotae* gen. et sp. nov. (Eupantotheria, Mammalia) aus dem Oberen Jura von Portugal. Berl geow Ab A 133:1- 110

Krebs B (1993) Das Gebiß von Crusafontia (Eupantotheria, Mammalia) —Funde aus der Unter-Kreide von Galve un Uña. Berl geow Ab E 9:233-252

Krebs B (1998) *Drescheratherium acutum* gen. et sp. nov., ein neuer Eupantotherier (Mammalia) aus dem Oberen Jura von Portugal. Berl geow Ab E 28:91-111

Ladevèze, S., Asher, R. J. & Sánchez-Villagra, M. R. 2008 Petrosal anatomy in the fossil mammal Necrolestes: evidence for metatherian affinities and comparisons with the extant marsupial mole. J. Anat. 213, 686–697.

Ladevèze S, de Muizon C, Colbert M, Smith T. 2010. 3D computational imaging of the petrosal of a new multituberculate mammal from the Late Cretaceous of China and its paleobiologic inferences. *Comptes Rendus Palevol* 9: 319–330.

Ladevèze S, Asher RJ, Sánchez-Villagra MR (2008) Petrosal anatomy in the fossil mammal *Necrolestes*: evidence for metatherian affinities and comparisons with the extant marsupial mole. J Anat 213:686-697

Ladéveze, S., Muizon, C. de, Colbert, M. & Smith, T. 3D computational imaging of the petrosal of a new multituberculate mammal from the Late Cretaceous of China and its paleobiologic inferences. *C. R. Palevol* **9**, 319-330 (2010).

Lapointe, F.-J. and Kirsch, J.A.W. 2001. Construction and verification of a large phylogeny of marsupials. Australian Mammalogy 23: 9-22.

Leche W (1907) Zur Entwicklungsgeschichte des Zahnsystems der Säugetiere, zugleich ein Beitrag zur Stammengeschichte dieser Tiergruppe. Teil 2. Zoologica (Stuttgart) 49:1-157

Li G, Luo Z-X (2006) A Cretaceous symmetrodont therian with some monotreme-like postcranial features. Nature 439:195-200

Lillegraven JA. 1969. Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupialplacental dichotomy in mammalian evolution. Univ Kansas Paleontol Contr. 50:1–122.

Lopatin AV, Averianov AO (2007) *Kielantherium*, a basal tribosphenic mammal from the Early Cretaceous of Mongolia, with new data on the aegialodontian dentition. Acta Palaeontol Pol 52:441-446.

Lucas SG, Luo ZX. 1993. Adelobasileus from the Upper Triassic of western Texas: the oldest mammal. *Journal of Vertebrate Paleontology* 13: 309–334.

Luo Z-X (2007) Transformation and diversification in early mammal evolution. Nature 450: 1011-1019.

Luo ZX, Crompton AW. 1994. Transformations of the quadrate (incus) through the transition from non-mammalian cynodonts to mammals. Journal of Vertebrate Paleontology 14: 341–374.

Luo Z. -X., Ruf, I., Schultz, J. A. & Martin, T. Fossil evidence on evolution of inner ear cochlea in Jurassic mammals. *Proc. R. Soc. B* **278**, 28-34 (2011).

PeerJ PrePrints

PeerJ PrePrints

Luo Z-X, Cifelli RL, Kielan-Jaworowska Z (2001a) Dual origin of tribosphenic mammals. Nature 409:53-57

Luo Z-X, Crompton AW, Sun A-L (2001b) A New Mammaliaform from the Early Jurassic and Evolution of Mammalian Characteristics. Science 292:1535-1540

Luo, Z-X. & J.R. Wible. 2005. A new Late Jurassic digging mammal and early mammalian diversification. Science 308: 103–107.

Luo Z-X, Ji Q, Yuan C-X (2007) Convergent dental adaptations in pseudotribosphenic and tribosphenic mammals. Nature 450:93-97

Luo Z-X, Kielan-Jaworowska Z, Cifelli RL (2002) In quest for a phylogeny of Mesozoic mammals. Acta Palaeontol Pol 47:1-78

Luo Z-X, Yuan C-X, Meng Q-J, Ji Q (2011) A Jurassic eutherian mammal and divergence of marsupials and placentals. Nature 476:442-445

Luo, Z. -X., Ji, Q., Wible, J. R. & Yuan, C. -X. An early Cretaceous tribosphenic mammal and metatherian evolution. *Science* **302**, 1934–1940 (2003).

Luo, Z.-X., Ruf, I. & T. Martin. 2012. The petrosal and inner ear of the Late Jurassic cladotherian mammal *Dryolestes leiriensis* and implications for ear evolution in therian mammals. *Zoological Journal of the Linnean Society*, 166: 433–463.

Marshall, L.G. (1979). Evolution of metatherian and eutherian (mammalian) characters: a review based on cladistic methodology. Zoological Journal of the Linnean Society 66: 369–410.

PeerJ PrePrints

Martin T (1995) Dryolestidae from the Kimmeridge of the Guimarota coal mine (Portugal) and their implications for dryolestid systematics and phylogeny. In Sun A-L, Wang Y (eds) Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota. Ocean Press, Beijing, pp 229-231

Martin T (1997) Tooth replacement in Late Jurassic Dryolestidae (Eupantotheria, Mammalia). J Mammal Evol 4:1-18

Martin T (1999) Dryolestidae (Dryolestoidea, Mammalia) aus dem Oberen Jura von Portugal. Abh Senckenb Naturf Gesell 550:1-119

Martin T, Rauhut OWM. 2005. Mandible and dentition of Asfaltomylos patagonicus (Australosphenida, Mammalia) and the evolution of tribosphenic teeth. J Vert Paleontol. 25(2):414–425.

Martinelli, A.G., Bonaparte, J.F., Schultz, C.L. and Rubert, R. 2007. A new tritheledontid (Therapsida, Eucynodontia) from the Late Triassic of Rio Grande do Sul (Brazil) and its phylogenetic relationships among carnivorous non-mammalian eucynodonts. Ameghiniana 42(1): 191-208.

Mason, M. J. Middle ear structures in fossorial mammals: a comparison with non-fossorial species. *J. Zool.* **255**, 467-486 (2001).

M.J. Mason, Morphology of the middle ear of golden moles (Chrysochloridae), J. Zool. 260 391-403. (2003).

M.J. Mason, Evolution of the middle ear apparatus in talpid moles, J. Morphol. 267 678-695. (2006).

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

McKenna, M.C. 1961. On the shoulder girdle of the mammalian subclass Allotheria. American Museum Novitates 2066: 1–27.

McKenna, M.C. (1975). Toward a phylogenetic classification of the Mammalia. Pp. 21–46 in Luckett, W.P. & Szalay, F.S. (eds) Phylogeny of the Primates. Plenum Press : New York

Meng J, Wyss A. 1995. Monotreme affinities and low frequency hearing suggested by multituberculate ear. Nature 377: 141–144.

Meng, J. Wang, Y. and Li, C. 2011. Transitional mammalian middle ear from a new Cretaceous Jehol eutriconodont. Nature 472 (7342): 181–185.

Meredith, R. W. et al. 2011. Impacts of the Cretaceous Terrestrial Revolution and KPg Extinction on Mammal Diversification. Science 334, 521

Meredith, R. W., Krajewski, C., Westerman, W. & Springer, M. S. 2009 Relationships and divergence times among the orders and families of marsupials. Mus. N. Ariz. Bull. 65, 383-406.

Meredith, R. W., Westerman, M., Case, J. A. & Springer, M. S. 2008 A phylogeny and timescale for marsupial evolution based on sequences for five nuclear genes. J. Mamm. Evol. 15, 1-36. - very strong molecular (nuclear) support for Notoryctes within crown-group Marsupialia

Mess, A. y Carter, A.M. 2006. Evolutionary Transformations of Fetal Membrane Characters in Eutheria with Special Reference to Afrotheria. Journal of Experimental Zoology 306B: 140–163.

PeerJ PrePrints

Muizon, C.de. 1998. Mayulestes ferox, a borhyaenoid (Metatheria, Mammalia) from the early Palaeocene of Bolivia. Phylogenetic and palaeobiologic implications. Geodiversitas 20: 19-142.

Nilsson, M. A., Arnason, U., Spencer, P. B. S. & Janke, A. 2004 Marsupial relationships and a timeline for marsupial radiation in South Gondwana. Gene 340, 189-196.

Nilsson, M. A., Churakov, G., Sommer, M., Tran, N.V., Zemann, A., Brosius, J. & Schmitz, J. 2010 Tracking marsupial evolution using archaic genomic retroposon insertions. PLoS Biol. 8, e1000436.

Novacek MJ. 1986. The skull of leptictid insectivorans and the higher-level classification of eutherian mammals. Bulletin of the American Museum of Natural History 183: 1–112.

Nowak, R. M. *Walker's Mammals of the World*. Sixth edition (The Johns Hopkins Univ. Press, Baltimore and London, 1999).

Ogilby, J.D. (1892). Catalogue of Australian Mammals, with Introductory notes on General Mammalogy. Catalogue No. 16. Australian Museum : Sydney 142 pp.

Páez Arango, N. 2008. Dental and craniomandibular anatomy of Peligrotherium tropicalis: the evolutionary radiation of South American dryolestoid mammals. Thesis of Master Of Science, Department of Anatomical Sciences and Neurobiology, School of Medicine, University of Louisville, Louisville, Kentucky. 232 pp.

Pascual R, Archer M, Ortiz-Jaureguizar E, Prado JL, Godthelp H, Hand SJ. 1992. First discovery of monotremes in South America. Nature 356:704–705.

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

Pascual R, Ortíz-Jaureguizar E (2007) The Gondwanan and South American Episodes: Two Major and Unrelated Moments in the History of the South American Mammals. J Mammal Evol 14:75-137

Patterson B (1956) Early Cretaceous mammals and the evolution of mammalian molar teeth. Fieldiana: Geology 13:1-105

Patterson B (1958) Affinities of the Patagonian fossil mammal, *Necrolestes*. Breviora 94:1-14

Phillips MJ, Pratt RC. 2008. Family-level relationships among the Australasian marsupial ‘herbivores’ (Diprotodontia: koala, wombats, kangaroos and possums). Molecular Phylogenetics and Evolution 46: 594–605.

Phillips, M. J., McLenachan, P. A., Down, C., Gibb, G. C. & Penny, D. 2006 Combined mitochondrial and nuclear DNA sequences resolve the interrelations of the major Australasian marsupial radiations. Syst. Biol. 55, 122-137.

Phillips MJ, Bennett TH, Lee MSY. 2009. Molecules, morphology, and ecology indicate a recent, amphibious ancestry for echidnas. Proc Natl Acad Sci USA. 106(40):17089–17094.

Presley, R. Pelvic problems for mammals. *Nature* **389**, 440-441 (1997).

Pridmore, P.A. 1985. Terrestrial locomotion in monotremes (Mammalia: Monotremata). Journal of Zoology 205(1): 53-73.

Pridmore, P.A., Rich, T.H., Vickers-Rich, P. & Gambaryan, P.P. 2005. A Tachyglossid-Like Humerus from the Early Cretaceous of South-Eastern Australia. Journal of Mammalian Evolution, 12 (3/4): 359-378.

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.715v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

Prothero, D.R. 1981. New Jurassic mammals from Como Bluff, Wyoming, and the interrelationships of non−tribosphenic Theria. Bulletin of the American Museum of Natural History 167: 277–326.

Reese, S., Pfuderer, U., Bragulla, H., Loeffer, K. & Budras, K. 2001. Topography, structure and fuction of the patella and the patelloid in marsupials. Anatomy, Histology and Embryology 30: 289-294.

Renfree, M.B. Ontology, Genetic Control, and Phylogeny of Female Reproduction in Monotreme and Therian Mammals. *In*: Szalay, F.S., Novacek, M.J., and McKenna, M.C. (eds.). *Mammal Phylogeny. Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians, and Marsupials*. Springer-Verlag. Pp. 4-20 (1993).

Rich, T.H., Flannery, T.F., Trusler, P., Kool, L., van Klaveren, N., and Vickers−Rich, P. 2001. Asecond placental mammal from the Early Cretaceous Flat Rocks site,Victoria, Australia. Records of the Queen Victoria Museum 110: 1–9.

Rich TH, Hopson JA, Musser AM, Flannery TF, Vickers-Rich P (2005) Independent Origins of Middle Ear Bones in Monotremes and Therians. Science 307:910-914

Riedelsheimer, B., Unterberger, P., Künzle, H. and U. Welsch. 2007. Histological study of the cloacal region and associated structures in the hedgehog tenrec *Echinops telfairi*. Mammalian Biology 72(6): 330-341.

Rougier GW, Wible JR, Hopson JA. 1992. Reconstruction of the cranial vessels in the early Cretaceous mammal Vincelestes neuquenianus: implications for the evolution of the mammalian cranial vascular system. J Vertebr Paleontol 12:188–216.

PeerJ PrePrints

PeerJ PrePrints

Rougier GW, Wible JR, Hopson JA. 1996. Basicranial anatomy of Priacodon fruitaensis (Triconodontidae, Mammalia) from the late Jurassic of Colorado, and a reappraisal of mammaliaform interrelationships. Am Mus Novit 3183: 1–38.

Rougier GW, Wible JR, Novacek MJ. 1998. Implications of Deltatheridium specimens for early marsupial history. Nature 396:459–463.

Rougier GW, Apesteguía S, Gaetano LC (2011) Highly specialized mammalian skulls from the Late Cretaceous of South America. Nature 479:98-102

Rougier GW, Wible JR, Beck RMD, Apesteguía S. 2012. The Miocene mammal *Necrolestes* demonstrates the survival of a Mesozoic nontherian lineage into the late Cenozoic of South America. Proc Natl Acad Sci USA. 109(49):20053–20058.

Rougier, G. W., Forasiepi, A. M., Hill, R. V. & Novaceck, M. New mammalian remains from the Late Cretaceous La Colonia Formation, Patagonia, Argentina. *Acta Paleontol. Pol.* **54**, 195-212 (2008).

Rougier, G.W., Chornogubsky, L., Casadío, S., Páez Arango, N. & Giallombardo, A. Mammals from the Allen Formation, Late Cretaceous, Argentina. *Cret. Res.* **30**, 223-238 (2009).

Rougier, G.W., Wible, J.R. & Hopson, J.A. 1992. Reconstruction of the cranial vessels in the Early Cretaceous mammal *Vincelestes neuquenianus*: implications for the evolution of the mammalian cranial vascular system. *J. Vert. Paleontol.* **12**, 188-216 (1992).

Rowe T. 1993. Phylogenetic systematics and the early history of mammals. In: Szalay FS, Novacek MJ, McKenna MC, editors. Mammalian phylogeny. Vol. 1. Mesozoic

PeerJ PrePrints

differentiation, multituberculates, monotremes, early therians, and marsupials. New York: Springer-Verlag. p 129–145.

Rowe T. 1996. Coevolution of the mammalian middle ear and neocortex. Science 273:651–654.

Rowe, T., T.E. Macrini, and Z.-X. Luo. 2011. Fossil evidence on origin of the mammalian brain. Science 332: 955–957.

Rowe, M.J. & Bohringer, R.C. Functional organization of the cerebral cortex in monotremes. In: Augee, M.L. (ed.). *Platypus and Echidnas*. Royal Zoological Society of New South Wales, Australia. Pp. 177-193 (1992).

Ruf, I., Luo, Z.-X., Wible, J. R. & Martin, T. 2009. Petrosal anatomy and inner ear structure of the Late Jurassic mammal *Henkelotherium* and the ear region characters of basal therian mammals. *J. Anat.* **214**, 679–693.

Sánchez-Villagra, M.R. 2001. Ontogenetic and phylogenetic transformations of the vomeronasal complex and nasal floor elements in marsupial mammals. Zoological Journal of the Linnean Society 131: 459–479.

Sánchez-Villagra MR, Smith KK. 1997. Diversity and evolution of the marsupial mandibular angular process. J Mammal Evol. 4:119–144.

Sanchez-Villagra, M. *et al.* Exceptionally preserved North American Paleogene metatherians: adaptations and discovery of a major gap in the opossum fossil record. *Biol. Lett.* **3**, 318-322 (2007).

Schmelzle T, Sánchez-Villagra MR, Maier W (2007) Vestibular labyrinth evolution in diprotodontian marsupial mammals. Mammal Study 32:83-97

PeerJ PrePrints

Schultz JA, Martin T (2011) Wear pattern and functional morphology of dryolestoid molars (Mammalia, Cladotheria). Paläontol Z 85:269-285

Scott WB (1905) Paleontology. Part II. Insectivora. Report of the Princeton University Expeditions to Patagonia 5:365-383

Segall, W. Morphological parallelisms of bulla and auditory ossicles in some insectivores and marsupials. *Field. Zool.* **51**, 169-205 (1970).

Sereno PC. 2006. Shoulder girdle and forelimb in multituberculates: evolution of parasagittal forelimb posture in mammals. In: Carrano MT, Gaudin TJ, Blob RW, Wible JR, eds. Amniote paleobiology: perspectives on the evolution of mammals, birds, and reptiles. Chicago, IL: University of Chicago Press, 315–366.

Sereno PC, McKenna MC (1995) Cretaceous multituberculate skeleton and the early evolution of the mammalian shoulder girdle. Nature 377:144-147

Shoshani, J. & Mckenna, M.C. 1998. Higher taxonomic relationships among extant mammals based on morphology, with selected comparisons of results from molecular data. Molecular Phylogenetics and Evolution 9(3): 572-584.

Sigogneau-Russell D (1998) Discovery of a Late Jurassic Chinese mammal in the upper Bathonian of England. C R Acad Sc 327:571-576

Sigogneau-Russell D (1999) Réévaluation des Peramura (Mammalia, Theria) sur la base de nouveaux spécimens du Crétacé inférieur d'Angleterre et du Maroc. Geodiversitas 21:93-127

Sigogneau-Russell D (2003) Holotherian mammals from the Forest Marble (Middle Jurassic of England). Geodiversitas 25: 501–537.

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

Smith, G. E. The comparative anatomy of the cerebrum of *Notoryctes typhlops*. *Trans. R. Soc. S Australia* **19**, 167–193 (1895).

Spencer, B. 1896b. Report on the work of the Horn Scientific Expedition to Central Australia. Part I: Introduction, Narrative, Summary of Results and Supplement to Zoological Report. Melville, Mullen and Slade, Melbourne.

Springer, M.S., Burk, A., Kavanagh, J.R., Maddell, V.G., Stanhope, M.J. 1997. The interphotoreceptor retinoid binding protein gene in therian mammals: Implications for higher level relationships and evidence for loss of function in the marsupial mole. PNAS 94(25): 13754–13759.

Springer, M.S., Westerman, M., Kavanagh, J.R., Burk, A., Woodburne, M.O., Kao, D.J. & Krajewski, C. 1998. The origin of the Australasian marsupial fauna and the monophyletic affinities of the enigmatic monito de monte and marsupial mole. *Proc. R. Soc. London B* **265**, 2381–2386.

Stirling, E. C. 1888 Preliminary notes on a new Australian mammal. Trans. R. Soc. South Aust. 11, 21–24.

Stirling, E.C. 1891. Description of a new genus and species of Marsupialia, *Notoryctes typhlops*. *Trans. R. Soc. S. Aus* **14**, 154-187 (1891).

Sweet, G. Contributions to our knowledge of the anatomy of *Notoryctes typhlops*. Parts IV and V. The skin, hair, and reproductive organs of *Notoryctes*. *Quart. J. Micr. Sc.* **51**, 325–344 (1907).

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

Szalay FS. 1982. A new appraisal of marsupial phylogeny and classification. In: Archer M, ed. Carnivorous marsupials. Mosman, NSW: Royal Zoological Society of New South Wales, 621–640.

Szalay, F.S. and Sargis, E.J. 2006. Cretaceous therian tarsals and the metatherian-eutherian dichotomy. Journal of Mammalian Evolution 13: 171-210.

Szalay, F.S. *Evolutionary history of the marsupials and an analysis of osteological characters*. Cambridge University Press, New York. 481 pp. (1994).

Temple-Smith, T.; Grant, T. 2001. Uncertain breeeding: a short history of reproduction in monotremes. Reprod. Fertil. Dev. 13, 487–497.

Thomas, O. *Notoryctes* in north-west Australia. *Ann. Mag. Nat. Hist.* **6**, 111–113 (1920).

Turnbull, W. D. in *Dental Morphology and Evolution* (ed A. A. Dahlberg) 151-179 (Univ. Chicago Press, Chicago, 1971).

Vaughan, T. A., Ryan, J. M. & Czaplewski, N. J. *Mammalogy*. 5th Edition. (Jones & Bartlett Learning, 2010).

Vázquez-Molinero, R., Martin, T., Fischer, M.S., Frey, R. 2001. Comparative anatomical investigations of the postcranial skeleton of *Henkelotherium guimarotae* Krebs, 1991 (Eupantotheria, Mammalia) and their implications for its locomotion. Mitt. Mus. Nat.kd. Berl., Zool. Reihe 77(2): 207-216.

von Koenigswald W, Goin FJ. 2000. Enamel differentiation in South American marsupials and a comparison of placental and marsupial enamel. Palaeontogr Abt A. 255:1–40.

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014
PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)

PeerJ PrePrints

Vullo R, Gheerbrant E, Muizon Cd, Néraudeau D (2009) The oldest modern therian mammal from Europe and its bearing on stem marsupial paleobiogeography. PNAS 106:19910-19915

Waddell, P.J., Okada, N., Hasegawa, M. 1999. Towards resolving the interordinal relationships of placental mammals. Systematic Biology 48: 1–5.

Warburton, N.M. *Functional morphology and evolution of marsupial moles (Marsupialia; Notoryctemorphia)*. (Unpublished PhD thesis, School of Animal Biology, Univ. Western Australia, 2003).

Werdelin, L.; Nilsonne, A. 1999. The evolution of the scrotum and testicular descent in mammals: a phylogenetic view. J. Theor. Biol. 196, 61–72.

Wible JR. 1990. Petrosals of Late Cretaceous marsupials from North America, and a cladistic analysis of the petrosal in therian mammals. J Vertebr Paleontol 10:183–205.

Wible, J.R., Miao, D. & Hopson, J.A. 1990. The septomaxilla of fossil and recent synapsids and the problem of the septomaxilla of monotre-mes and armadillos. zoological Journal of the Linnean Society (1990), 98: 203-228.

Wible, J.R. & Hopson, J.A. Basicranial Evidence for Early Mammal Phylogeny. *In*: Szalay, F.S., Novacek, M.J. & McKenna, M.C. (eds.). *Mammal Phylogeny. Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians, and Marsupials*. Springer-Verlag. Pp. 45-62 (1993).

Wible, J.R., Rougier, G.W., Novacek, M.J. & McKenna, M.C. Earliest Eutherian Ear Region: A Petrosal Referred to *Prokennalestes* from the Early Cretaceous of Mongolia. American Museum Novitates **3322**, 1-44 (2001).

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

Wible JR, Rougier GW, Novacek MJ, Asher RJ. 2009. The eutherian mammal Maelestes gobiensis from the Late Cretaceous of Mongolia and the phylogeny of cretaceous Eutheria. Bull Amer Mus Nat Hist. 327:1–123.

Wood, C.B. & Rougier, G.W. 2005. Updating and recoding enamel microstructure in mesozoic mammals: in search of discrete characters for phylogenetic reconstruction. Journal of Mammalian Evolution, 12: 433-460.

Woodburne, M. O. & Case, J. A. Dispersal, vicariance, and the Late Cretaceous to early Tertiary land mammal biogeography from South America to Australia. *J. Mammal. Evol.* **3**, 121-161 (1996).

Worthy TH, Tennyson AJD, Archer M, Musser AM, Hand SJ, Jones C, Douglas BJ, McNamara JA, Beck RMD. 2006. Miocene mammal reveals a Mesozoic ghost lineage on insular New Zealand, southwest Pacific. Proc Natl Acad Sci USA. 103:19419–19423.

Wroe, S., Ebach, M., Ahyong, S., de Muizon, C., and Muirhead, J. (2000). Phylogeny of Dasyuromorphia:a cladistic analysis using cranial and dental data. Journal of Mammalogy 81, 1008 – 1024.

Zeller U. 1993. Ontogenetic evidence for cranial homologies in monotremes and therians, with special reference to Ornithorhynchus. In: Szalay FS, Novacek MJ, McKenna MC, eds. Mammal phylogeny – Mesozoic differentiation, multituberculates, monotremes, early therians, and marsupials. New York: Springer-Verlag, 95–107.

PeerJ PrePrints

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

Figures.

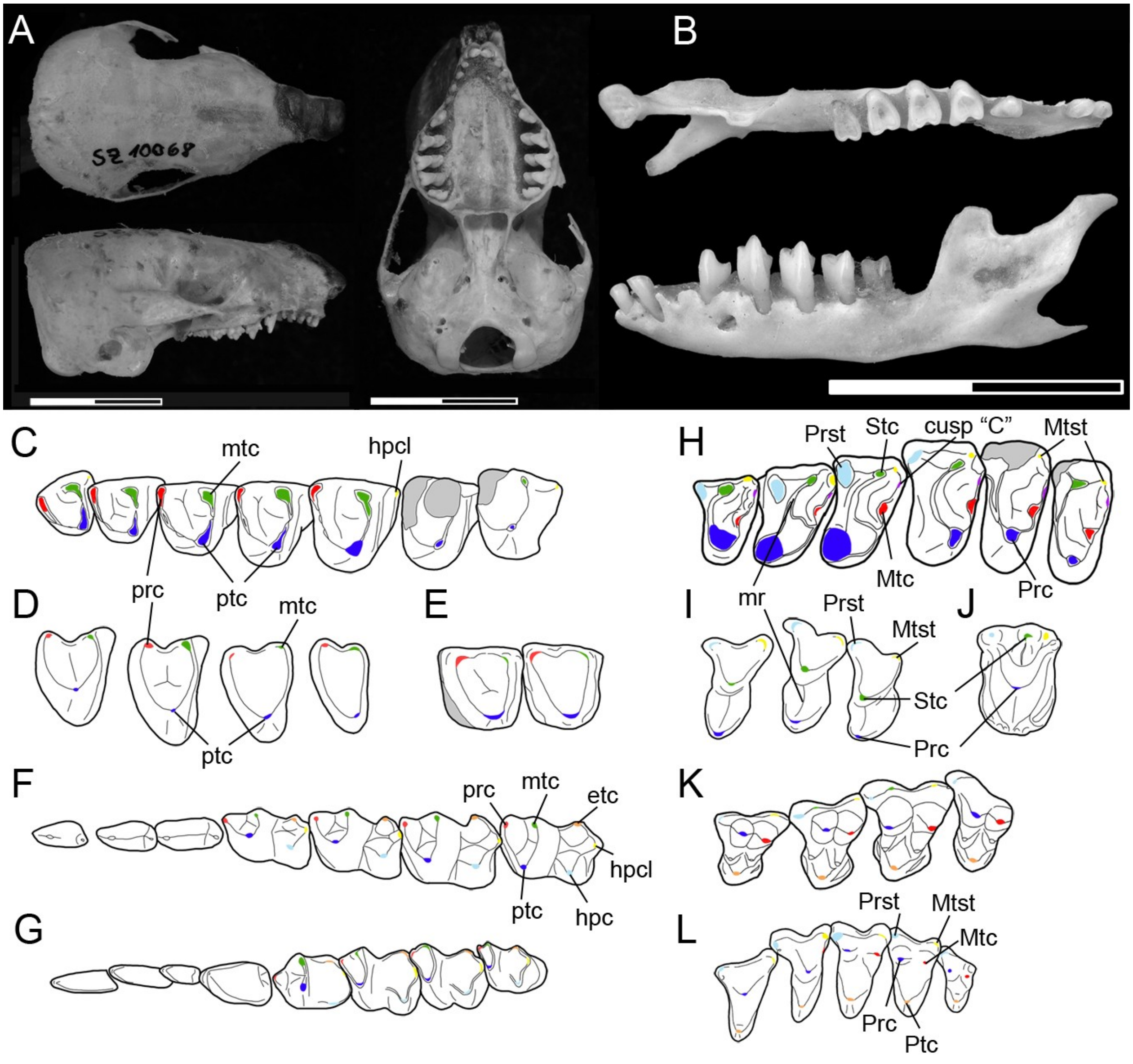


Figure 1. Skull and dentition of *Notoryctes typhlops* compared with selected therian and non-therian mammals. A, *Notoryctes typhlops* (ZIUT-SZ10068, Zoologisches Institut Universitat Tübingen, Germany) skull in dorsal (left above), lateral (left below), and ventral (central) views, **B**, *Notoryctes typhlops* (BMNH 39.4210, British Museum of Natural History, England) right mandible in oclusal (above) and lateral (below) views. **C-G**, lower dentitions: **C**, m1-m7 of *Dryolestes* (Dryolestoidea); **D**, m1-m4 of *Notoryctes*; **E**, ?m2-3 of *Mesungulatum*

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

(Meridiolestida); **F**, p1-m3 of *Asiatherium* (Metatheria); **G**, p1-m4 of *Zalambdalestes*. **H-L**, upper dentition of selected mammals: **H**, M1-M7 of *Dryolestes* (Dryolestoidea); **I**, M1-M3 of *Notoryctes*; **J**, molariform of *Mesungulatum* (Meridiolestida); **K**, M1-M4 of *Asiatherium* (Metatheria); **l**, P3-M3 of *Zalambdalestes* (Eutheria). D, based on BMNH 39.4210; I, based on ZIUT-SZ10068. A-B, scale bar: 10 mm; C-L, not to scale.

PeerJ PrePrints

PeerJ PrePrints

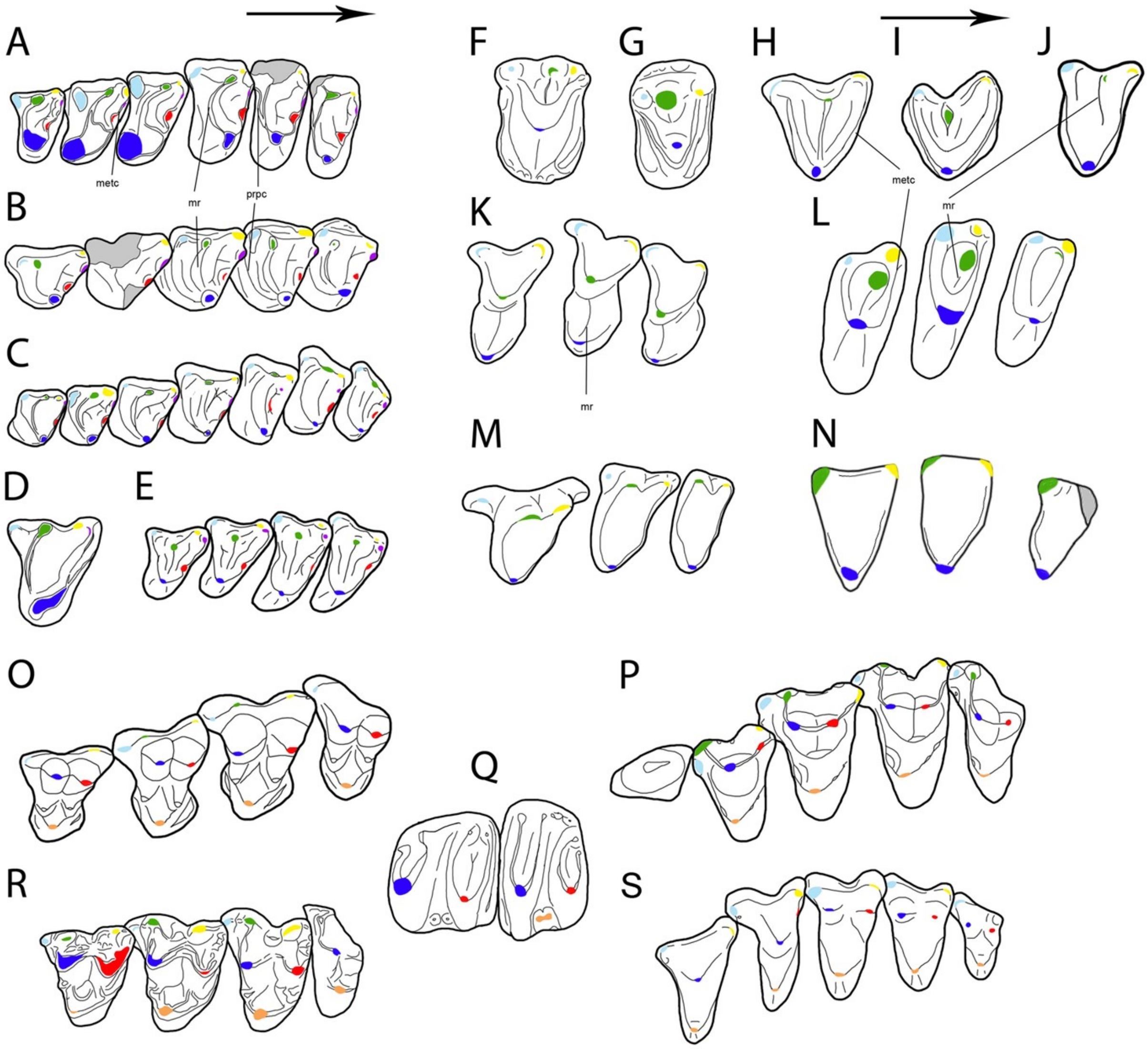


Figure 2. Upper dentitions of selected mammaliaforms in oclusal view. **A**, M1-M7 of *Dryolestes* (Dryolestoidea); **B**, M1-M5 of *Henkelotherium* (Dryolestoidea); **C**, M1-M7 of *Krebsotherium* (Dryolestoidea); **D**, ?M of *Crusafontia* (Dryolestoidea); **E**, ?M of *Laolestes* (Dryolestoidea); **F**, ?M3 of *Mesungulatum* (Dryolestoidea); **G**, ?M3 of *Coloniatherium* (Meridiolestida); **H**, ?M of *Brandonia* (Meridiolestida); **I**, ?M of *Casamiquelia* (Meridiolestida); **J**, ?M of *Groebertherium* (Meridiolestida); **K**, M1-M3 of *Notoryctes* (Meridiolestida); **L**, ?M1-3 of *Leonardus* (Meridiolestida); **M**, M1-M3 of *Cronopio* (Meridiolestida); **N**, P4-M2 of *Necrolestes* (Meridiolestida); **O**, M1-M4 of *Asiatherium* (Metatheria); **P**, P3-M3 of *Prokennalestes* (Eutheria); **Q**, M1-M2 of *Obdurodon* (Monotremata); **R**, M1-M4 of *Alphadon* (Metatheria); **S**, P3-M3 of *Zalambdalestes* (Eutheria). A-J, L-S modified from Chimento et al. (2012), K,

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014
PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)

based on ZIUT-SZ10068. Arrow indicates distal tooth face. References: **blue**, paracone; **red**, metacone; **green**, stylocone; **yellow**, metastyle; **light blue**, parastyle; **orange**, protocone; **violet**, cusp "C". Abbreviations: **metc**, metacrista; **mr**, median ridge; **prpc**, preparacrista. Not to scale.

PeerJ PrePrints

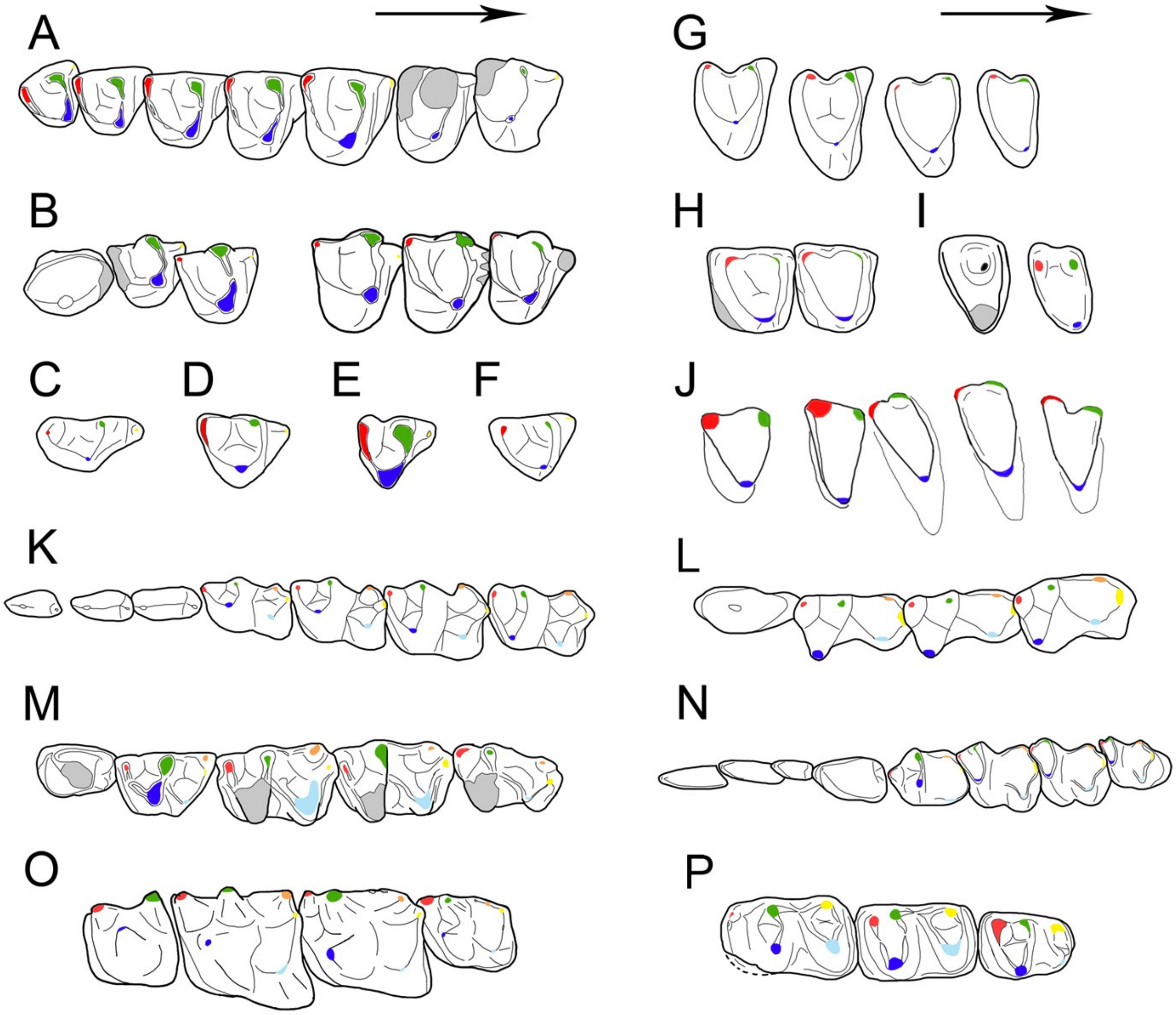


Figure 3. Lower dentitions of selected mammaliaforms in oclusal view. **A**, m1-m7 of *Dryolestes* (Dryolestoidea); **B**, p4-m2 and m5-m8 of *Guimarotodus* (Dryolestoidea); **C**, ?m of *Chunnelodon* (Dryolestoidea); **D**, ?m of *Tathiodon* (Dryolestoidea); **E**, ?m of *Laolestes* (Dryolestoidea); **F**, ?m of *Amblotherium* (Dryolestoidea); **G**, m1-m4 of *Notoryctes* (Meridiolestida); **H**, p4-m1 of *Mesungulatum* (Dryolestoidea); **I**, two molars of *Leonardus* (Meridiolestida); **J**, P2-M3 of *Necrolestes* (Meridiolestida); **K**, p3-m4 of *Asiatherium* (Metatheria); **L**, p4-m3 of *Prokennalestes* (Eutheria); **M**, p3-m4 of *Alphadon* (Metatheria); **N**, dentition of *Zalambdalestes* (Eutheria); **O**, p4-m3 of *Aukstribosphenos* (Australosphenida); **P**, m1-m3 of *Steropodon* (Australosphenida). A-F, H-P modified from Chimento et al. (2012); G, based on BMNH 39.4210. Arrows indicate distal face of tooth. References: **blue**, protoconid;

PeerJ PrePrints

red, paraconid; **green**, metaconid; **yellow**, hipoconulid; **orange**, entoconid; **light blue**, hipoconid. Not to scale.

PeerJ PrePrints

PeerJ PrePrints

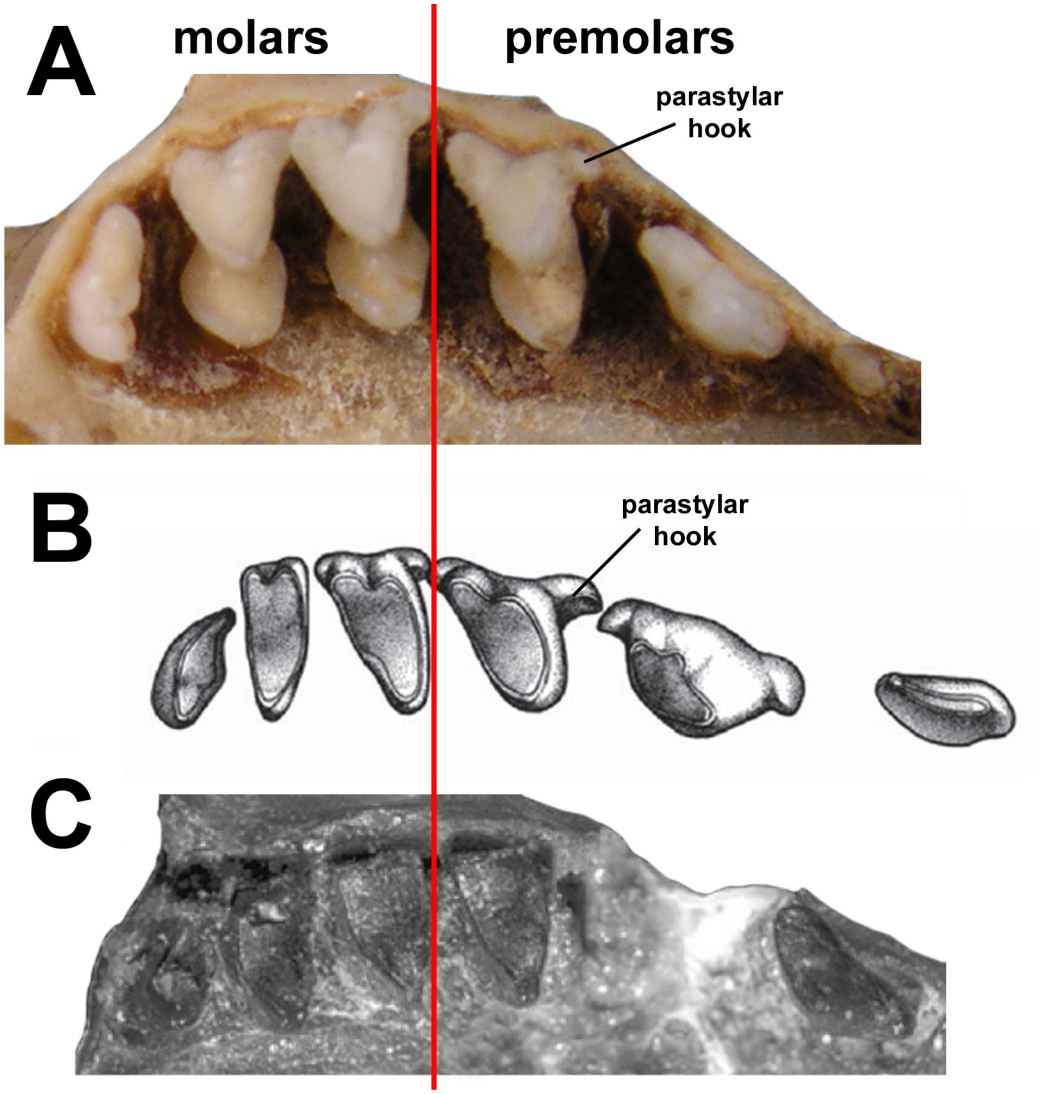


Figure 4. Compared oclusal views of the maxillar check-teeth of *Notoryctes* (A), *Cronopio* (B) and *Necrolestes* (C). A correspond to ZIUT-SZ10068; B modified from Rougier et al. (2011); C modified from Asher et al. (2007).

PeerJ PrePrints

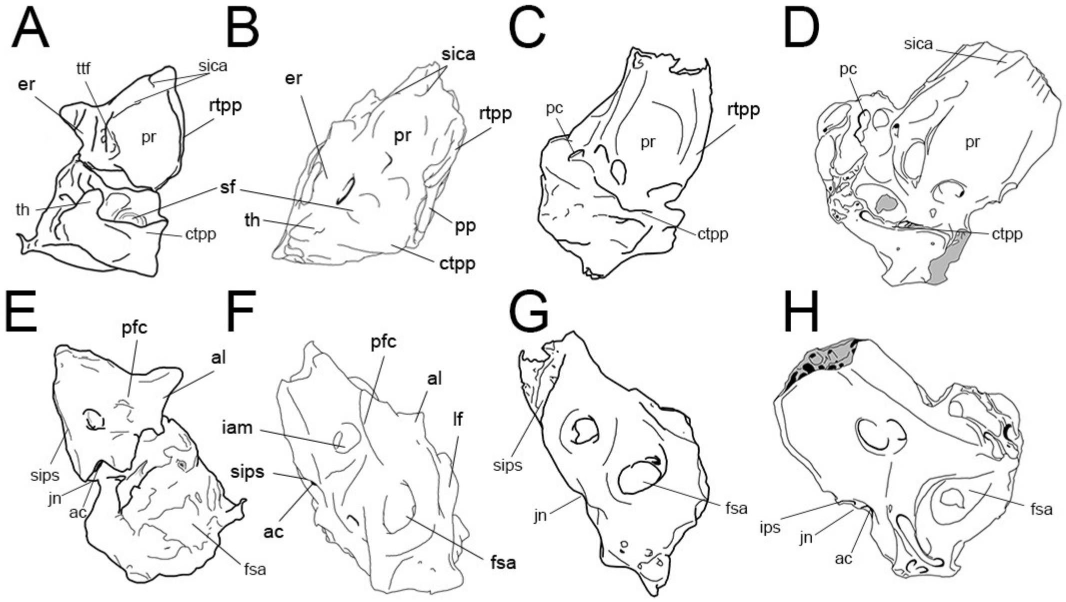


Figure 5. Comparisons of petrosal anatomy of selected mammals in ventral (above) and dorsal views (below). A,E, *Necrolestes*; B,F, *Notoryctes*; C,G, *Mimoperadectes*; D,H, *Prokennalestes*. A,B,E,F modified from Ladevèze et al. (2008); C,G modified from Horovitz et al. (2009); D,H, modified from Wible et al. (2001).

PeerJ PrePrints

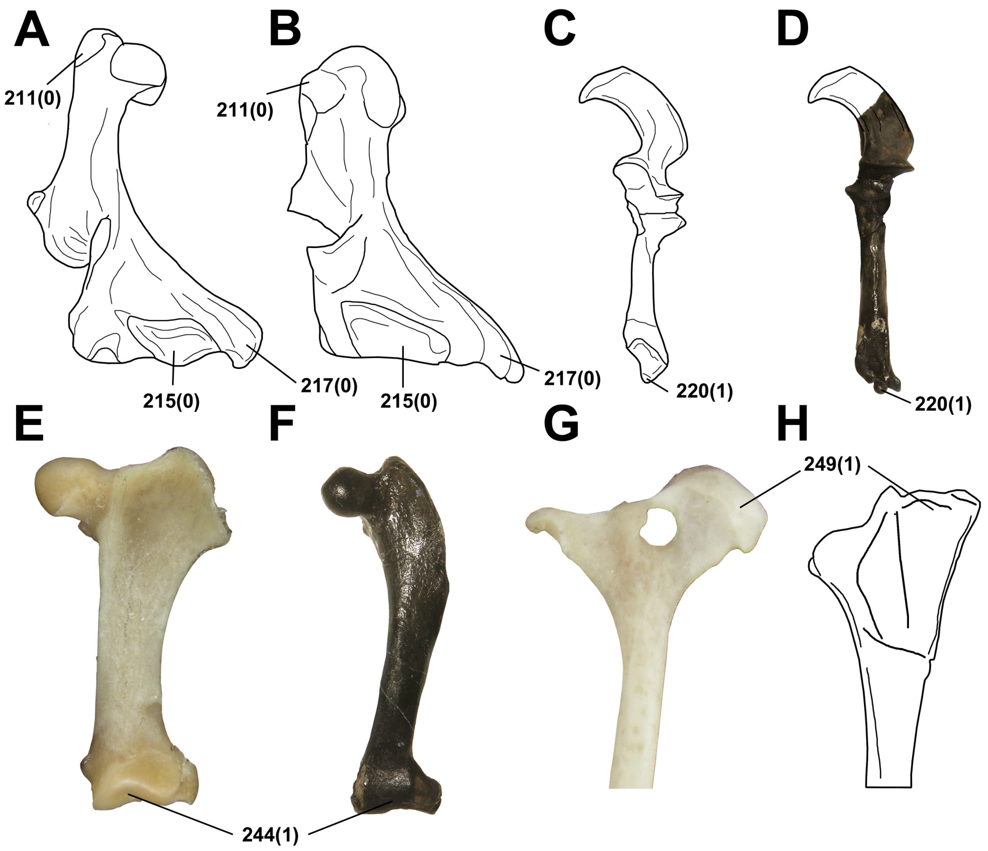
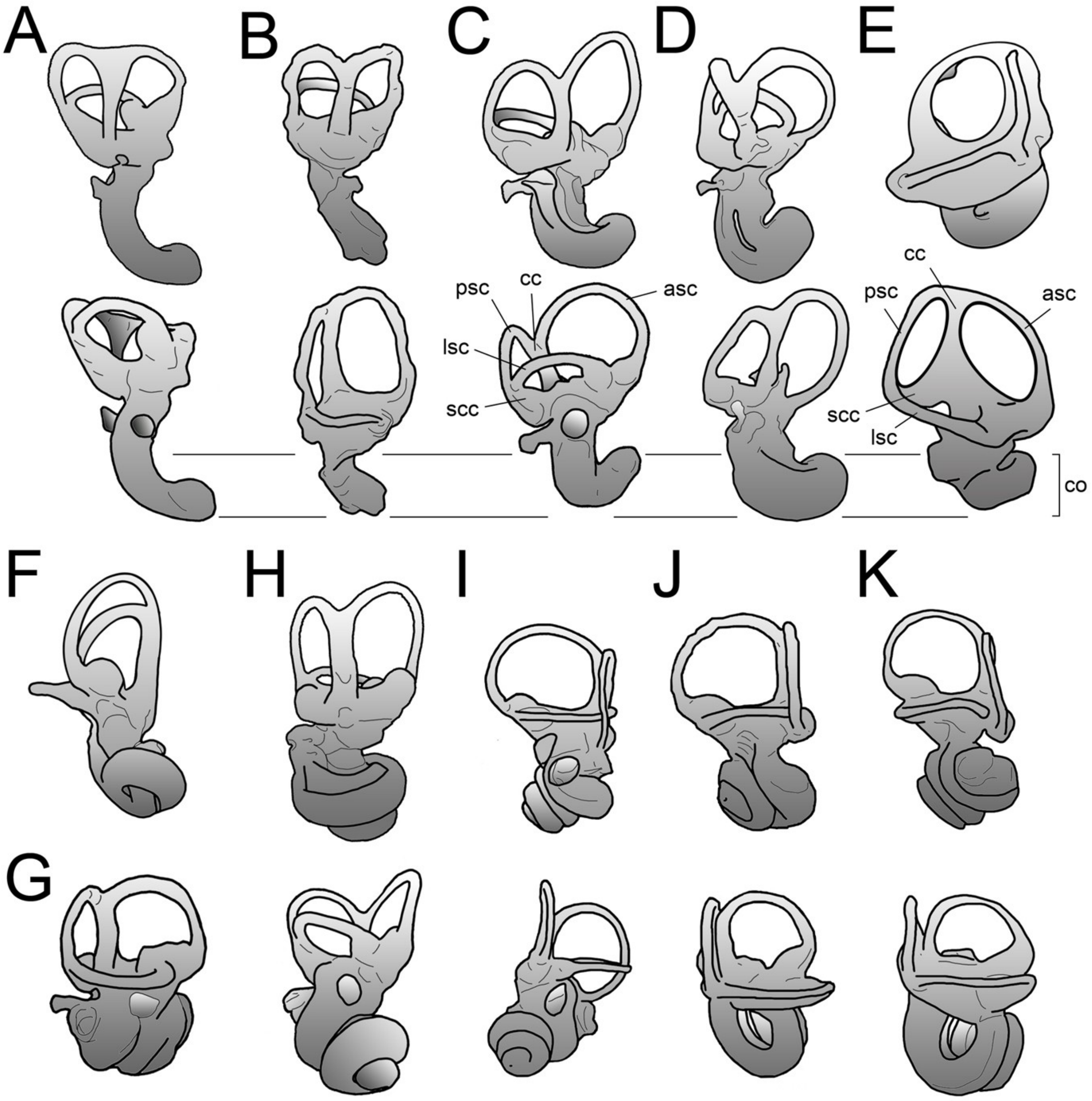


Figure 6. Selected post-cranial bones of *Notoryctes* compared with *Necrolestes*. **A**, femur of *Notoryctes*; **B**, femur of *Necrolestes*; **C**, left ulna of *Notoryctes*; **D**, right ulna of *Necrolestes* (reversed); **E**, left femur of *Notoryctes*; **F**, right femur of *Necrolestes* (reversed); **G**, left fibula of *Notoryctes*; **H**, fibula of *Necrolestes*. **Character numbers and states**: 211(0), lesser tubercle of the humerus relative to the greater tubercle, narrower; 215(0), ulnar articulation on the distal humerus, bulbous; 217(0), entepicondyle (medial epicondyle) and ectepicondyle (lateral epicondyle) of the humerus, robust; 220(1), styloid process of the radius, strong; 244(1), patellar facet ('groove') of the femur shallow and weakly developed; 249(1), parafibular process of the fibula fused to fibula and enlarged. A, B, C, H, modified from Asher et al. (2007); D and F correspond to MACN A-5751 and MACN A-5747, respectively; E and G correspond to ZMB 35694.

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.715v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014



1967

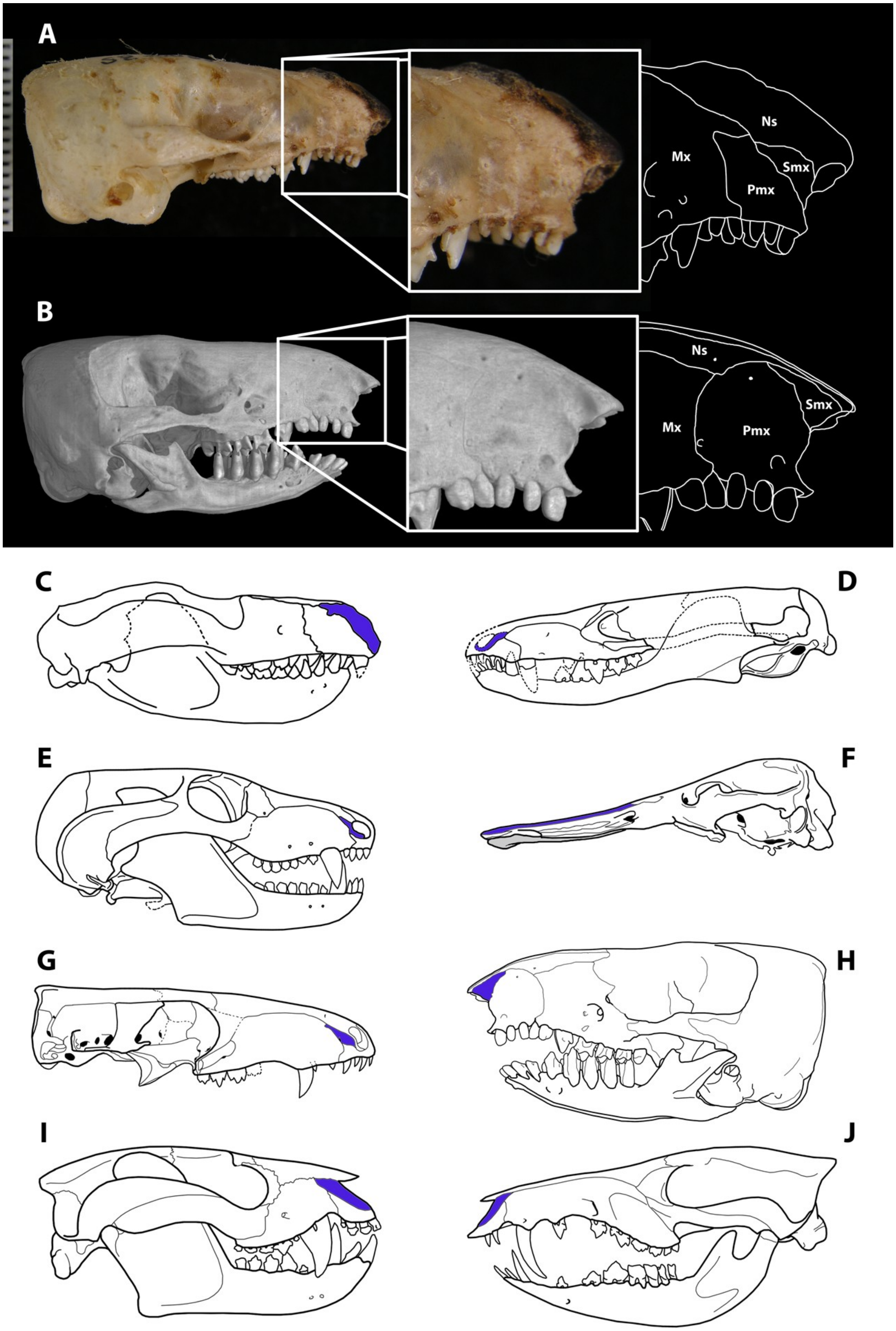
1968 **Figure 7. Inner ear morphology of selected mammals**. **A**, *Ornithorhynchus* (Monotremata) in median (above) and ventral (below) views; **B**, cf. *Tombaatar* (Multituberculata) in median (above) and ventral (below) views; **C**, *Dryolestes* (Dryolestoidea) in median (above) and ventral (below) views; **D**, *Henkelotherium* (Dryolestoidea) in dorsomedian (above) and median (below) views; **E**, *Notoryctes* (Dryolestoidea) in dorsal (above) and lateral (below) views; **F**, *Herpetotherium* (Dryolestoidea) in anterior view; **G**, *Mimoperadectes* (Metatheria) in lateral

PeerJ PrePrints

view; **H**, *Didelphys* (Metatheria) in median (above) and ventral (below) views; **I**, *Petauroides* (Metatheria) in lateral (above) and anterior (below) views; **J**, *Loris* (Eutheria) in lateral (above) and anterior (below) views; **K**, *Adapis* (Eutheria) in lateral (above) and anterior (below) views. A, C, and H modified from (*50*); B modified from (*82*); D modified from (*49*); E modified from (*48*); F modified from (*80*); G modified from (*83*); I modified from (*84*); J-K modified from (*85*). **Abbreviations**: **asc**, anterior semicircular canal; **cc**, crus commune; **co**, cochlea; **lsc**, lateral semicircular canal; **psc**, posterior semicircular canal; **scc**, secondary crus commune. Not to scale.

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints



PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

Figure 8. **A-B,** lateral view of skulls of *Notoryctes* in right lateral view, showing a detail of the snout; **A**, *Notoryctes typhlops* (ZIUT-SZ10068); **B**, *Notoryctes typhlops* (AMNH 202107, modified from Rodgers, 2008). **C-J,** lateral view of the skull of basal mammaliaforms; **C**, *Repenomamus* (modified from Hu et al., 2005); **D**, *Hadrocodium* (modified from Luo et al., 2001); **E**, *Probainognathus* (modified from Bonaparte & Migale, 2010); **F**, *Ornithorhynchus* (modified from Kielan-Jaworowska et al., 2004); **G**, *Sinoconodon* (modified from Kielan-Jaworowska et al., 2004); **H**, *Notoryctes* (modified from Rodgers, 2008); **I**, *Vincelestes* (modified from Kielan-Jaworowska et al., 2004); **J**, *Cronopio* (modified from Rougier et al., 2011). Septomaxilla indicated in colour blue. Abbreviations: **Mx**, maxilla; **Pmx**, premaxilla; **Smx**, septomaxilla; **Ns**, nasal. Not to scale.

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

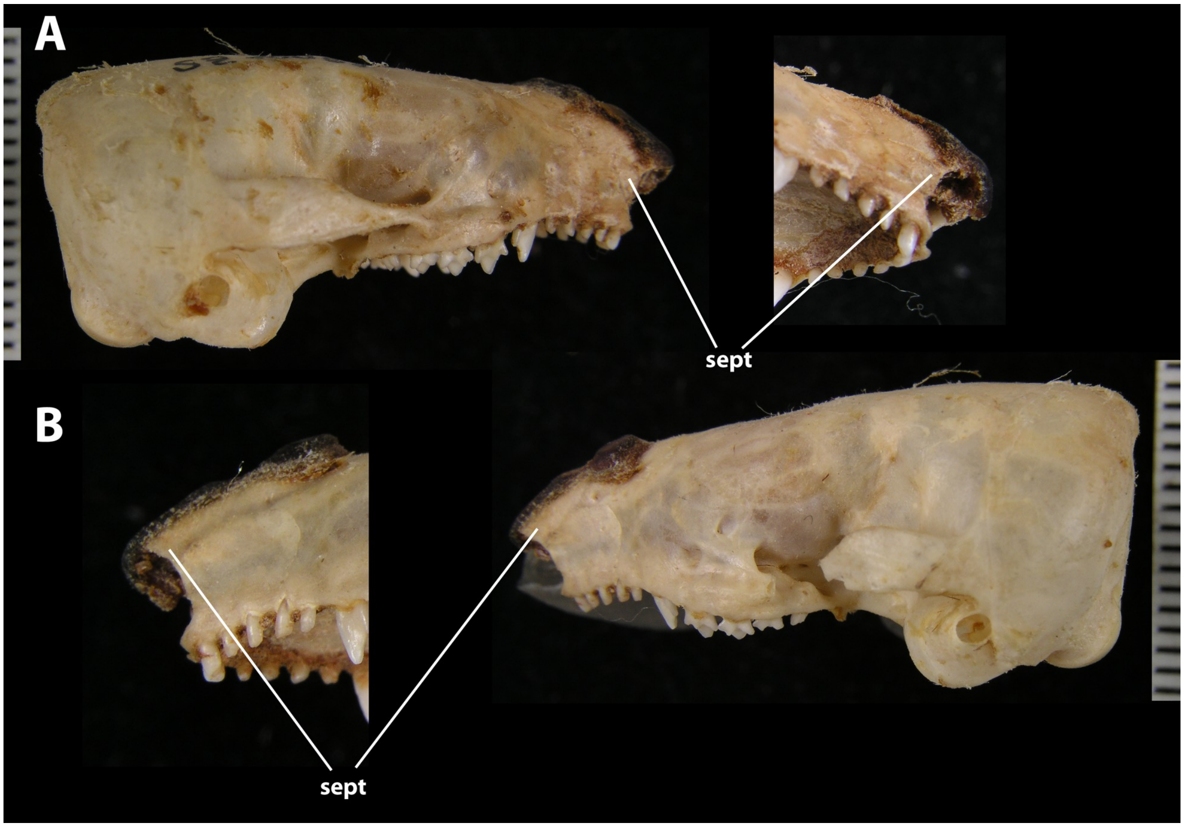


Figure 9. A, skull of *Notoryctes typhlops* (ZIUT-SZ10068) in right lateral view (at left), ventrolateral view of the snout (at right); **B,** skull of *Notoryctes typhlops* (ZIUT-SZ10068) in left lateral view (at right), ventrolateral view of the snout (at left). Abbreviations: **sept**, septomaxilla.

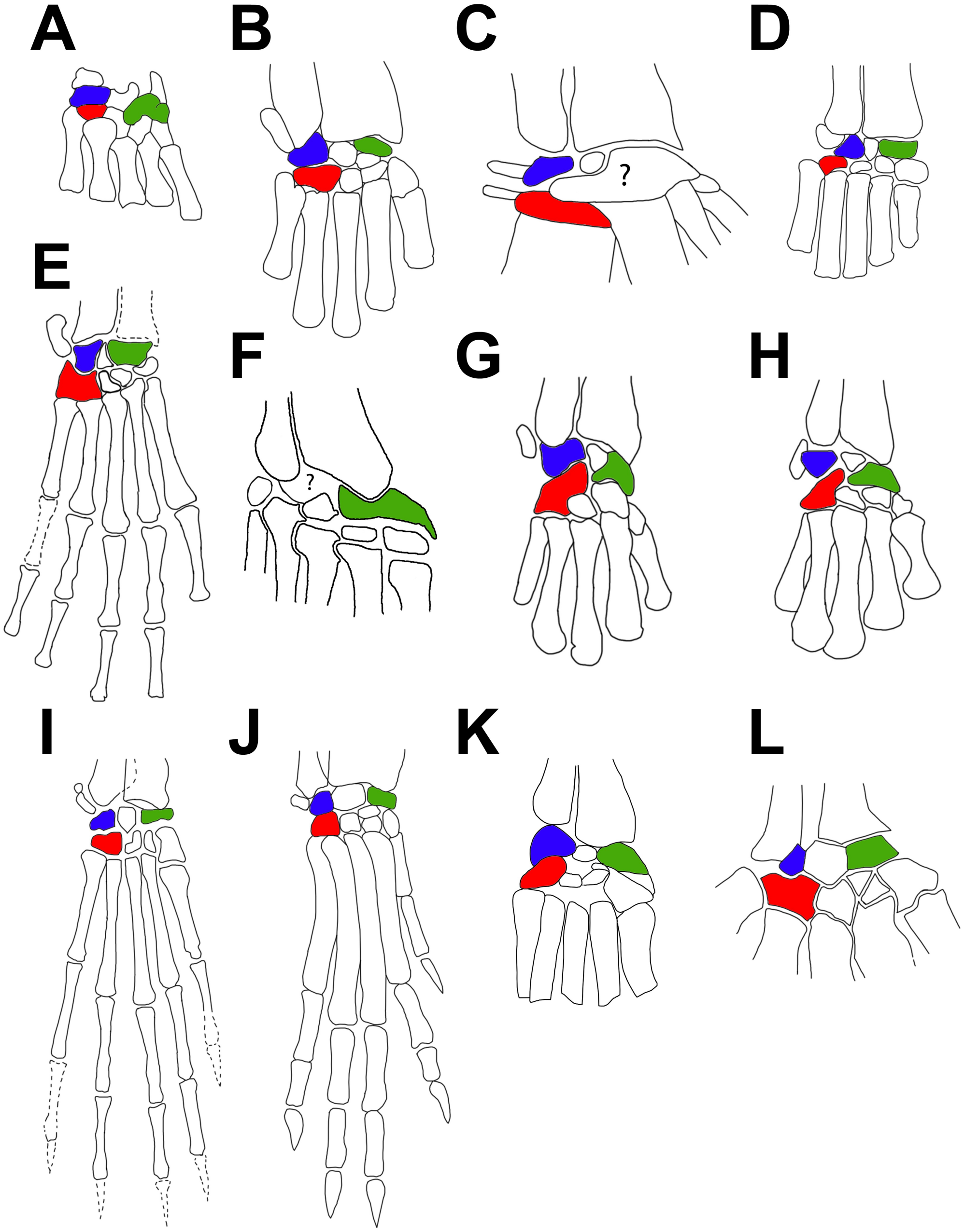


Figure 10. Comparisons between carpal manual elements of selected mammaliaforms. A, *Ornithorhynchus* (Monotremata); **B**, *Zhangheotherium* (Symmetrodonta); **C**, *Notoryctes* (Dryolestoidea); **D**, *Jeholodens* (Mammaliaformes); **E**, *Sinodelphys* (Metatheria); **F**, *Asiatherium* (Metatheria); **G**, *Didelphys* (Metatheria); **H**, *Dromiciops* (Metatheria); **I**, *Eomaia* (Eutheria); **J**, *Zalambdalestes* (Eutheria); **K**, *Asioryctes* (Eutheria); **L**, *Talpa* (Eutheria) (A-B, D, G- J modified from Ji et al., 2002; C modified from Szalay, 1994; E modified from Luo et al., 2003; F modified

PeerJ PrePrints

from Szalay & Trofimov, 1996; K modified from Kielan-Jaworowska et al., 2004; L modified from Holmgren, 1952). References: **red**, hamate; **blue**, triquetrum; **green**, scaphoid. Not to scale.

PeerJ PrePrints

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

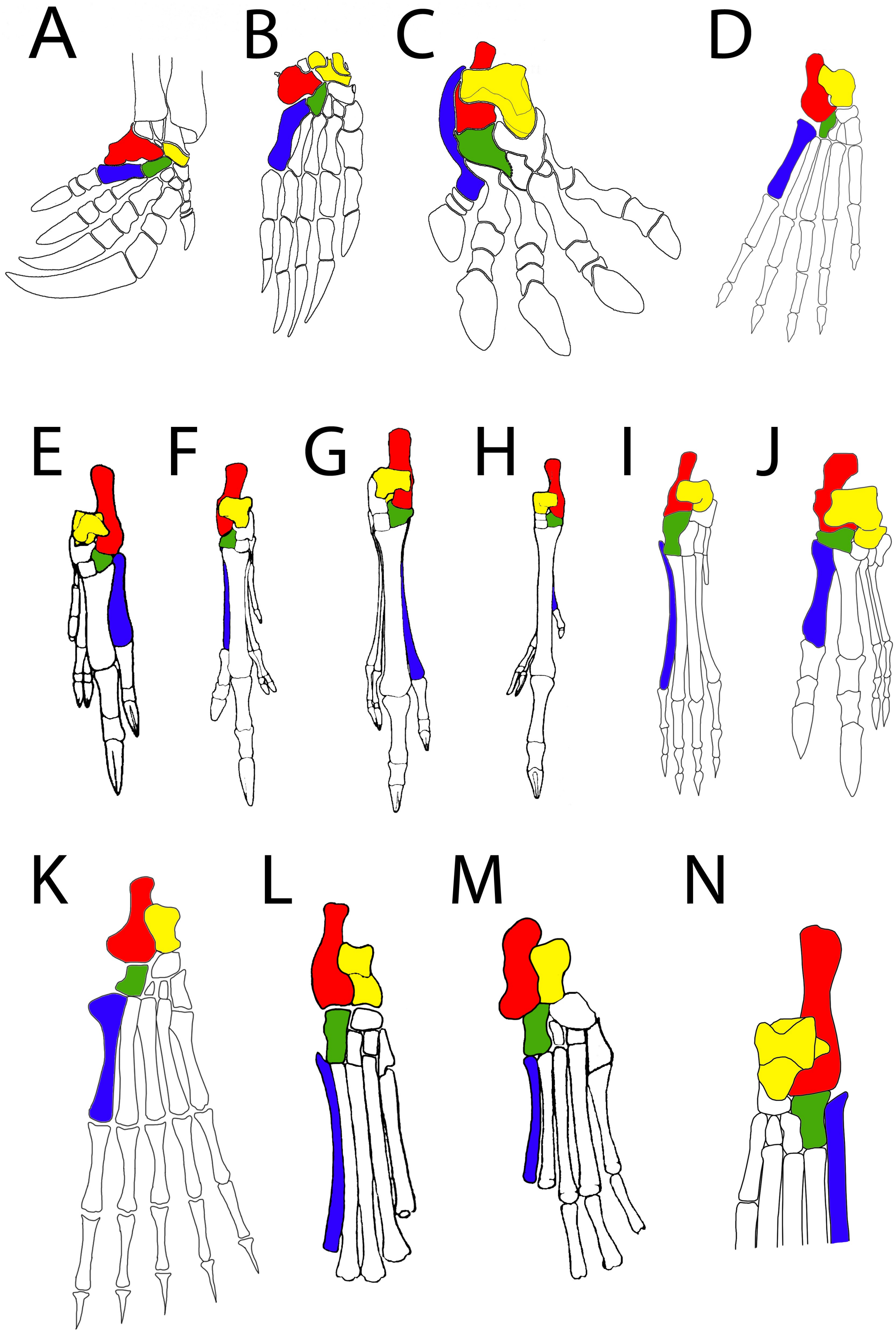


Figure 11. Comparisons between tarsal pedal elements of selected mammaliaforms.

Monotremata: **A**, *Tachyglossus*; **B**, *Ornithorhynchus*; **Dryolestoidea: C**, *Notoryctes*;

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

Mammaliaformes: D, *Jeholodens*; **Theria: E**, *Echymipera*; **F**, *Perameles*; **G**, *Macrotis*; **H**, *Chaeropus*; **I**, *Dasyurus*; **J**, *Dendrolagus*; **K**, *Eomaia*; **L**, *Tupaia*; **M**, *Asioryctes*; **N**, *Zalambdalestes* (A-C, E-H, modified from Szalay, 1994; D, K-N, modified from Ji et al., 2002; I-J modified from Vaughan et al., 2010). References: **red**, calcaneus; **blue**, fifth metatarsal; **green**, cuboid; **yellow**, astragalus. Not to scale.

PeerJ PrePrints

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

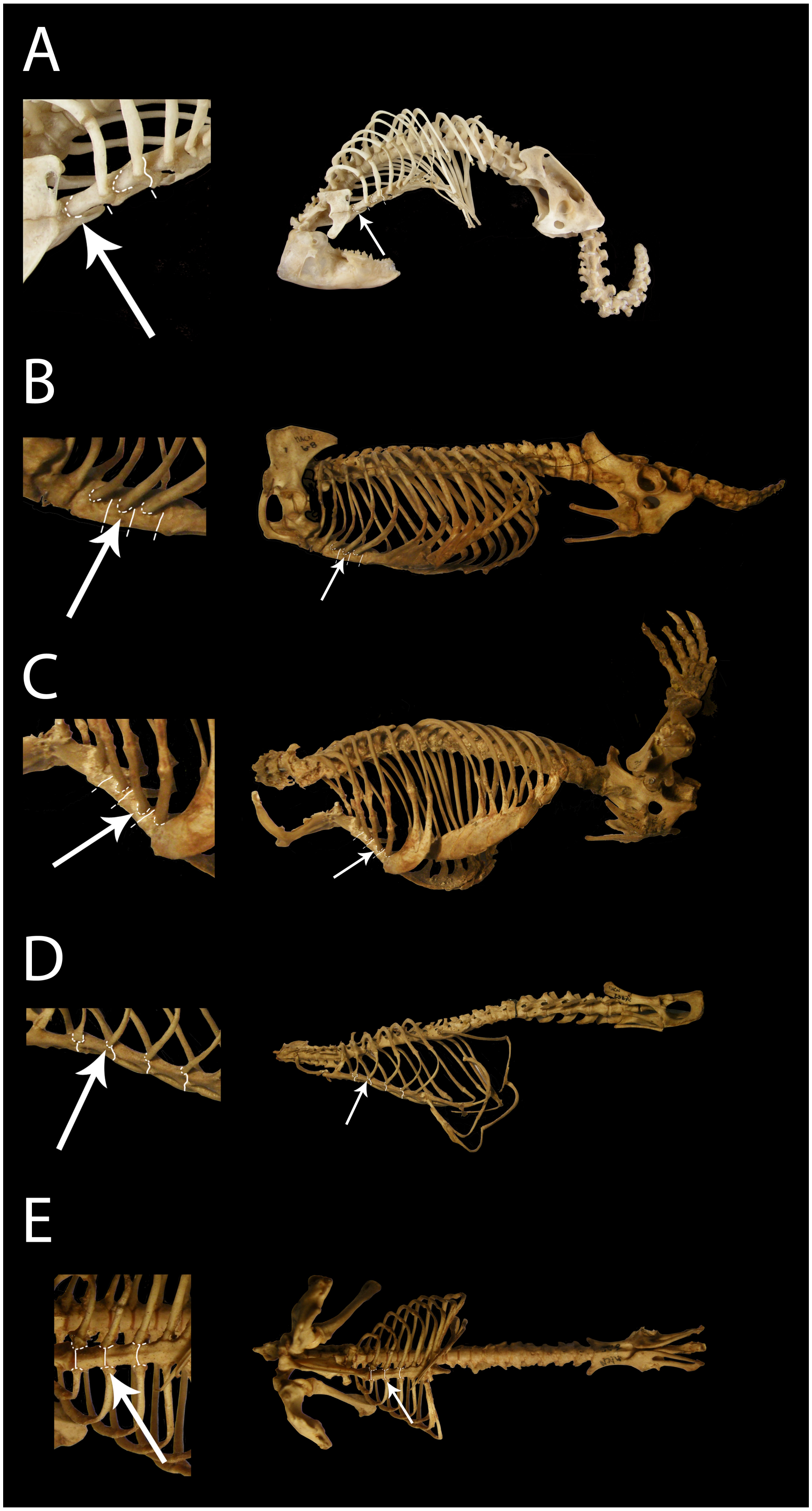


Figure 12. Thoracic ribs and sternal articulation of selected mammals. **A**, *Notoryctes* (ZMB35694); **B**, *Tachyglossus* (MACN 6.8); **C**, *Ornithorynchus* (MACN 26.76); **D**, *Dasyurus* (MACN 23.572); **E**, *Talpa* (MACN 6.35). Arrow indicate articulation between thoraci ribs and sternebrae. Note that each thoracic rib articulates with a single sternebra in Monotremata and *Notoryctes*, whereas in Theria at least to sternebrae are contacted by each rib (based on Horovitz & Sánchez-Villagra, 2003).

PeerJ PrePrints

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

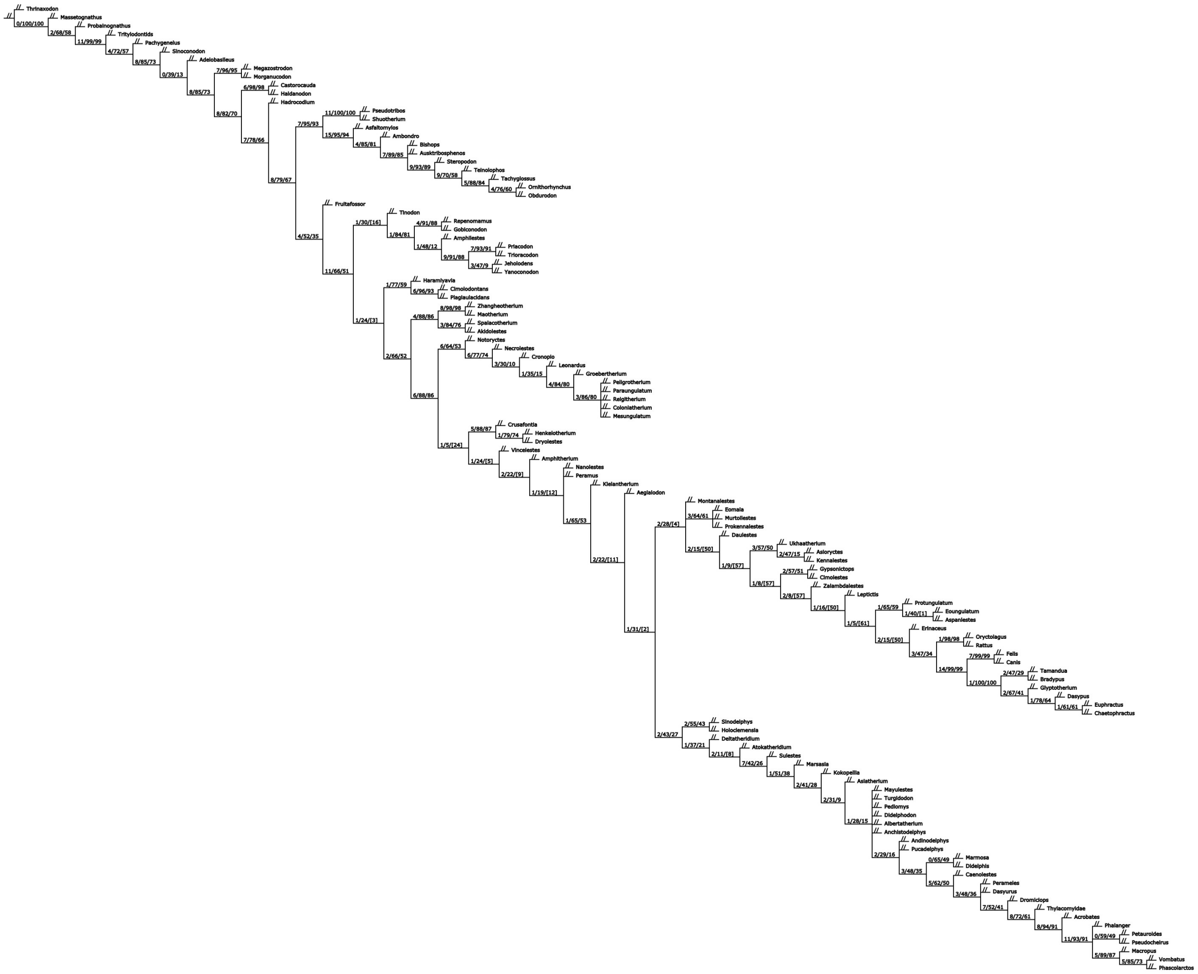


Figure 13. Phylogenetic analysis of Mammaliaformes. Strict-consensus tree of higher-level mammaliaform relationships. **References**: yellow, Yinotheria; red, Dryolestoidea; green, Eutheria; blue, Metatheria.

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.715v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

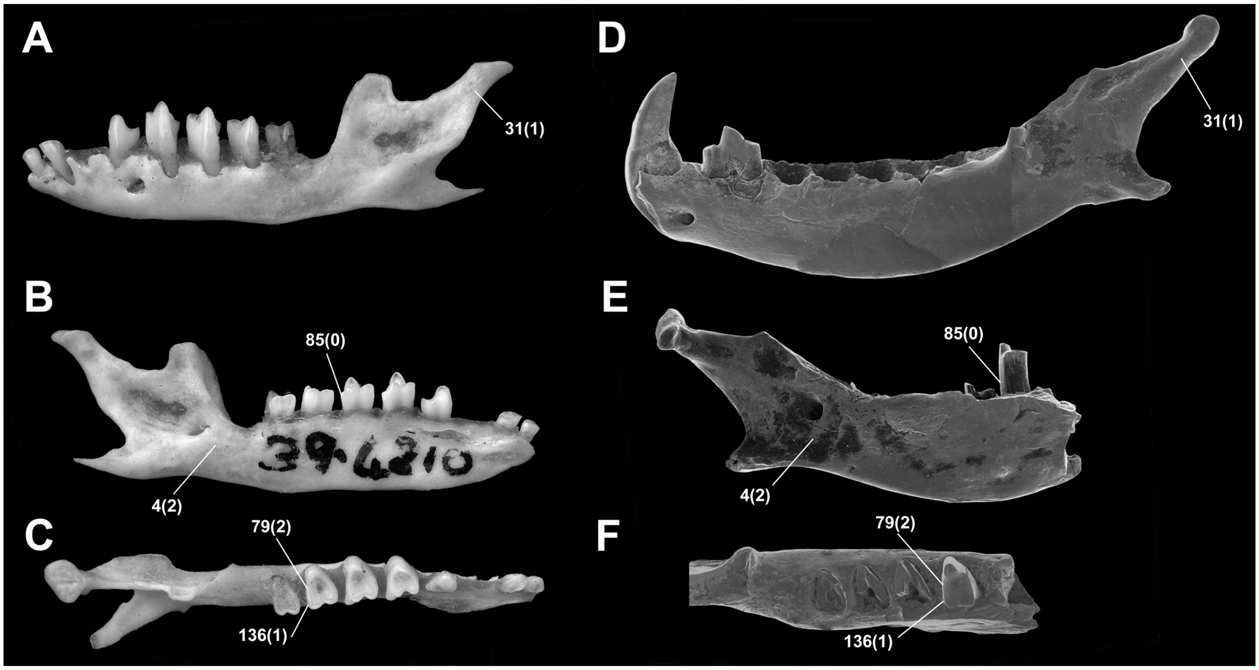


Figure 14. Hemimandible of *Notoryctes* (left) compared with *Necrolestes* (right), in medial (A,D), lateral (B,E) and oclusal views (C,F). A, B and C correspond to BMNH 39.4210; D, E and F correspond to MACN-A5742 (holotipe). **Character numbers and states**: 4(2), absent of Meckel's sulcus; 31(1), presence of gracile and elongate dentary peduncle; 79(2), paracristid nearly transverse relative to the longitudinal axis of the molar; 85(0), absence of talonid; 136(1), absence of distal metacristid.

PeerJ PrePrints

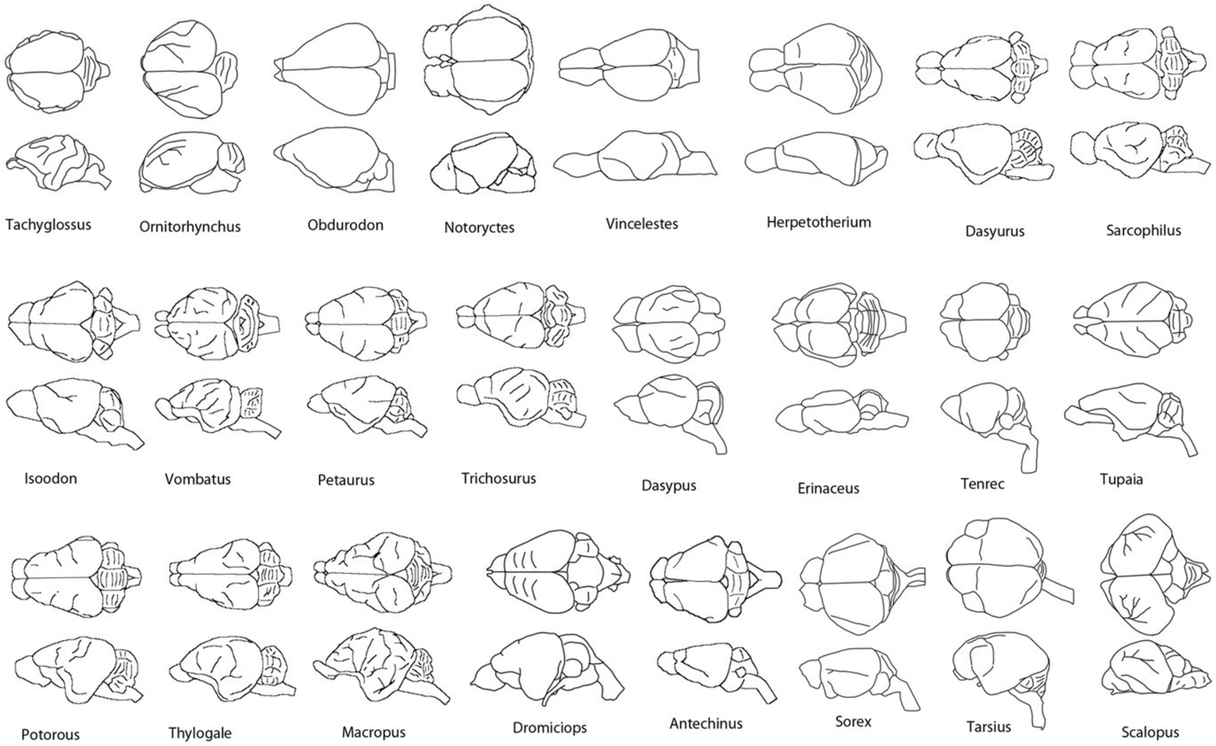


Figure 15. Comparison of selected mammalian brains. **Monotremata**: *Tachyglossus*, *Ornitorynchus*, *Obdurodon*. **Dryolestoidea**: *Notoryctes*. **Stem-Zatheria**: *Vincelestes*. **Metatheria**: *Herpetotherium*, *Dasyurus*, *Sarcophilus*, *Isoodon*, *Vombatus*, *Petaurus*, *Trichosurus*, *Potorous*, *Thylogale*, *Macropus*, *Dromiciops*, *Antechinus*. **Eutheria**: *Dasypus*, *Erinaceus*, *Tenrec*, *Tupaia*, *Sorex*, *Tarsius*, *Scalopus*. Modified from brain photographs of the University of Wisconsin and Michigan State Comparative Mammalian Brain Collections, available at: http://www-brainmuseum.org (specimens 65-46; 60-465; 65-60; 70-96; 61-559; 64-32; 64-033; 73-4; 64-20; 65-55; 65-65; 59-267; 64-25; 64-232; 64-193; 69-503; 65-59; 64-29; 62-279; 64-11) (Additional data taken from Smith, 1895a,b,c; 1995; Moeller, 1970; Rowe & Bohringer, 1992; Bohringer, 1992; Karlen & Krubitzer, 2007; Macrini et al., 2007; Sanchez-Villagra et al., 2007; Ashwell, 2010).

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

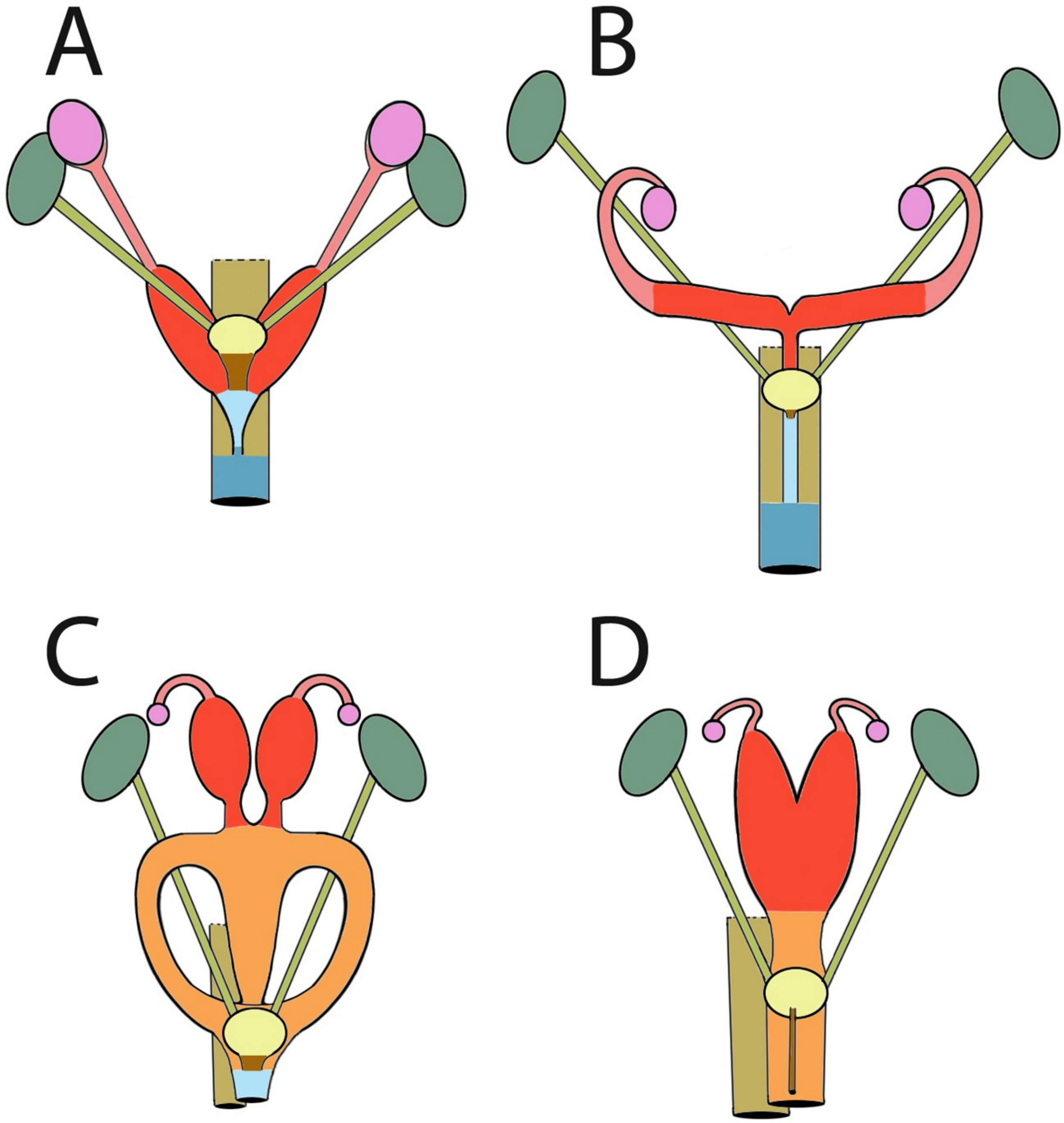


Figure 16. Comparisons between female reproductive systems of main mammalian clades.

Diagrammatic figures of female reproductive system of Mammalia: **A**, Monotremata; **B**, *Notoryctes*; **C**, Metatheria; **D**, Eutheria (based on Stirling, 1891; Gadow, 1892; Weichert & Presch, 1981; Renfree, 1993; Presley, 1997; Vaughan et al., 2010). References: **green**, kidneys; **pink**, ovaries; **light red**, oviducts; **deep red**, uterines; **orange**, vagina; **light green**, ureters; **yellow**, bladder; **brown**, urethra; **light brown**, rectum; **light blue**, urogenital sinus; **deep blue**, cloaca. Not to scale.

PeerJ PrePrints

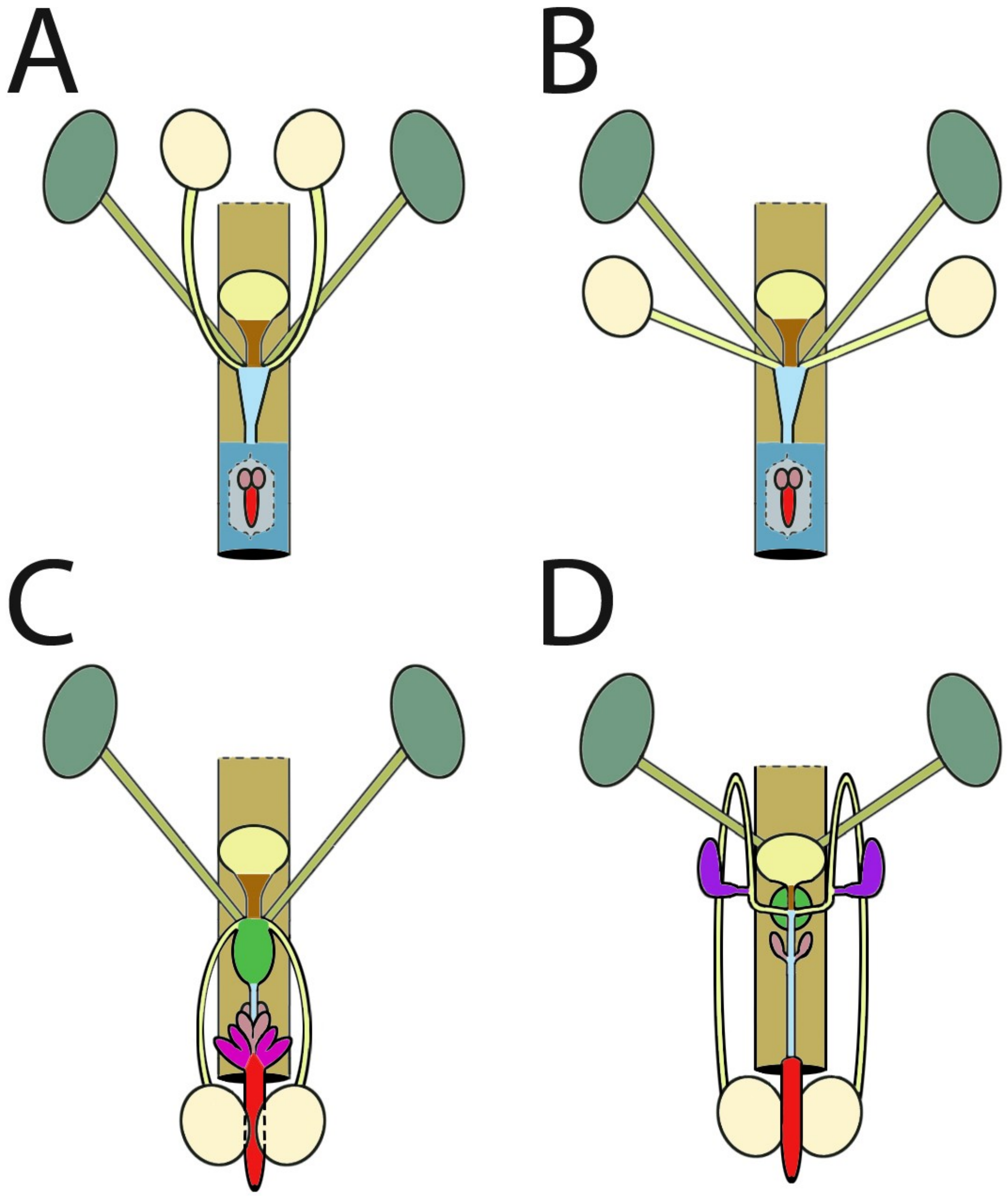


Figure 17. Comparisons between male reproductive systems. Diagrammatic figures of male reproductive system of Mammalia: **A**, Prototheria; **B**, *Notoryctes*; **C**, Metatheria; **D**, Eutheria (based on Gadow, 1892; Linzey & Layne, 1969; Frey, 1991; Jones et al., 1992; Vaughan et al., 2010). References: **dark green**, kidneys; **light green**, ureters; **green**, prostate gland; **cream**, testis; **yellow fluorescent**, vas deferens; **yellow**, bladder; **brown**, urethra; **light brown**,

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

rectum; **light blue**, urogenital sinus; **blue**, cloaca; **fuchsia**, urethral glands; **dark red**, bulbourethral glands; **violet**, vesicular glands; **red**, penis. Not to scale.

PeerJ PrePrints

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

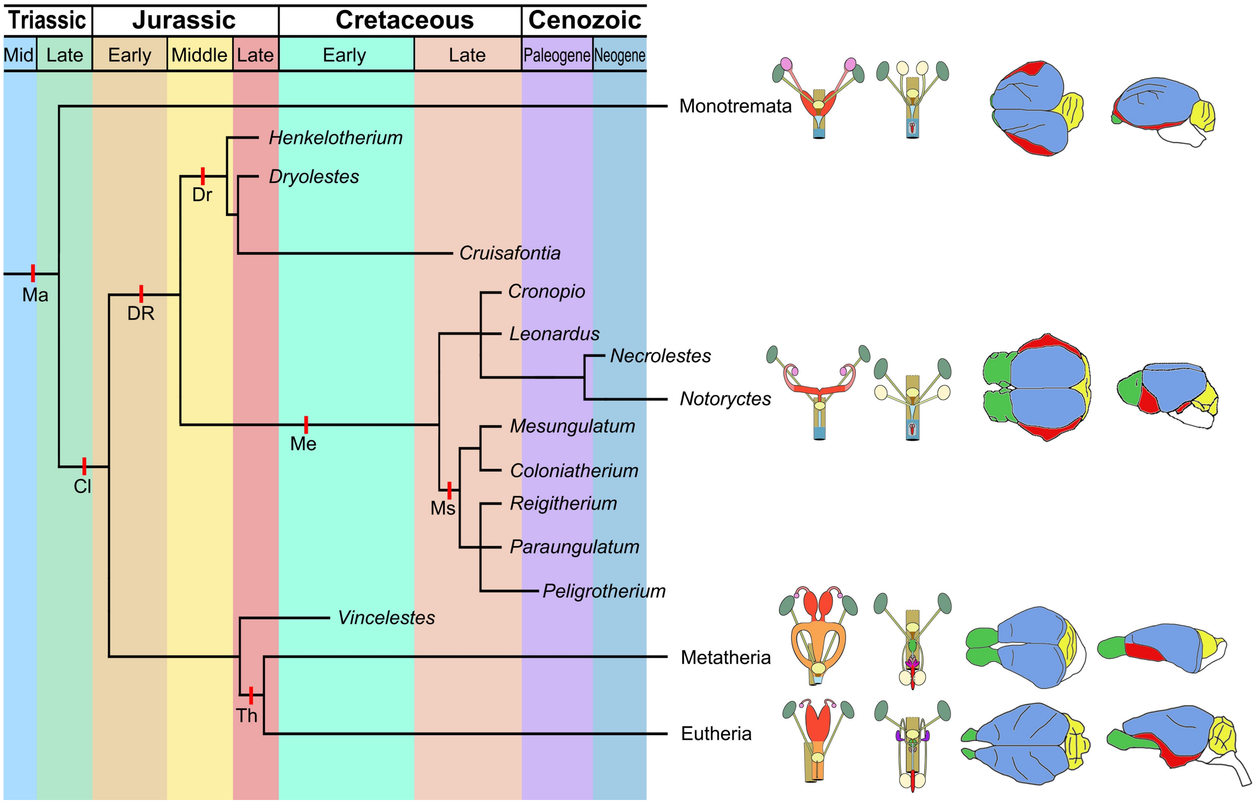


Figure 18. Simplified phylogeny of Mammalia illustrating key-features, as present in *Notoryctes* and main mammalian clades. Selected mammalian soft organs: from left to right: left female reproductive system, male reproductive system, brain in dorsal view, and brain in left lateral view. Upper row: Monotremata; mid-upper row: *Notoryctes*; mid-lower row: Marsupialia; lower row: Eutheria. Brain colouration: **green**, olfactory bulb; **blue**, neopallium; **red**, paleopallium; **yellow**, cerebellum. Abbreviations: **Tr**, Triassic; **Jur**, Jurassic; **Cr**, Cretaceous; **Tc**, Tertiary; **E**, early; **M**, middle; **L**, late; **Ma**, Mammalia; **Cl**, Cladotheria; **DR**, Dryolestoidea; **Dr**, Dryolestida; **Me**, Meridiolestida; **Ms** Mesungulatinae; **Th**, Theria. Not to scale.

PeerJ PrePrints

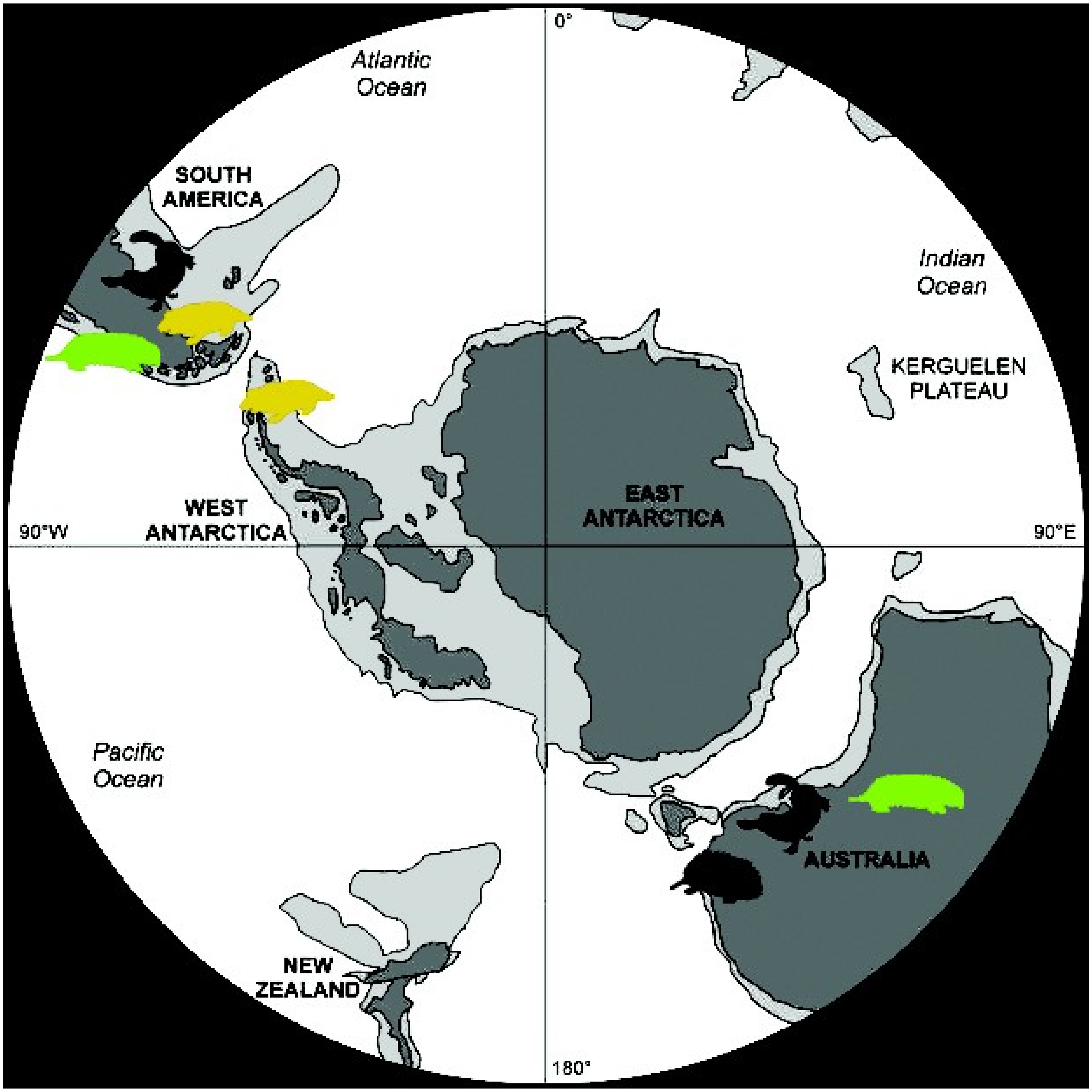


Figure 19. Map of southern Gondwanan continents by the Late Paleogene. Location of typically Mesozoic mammalian lineages that survived the Cretaceous-Tertiary extinction event is indicated. Green silhouette represent dryolestoids; Yellow silhouette represent gondwanatheres; Black silhouette represent monotremes.

PeerJ PrePrints

Appendix 1. List of characters

MANDIBLE

1. Post-dentary trough (behind the tooth row):

(0) Present; (1) Absent.

***Notoryctes*: 1, absent.**

2. Separate scars for the surangular/prearticular in the mandible:

(0) Present; (1) Absent.

***Notoryctes*: 1, absent.**

3. Overhanging medial ridge above the post-dentary trough (behind the tooth row):

(0) Present; (1) Absent.

***Notoryctes*: 1, absent.**

4. Degree of development of Meckel's sulcus:

(0) Well developed; (1) Weakly developed; (2) Vestigial or absent.

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

***Notoryctes*: 2, absent.**

5. Curvature of Meckel's sulcus (under the tooth row):

(0) Parallel to the ventral border of the mandible; (1) Convergent on the ventral border of the mandible.

***Notoryctes*: ?, inapplicable.**

6. Groove for the replacement dental lamina (= Crompton's groove):

(0) Present; (1) Absent.

***Notoryctes*: 1, absent.**

7. Angular process of the dentary:

(0) Weakly developed to absent; (1) Present, distinctive but not inflected; (2) Present and transversely flaring (This is different from character state {4} in having a lateral expansion of the angle and in lacking the anterior shelf); (3) Present and slightly inflected; (4) Present, strongly inflected, and continuing anteriorly as the mandibular shelf.

***Necrolestes*: 2, 3 transversely flaring and inflected.**

***Notoryctes*: 2, transversely flaring and inflected.**

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

8. Position of the angular process of the dentary relative to the dentary condyle:

(0) Anterior position (the angular process is below the main body of the coronoid process, separated widely from the dentary condyle); (1) Posterior position (the angular process is positioned at the level of the posterior end of the coronoid process, either close to, or directly under the dentary condyle).

***Necrolestes*: 1, posterior position.**

***Notoryctes*: 1, posterior position.**

9. Vertical elevation of the angular process of the dentary relative to the molar alveoli:

(0) Angular process low, at or near the level of the ventral border of the mandibular horizontal ramus; (1) Angular process high, at or near the level of the molar alveolar line (and far above the ventral border of the mandibular horizontal ramus).

***Notoryctes*: 0, angular process low.**

10. Flat ventral surface of the mandibular angle:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

11. Exoflection of the angular process of mandible:

(0) Absent; (1) Present.

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.755v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

***Notoryctes*: 0, absent.**

12. Coronoid bone (or its attachment scar):

(0) Present; (1) Absent.

***Notoryctes*: 1, absent.**

13. Location of the mandibular foramen (posterior opening of the mandibular canal):

(0) Within the postdentary trough or in the posterior part of Meckel’s sulcus; (1) In the pterygoid fossa and offset from Meckel’s sulcus (the intersection of Meckel’s sulcus at the pterygoid margin is ventral and posterior to the foramen); (2) In the pterygoid fossa and in alignment with the posterior end of Meckel’s sulcus; (3) In the pterygoid fossa but not associated with Meckel’s sulcus; (4) Not associated with any of the above structures.

***Notoryctes*: 4, mandibular foramen not associated with any structure.**

14. Vertical position of the mandibular foramen:

(0) Below the alveolar plane; (1) At or above the alveolar plane.

***Notoryctes*: 1, mandibular foramen at the alveolar plane.**

15. Concavity (fossa) for the reflected lamina of the angular bone on the dentary angular process:

(0) Present the medial side; (1) Present on the posterior aspect; (2) Absent.

***Notoryctes*: 2, absent.**

16. Splenial bone as a separate element (as indicated by its scar on the dentary):

(0) Present; (1) Absent.

***Notoryctes*: 1, absent.**

17. Relationship of the “postdentary” complex (surangular-articular-prearticular) to the craniomandibular joint (CMJ):

(0) Participating in CMJ; (1) Excluded from CMJ.

***Notoryctes*: 1, excluded from CMJ.**

18. Contact of the surangular bone (or associated postdentary element) with the squamosal:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

19. Pterygoid muscle fossa on the medial side of the ramus of the mandible:

(0) Absent; (1) Present.

PeerJ PrePrints

***Notoryctes*: 1, present.**

20. Medial pterygoid ridge (shelf) along the ventral border of the ramus of the mandible:

(0) Absent; (1) Present; (2) Pterygoid shelf present and reaching the dentary condyle via a low crest.

***Notoryctes*: 0, absent.**

21. Ventral border of the masseteric fossa:

(0) Absent; (1) Present as a low and broad crest; (2) Present as a well-defined and thin crest.

***Notoryctes*: 1, present as a low and broad crest.**

22. Crest of the masseteric fossa along the anterior border of the coronoid process:

(0) Absent or weakly developed; (1) Present and distinctive; (2) Hypertrophied and laterally flaring.

***Notoryctes*: 1, present and distinctive.**

23. Anteroventral extension of the masseteric fossa:

(0) Absent; (1) Extending anteriorly onto the body of the mandible; (2) Further anterior extension below the ultimate premolar.

PeerJ PrePrints

PeerJ PrePrints

***Notoryctes*: 0, absent.**

24. Labial mandibular foramen inside the masseteric fossa:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

25. Posterior vertical shelf of the masseteric fossa connected to the dentary condyle:

(0) Absent; (1) Present as a thin crest along the angular margin of mandible; (2) Present as a thick, vertical crest.

***Notoryctes*: 1, present.**

26. Posterior-most mental foramen:

(0) In the canine and anterior premolar (premolariform) region (in the saddle behind the canine eminence of the mandible); (1) Below the penultimate premolar (under the anterior end of the functional postcanine row); (2) Below the ultimate premolar; (3) At the ultimate premolar and the first molar junction; (4) Under the first molar.

***Notoryctes*: 1, below the penultimate premolar.**

27. Articulation of the dentary and the squamosal:

(0) Absent; (1) Present, but without condyle/glenoid; (2) Present, but with condyle/glenoid.

***Notoryctes*: 2, present, but with condyle/glenoid.**

28. Shape and relative size of the dentary articulation:

(0) Condyle small or absent; (1) Condyle massive, bulbous, and transversely broad in its dorsal aspect; (2) Condyle mediolaterally narrow and vertically deep, forming a broad arc in lateral outline, either ovoid or triangular in posterior view.

***Notoryctes*: 1, condyle massive.**

29. Orientation of the dentary peduncle (condylar process) and condyle:

(0) Dentary peduncle more posteriorly directed; (1) Dentary condyle continuous with the semicircular posterior margin of the dentary; the condyle is facing up due to the upturning of the posterior-most part of the dentary; (2) Dentary articulation extending vertically for the entire depth of the posterior mandibular ramus; it is confluent with the ramus and without a peduncle; the dentary articulation is posteriorly directed; (3) More vertically directed dentary peduncle.

***Notoryctes*: 3, More vertically directed dentary peduncle.**

30. Ventral (inferior) border of the dentary peduncle:

PeerJ PrePrints

PeerJ PrePrints

(0) Posteriorly tapering; (1) Columnar and with a lateral ridge; (2) Ventrally flaring; (3) Robust and short; (4) Ventral part of the peduncle and condyle continuous with the ventral border of the mandible.

***Necrolestes*: 1, Columnar and with a lateral ridge**.

***Notoryctes*: 1, Columnar and with a lateral ridge.**

31. Gracile and elongate dentary peduncle:

(0) Absent; (1) Present.

***Notoryctes*: 1, present.**

32. Position of the dentary condyle relative to the level of the postcanine alveoli:

(0) Below or about the same level; (1) Above.

***Notoryctes*: 1, above.**

33. Tilting of the coronoid process of the dentary (measured as the angle between the anterior border of the coronoid process and the horizontal alveolar line of all molars):

(0) Coronoid process strongly reclined and the coronoid angle obtuse (≥150º); (1) Coronoid process less reclined (135º-145º); (2) Coronoid process less than vertical (110º-125º); (3) Coronoid process near vertical (95º to 105º).

***Necrolestes*: 3, Coronoid process near vertical (95º to 105º).**

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

***Notoryctes*: 3, Coronoid process near vertical (95º to 105º).**

34. Gracile base of the coronoid process:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

35. Height of the coronoid process of the dentary:

(0) Not reduced; (1) reduced.

***Notoryctes*: 0, not reduced.**

36. Alignment of the ultimate molar (or posteriormost postcanine) to the anterior margin of the dentary coronoid process (and near the coronoid scar if present):

(0) Ultimate molar medial to the coronoid process; (1) Ultimate molar aligned with the coronoid process.

***Notoryctes*: 0, Ultimate molar medial to the coronoid process.**

37. Direction of lower jaw movement during occlusion (as inferred from teeth):

(0) Dorsal movement; (1) Dorsomedial movement with a significant medial component; (2) Dorsoposterior movement.

PeerJ PrePrints

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)

PeerJ PrePrints

***Notoryctes*: 1, dorsomedial movement.**

38. Dentary symphysis:

(0) Fused; (1) Unfused.

***Notoryctes*: 1, unfused.**

39. Rostral mandibular spout:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

PREMOLARS

40. Ultimate upper premolar - metastylar lobe:

(0) Reduced or absent; (1) Enlarged and wing-like.

***Notoryctes*: 0, reduced.**

41. Ultimate upper premolar - metacone or metaconal swelling:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

42. Ultimate upper premolar - protocone or protoconal swelling:

(0) Little or no lingual swelling; (1) Present.

***Notoryctes*: 0, no lingual swelling.**

43. Penultimate upper premolar - protocone or protoconal swelling:

(0) Little or no lingual swelling; (1) Protoconal swelling; (2) Distinctive and functional protocone.

***Notoryctes*: ?, unknown.**

44. Position of the tallest posterior upper premolar within the premolar series:

(0) No premolar standing out; (1) In ultimate premolar position; (2) In penultimate premolar position.

***Notoryctes*: 0, no premolar standing out.**

45. Diastema posterior to the first upper premolar (applicable to taxa with premolar-molar differentiation):

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

46. Ultimate lower premolar - symmetry of the main cusp a (= protoconid):

(0) Asymmetrical (anterior edge of cusp a is more convex in outline than the posterior edge); (1) Symmetrical (anterior and posterior cutting edges are equal or subequal in length; neither edge is more convex or concave than the other in lateral profile).

***Notoryctes*: ?.**

47. Ultimate lower premolar - anterior cusp b (= paraconid):

(0) Absent or indistinctive; (1) Present and distinctive; (2) Enlarged.

***Notoryctes*: 1, present and distinctive.**

48. Ultimate lower premolar - arrangement of principal cusp a, cusp b (if present), and cusp c (assuming the cusp to be c if there is only one cusp behind the main cusp a):

(0) Aligned in a single straight line or at a slight angle; (1) Distinctive triangulation; (2) Premolar multicuspate in longitudinal row(s).

***Notoryctes*: ?.**

49. Ultimate lower premolar - posterior (distal) cingulid or cingular cuspule (in addition to cusp c or the metaconid if the latter cusp is present on a triangulated trigonid).

PeerJ PrePrints

(0) Absent or indistinctive; (1) Present; (2) Present, in addition to cusp c or the c swelling; (3) Presence of the continuous posterior (distal) cingulid at the base of the crown.

***Notoryctes*: ?.**

50. Ultimate lower premolar - outline:

(0) Laterally compressed (or slightly angled); (1) Transversely wide (by trigonid); (2) Transversely wide (by talonid).

***Notoryctes*: 1, ultimate lower premolar transversely wide by trigonid.**

51. Ultimate lower premolar - labial cingulid:

(0) Absent or vestigial; (1) Present (at least along the length of more than half of the crown).

***Notoryctes*: 0, absent.**

52. Ultimate lower premolar - lingual cingulid:

(0) Absent or vestigial; (1) Present.

***Notoryctes*: 0, absent.**

53. Ultimate lower premolar - relative height of primary cusp a to cusp c (measured as the height ratio of a and c from the bottom of the valley between the two adjacent cusps):

PeerJ PrePrints

(0) Indistinctive; (1) Posterior cusp c distinctive but less than 30% of the primary cusp a; (2) Posterior cusp c and primary cusp a equal or subequal in height (c is 40%-100% of a).

***Notoryctes*: ?.**

54. Penultimate lower premolar - paraconid (=cusp b):

(0) Absent; (1) Present but not distinctive; (2) Distinctive and slightly enlarged.

***Notoryctes*: ?.**

55. Penultimate lower premolar - arrangement of principal cusp a, cusp b (if present), and cusp c (we assume the cusp to be c if there is only one cusp behind the main cusp a):

(0) Cusps in straight alignment (for a tooth with a single cusp, the anterior and posterior

crests from the main cusp are in alignment); (1) Cusps in reversed triangulation; (2) With multicusps in longitudinal row(s).

***Notoryctes*: 0, alignment.**

56. Elongation of posterior premolars:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

PeerJ PrePrints

PeerJ PrePrints

MOLAR MORPHOLOGY

57. Alignment of the main cusps of the anterior lower molar(s):

(0) Single longitudinal row; (1) Reversed triangle–acute (≤90o); (2) Multiple longitudinal multicuspate rows.

***Notoryctes*: 1, reversed triangle-acute.**

58. Triangulation of cusps in the posterior molars:

(0) Absent; (1) Multi-row and multi-cuspate; (2) Posterior molars slightly triangulated; (3) Posterior molars fully triangulated.

***Notoryctes*: 3, posterior molars fully triangulated.**

59. B1 cusp on the upper molar (applicable to molars with triangulation):

(0) Absent; (1) Present:

***Notoryctes*: 0, absent.**

60. Postvallum/prevallid shearing (angle of the main trigonid shear facets, based on the second lower molar):

(0) Absent; (1) Present, weakly developed, slightly oblique; (2) Present, strongly developed and more transverse; (3) Present, strongly developed, short and slightly oblique.

***Notoryctes*: 1, present, weakly developed.**

61. Rank of postvallum shear (on the upper second molar; applicable to molars with reversed triangulation of cusps):

(0) Present but only by the first rank: postmetacrista; (1) Present, with the addition of a second rank (postprotocrista below postmetacrista) but the second rank does not reach labially below the base of the metacone; (2) Metacingulum/metaconule present, in addition to postprotocrista, but the metacingulum crest does not extend beyond the base of the metacone; (3) Metacingulum extended beyond metacone; (4) Metacingulum extended to the metastylar lobe; (5) Second rank postvallum shear forming a broad shelf.

***Notoryctes*: 1, Present.**

62. Postcingulum:

(0) Absent or weak; (1) Present; (2) Present and reaching past the metaconule; (3) Formed by the hypoconal shelf raised to near the level of the protocone.

***Notoryctes*: 0, absent.**

63. Precise opposition of the upper and lower molars:

(0) Absent; (1) Present (either one-to-one, or occluding at the opposite embrasure or talonid); (2) Present (one lower molar contacts sequentially more than one upper molar).

PeerJ PrePrints

***Notoryctes*: 1, present.**

64. Relationships between the cusps of the opposing upper and lower molars:

(0) Absent; (1) Present, lower primary cusp a occludes in the groove between upper cusps A, B; (2) Present, lower main cusp a occludes in front of the upper cusp B and into the embrasure between the opposite upper tooth and the preceding upper tooth; (3) Present, parts of the talonid occluding with the lingual face (or any part) of the upper molar; (4) Lower multicuspate rows alternately occluding between the upper multicuspate rows; (5) Columnar tooth without cusps and with beveled wear across the entire crown contact surface.

***Notoryctes*: ?.**

65. Protoconid (cusp a) and metaconid (cusp c) height ratio (on the lower second molar):

(0) Protoconid distinctively higher; (1) Protoconid and metaconid nearly equal in height.

***Notoryctes*: 1, nearly equal in height.**

66. Relative height and size of the base of the paraconid (cusp b) and metaconid (cusp c)(on the lower second molar):

(0) Paraconid distinctively higher than the metaconid; (1) Paraconid and metaconid nearly equal in height; (2) Paraconid lower than metaconid; (3) Paraconid reduced or absent.

***Notoryctes*: 1, nearly equal in height.**

PeerJ PrePrints

67. Elevation of the cingulid base of the paraconid (cusp b) relative to the cingulid base of the metaconid (cusp c) on the lower molars:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

68. Cristid obliqua, presence vs. absence and orientation (applicable only to the molar with at least a hypoconid on the talonid or a distal cingulid cuspule):

(0) Absent; (1) Present, contact closest to the middle posterior of the metaconid; (2) Present, contact closest to the lowest point of the protocristid; (3) Present, contact closest to the middle posterior of the protoconid.

***Notoryctes*: 0, absent.**

69. Lower molar - medial and longitudinal crest (=‘pre-entocristid’ or ‘pre-hypoconulid’) on the talonid heel (only applicable to taxa with talonid or at least a cusp d):

(0) Talonid (or cusp d) has no medial and longitudinal crest; (1) Medial-most cristid (‘pre-entoconid cristid’) of the talonid in alignment with the metaconid or with the postmetacristid if the latter is present (the postmetacristid is defined as the posterior crest of metaconid that is parallel to the lingual border of the crown), but widely separated from the latter; (2) Medial-most cristid of the talonid (‘pre-hypoconulid’ cristid, based on cusp designation) is hypertrophied and in alignment with the postmetacristid and abuts the latter by a V-notch; (3) ‘Pre-entocristid’ crest

PeerJ PrePrints

is offset from the metaconid (and postmetacristid if present), and the 'pre-entocristid' extending anterolingually past the base of the metaconid.

***Necrolestes*: 0, talonid has no medial and longitudinal crest.**

***Notoryctes*: 0, talonid has no medial and longitudinal crest.**

70. Posterior lingual cingulid of the lower molars:

(0) Absent or weak; (1) Distinctive; (2) Strongly developed, crenulated with distinctive cuspules (such as the kuhneocone).

***Notoryctes*: 0, absent.**

71. Anterior internal (mesio-lingual) cingular cuspule (e) on the lower molars:

(0) Present as an anterior cuspule but not at the cingulid level; (1) Present, at the cingulid level; (2) Present, positioned above the cingulid level; (3) hypertrophied cusp e = pseudo-hypoconulid; (4) Absent.

***Notoryctes*: 4, absent.**

72. Anterior and labial (mesio-buccal) cingular cuspule (f):

(0) Absent; (1) Present; (2) Hypertrophied to form pseudo-hypoconid.

***Notoryctes*: 0, absent.**

PeerJ PrePrints

PeerJ PrePrints

73. Mesial cingulid features above the gum:

(0) Absent; (1) Weak and discontinuous, with individualized cuspules below the trigonid (as individual cuspule e, f, or both, but e and f are not connected); (2) Present, in a continuous shelf below the trigonid (with no relations to the protoconid and paraconid), without occlusal function; (3) Present, with occlusal contact to the upper molar.

***Notoryctes*: 0, absent.**

74. Cingulid shelf wrapping around the anterolingual corner of the molar to extend to the lingual side of the trigonid below the paraconid:

(0) Absent; (1) Present, without occlusal function to the upper molars; (2) Present, with occlusal function to the upper molars.

***Notoryctes*: 0, absent.**

75. Postcingulid (distal transverse cingulid above the gum level) on the lower molars:

(0) Absent; (1) Present, horizontal above the gum level.

***Notoryctes*: 0, absent.**

76. Interlocking mechanism between two adjacent lower molars:

PeerJ PrePrints

(0) Absent; (1) Present, posterior cingular cuspule d (or the base of the hypoconulid) of the preceding molar fits in between cingular cuspules e and f of the succeeding molar; (2) Present, posterior cingular cuspule d fits between cingular cuspule e and cusp b of the succeeding molar; (3) Present, posterior cingular cuspule d of the preceding molar fits into an embayment or vertical groove of the anterior aspect of cusp b of the succeeding molar (without any involvement of distinctive cingular cuspules in interlocking). (4) Anterior corner of succeeding lower molar overlapping posterior corner of preceding lower molar.

***Notoryctes*: 0, absent.**

77. Size ratio of the last three lower molars:

(0) Ultimate molar is smaller than the penultimate molar ($m1 \geq m2 \geq m3$; or $m2 \geq m3 \geq m4$; or $m3 \geq m4 \geq m5$; or $m4 \geq m5 \geq m6$); (1) Penultimate molar is the largest of the molars ($m1 \leq m2 \leq m3 \geq m4$; or $m1 \leq m2 > m3$); (2) Ultimate molar is larger than the penultimate molar ($m1 \leq m2 \leq m3$); (3) Equal size.

***Notoryctes*: 0, ultimate molar is smaller than the penultimate molar.**

78. Paraconid position relative to the other cusps of the trigonid on the lower molars (based on the lower second molar):

(0) Paraconid in anterolingual position; (1) Paraconid lingually positioned (within lingual 1/4 of the trigonid width); (2) Paraconid lingually positioned and appressed to the metaconid; (3) Paraconid reduced in the selenodont/lophodont patterns.

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014
PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)

***Notoryctes*: 0, anterolingual position.**

79. Orientation of the paracristid (or the crest between cusps a and b) relative to the longitudinal axis of the molar:

(0) Longitudinal orientation; (1) Oblique; (2) Nearly transverse.

***Notoryctes*: 2, nearly transverse.**

80. Angle of the paracristid (b-a crest) and the protocristid (a-c crest) on the lower molar:

(0) > 90º; (1) 90º ~ 50º; (2) < 35º.

***Notoryctes*: 1, 90º ~ 50º.**

81. Mesiolingual vertical crest of the paraconid on the lower molars:

(0) Rounded; (1) Forming a keel.

***Notoryctes*: 0, rounded.**

82. Anteroposterior shortening at the base of the trigonid relative to the talonid:

(0) Trigonid long (extending over 3/4 of the tooth length); (1) Swelling on the side walls of the trigonid (taxa assigned to this character state have a trigonid length ratio 45%~50%; but their morphology is different from all other states in that their side walls are convex); (2) No

PeerJ PrePrints

shortening (trigonid 50-65% of tooth length); (3) Some shortening (the base of trigonid < 50% of tooth length); (4) Anteroposterior compression of trigonid (trigonid 40~45% of the tooth length).

***Notoryctes*: 0, trigonid long.**

83. Molar (the lower second molar measured where possible) trigonid/talonid heel width ratio:

(0) Narrow (talonid ≤40% of trigonid); (1) Wide (talonid is 40-70% of the trigonid in width); (2) Talonid is equal or wider than trigonid.

***Necrolestes*: 0, narrow.**

***Notoryctes*: 0, narrow.**

84. Lower molar hypoflexid (concavity anterolabial to the hypconid or cusp d):

(0) Absent or shallow (all "triconodont-like" teeth are coded as "0" here as long as they have cuspule d); (1) Deep (40~50% of talonid width); (2) Very Deep (>65%); (3) Pseudo-hypoflexid (40% to 65% of the pseudo-talonid width).

***Notoryctes*: 0, absent.**

85. Morphology of the talonid (or the posterior heel) of the molar:

(0) Absent; (1) Present, as an incipient heel, a cingulid, or cingular cuspule (d); (2) Present, as a transverse ‘V-shaped’ basin with two functional cusps; (3) Present, as an obtuse ‘V-shaped’

PeerJ PrePrints

triangle; (4) Present, as a functional basin, rimmed with 3 functional cusps (if the entoconid is vestigial, there is a functional crest to define the medial rim of the basin).

***Notoryctes*: 1, incipient heel.**

86. Hypoconid (we designate the distal cingulid cuspule d as the homolog to the hypoconid in the teeth with linear alignment of the main cusps; we assume the cusp to be the hypoconid if there is only a single cusp on the talonid in the teeth with reversed triangulation):

(0) Present, but not elevated above the cingulid level; (1) Present [as distal cusp d, sensu Crompton (*122*)], elevated above the cingulid level, labially positioned (or tilted in the lingual direction); (2) Present, elevated above the cingulid level, labially positioned; (3) Absent.

***Notoryctes*: 0, absent.**

87. Hypoconulid:

(0) Absent; (1) Present, and median (near the mid-point of the transverse talonid width); (2) Present, and placed within the lingual 1/3 of the talonid basin; (3) Incorporated into the crest of lophodont or selenodont conditions.

***Notoryctes*: 0, absent.**

88. Anterior lower molar- hypoconulid - anteroposterior orientation: procumbent vs. reclined:

PeerJ PrePrints

(0) Cusp tip reclined and the posterior wall of the hypoconulid is slanted and overhanging the root; (1) Cusp tip procumbent and the posterior wall of the cusp is vertical; (2) Cusp tip procumbent and the posterior wall is gibbous.

***Notoryctes*: ?, not applicable.**

89. Hypoconulid labial postcingulid (shelf) on the lower molars:

(0) Absent; (1) Present as a crest descending mesiolabially from the apex of the hypoconulid to the base of the hypoconid.

***Notoryctes*: 0, absent.**

90. Last lower molar - hypoconulid - orientation and relative size:

(0) Short and erect; (1) Tall (higher than hypoconid) and recurved.

***Notoryctes*: ?, not applicable.**

91. Entoconid:

(0) Absent; (1) Present, about equal distance to the hypoconulid as to the hypoconid; (2) Present, with slight approximation to the hypoconulid (distance between the hypoconulid and entoconid noticeably shorter than between the hypoconulid and hypoconid); (3) Present, and twinned with the hypoconulid.

***Notoryctes*: 0, absent.**

PeerJ PrePrints

92. Height ratio of the medial side of the crown vs. the most lingual cusp on the talonid to the base of the labial crown:

(0) Entoconid absent on the talonid heel; (1) Entoconid lower than the hypoconid; (2) Entoconid near the height of the hypoconid; (3) Entoconid near the height of the hypoconid and linked to the hypoconid by a transverse crest.

***Notoryctes*: 0, absent.**

93. Alignment of the paraconid, metaconid, and entoconid on the lower molars (applicable only to taxa with triangulation of the trigonid cusps and the entoconid present on the talonid):

(0) Cusps not aligned; (1) Cusps aligned.

***Notoryctes*: ?, not applicable.**

94. The length vs. width ratio of the functional talonid basin of the lower molars:

(0) Longer than wide (or narrows posteriorly); (1) Length equals width; (2) Wider than long.

***Notoryctes*: ?, not applicable.**

95. Elevation of the talonid relative to the trigonid: (0) Hypoconid/protoconid height ratio less than 20% (hypoconid or cusp d is on the cingulid); (1) Hypoconid/protoconid height ratio between 25% and 35% (talonid cusp elevated above the cingulid level); (2)

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.735v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

Hypoconid/protoconid height ratio between 40% and 60%; (3) Hypoconid/protoconid height ratio between >60% and 80%; (4) Equal height.

***Notoryctes*: ?, not applicable.**

96. Size of the upper molar labial stylar shelf on the penultimate molar:

(0) Absent; (1) Present and narrow; (2) Present and broad.

***Notoryctes*: 2, present and broad.**

97. Presence vs. absence of the ectoflexus on the upper second molar (or postcanines in the middle portion of the postcanine row):

(0) Absent or weakly developed; (1) Present.

***Notoryctes*: 0, absent.**

98. Ectoflexus gradient along the molar series:

(0) Present on penultimate molar, but weakly developed or absent on the anterior molars; (1) Present on the penultimate and preceding molars.

***Notoryctes*: ?, not applicable.**

PeerJ PrePrints

PeerJ PrePrints

99. Morphological features on the labial cingulum or stylar shelf of the upper molars (excluding the parastyle and metastyle):

(0) Indistinctive; (1) Distinctive cingulum, without cuspules; (2) Individualized or even hypertrophied cuspules; (3) W-pattern on stylar shelf; (4) Cingulum crenulated with distinctive and even-sized multiple cuspules.

***Notoryctes*: 0, indistinctive.**

100. Upper molar protocone:

(0) Functional cusp and lingual swelling absent; (1) Functional cusp absent, but the lingual side is more swollen than the labial side at the cingular level; (2) Functional cusp present.

***Notoryctes*: ?.**

101. Degree of labial shift of the protocone (distance from the protocone apex to the lingual border vs. the total tooth width, in %):

(0) Protocone present but no labial shift (10%-20%); (1) Moderate labial shift (25%- 30%); (2) Substantial labial shift (≥ 40%).

***Notoryctes*: ?, not applicable.**

102. Morphology of the protocone:

(0) Protoconal region present but no distinct protocone; (1) Protocone present, its apical portion anteroposteriorly compressed; (2) Apical portion slightly expanded; (3) Apical portion expanded; (4) Apical portion forming an obtuse triangle with the protoconal cristae.

***Notoryctes*: ?, not applicable.**

103. Height of the protocone relative to the paracone and metacone (whichever is highest of the latter two):

(0) Protocone markedly lower (less than 70%); (1) Protocone of intermediate height (70%~80%); (2) Protocone near the height of paracone and metacone (within 80%).

***Notoryctes*: ?, not applicable.**

104. Height and size of the paracone (cusp B) and metacone (cusp C) (based on the upper second molar if available):

(0) Paracone noticeably higher and larger at the base than metacone; (1) Paracone slightly larger than metacone; (2) Paracone and metacone of equal size or paracone lower than metacone, (3) metacone absent.

***Notoryctes*: 3, metacone absent.**

105. Metacone position relative to paracone:

PeerJ PrePrints

(0) Metacone labial to paracone; (1) Metacone about the same level as paracone; (2) Metacone lingual to paracone.

***Notoryctes*: ?, not applicable.**

106. Base of the paracone and metacone (based on the upper second molar if available, applicable only to triangulated molars):

(0) Merged; (1) Separated.

***Notoryctes*: ?, not applicable.**

107. Centrocrista between the paracone and the metacone of the upper molars (applicable only to taxa with well-developed metacone and distinctive wear facets 3 and 4):

(0) Straight; (1) V-shaped, with labially directed postparacrista and premetacrista.

***Notoryctes*: ?, not applicable.**

108. Anteroposterior width of the conular region (with or without conules) on the upper molars:

(0) Narrow (anteroposterior distance medial to the paracone and metacone less than 0.30 of total tooth length); (1) Moderate development (distance between position of conules = 0.31—0.50 of total tooth length); (2) Wide (distance between conules greater than 0.51 of total tooth length); (3) Expanded.

PeerJ PrePrints

PeerJ PrePrints

***Notoryctes*: ?, not applicable.**

109. Presence of the paraconule and metaconule on the upper molars:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

110. Relative position of the paraconule and metaconule on the upper first and second molars:

(0) Paraconule and metaconule closer to the protocone; (1) Both positioned near the midpoint of the protocone-metacone; (2) Paraconule and metaconule labial to the midpoint.

***Notoryctes*: ?, not applicable.**

111. Internal conular cristae (conular wing):

(0) Cristae indistinctive; (1) Cristae distinctive and wing-like.

***Notoryctes*: ?, not applicable.**

112. Parastylar groove (on upper second molar):

(0) Weak or absent; (1) Moderately to well developed.

***Notoryctes*: ?.**

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014
PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)

PeerJ PrePrints

113. Stylar cuspule “A”, the parastyle, on the upper molars (of the Bensley-Simpson system):

(0) Present (at least a swelling is present); (1) Absent.

***Notoryctes*: ?.**

114. Preparastyle on the upper first molar:

(0) Absent; (1) Present.

***Notoryctes*: ?.**

115. Stylar cuspule “B” (opposite the paracone) (based on the upper second molar if available):

(0) Vestigial to absent; (1) Small but distinctive; (2) Subequal to the parastyle; (3) Large (subequal to parastyle), with an extra "B-1" cuspule in addition to "B".

***Notoryctes*: ?.**

116. Stylar cuspule "C" (near the ectoflexus) on the penultimate upper molar:

(0) Absent; (1) Present.

***Notoryctes*: ?.**

PeerJ PrePrints

117. Stylar cuspule "D" (opposite the metacone) on the penultimate upper molar:

(0) Absent; (1) Present.

***Notoryctes*: ?.**

118. Absence vs. presence and size of the stylar cuspule “E”:

(0) Absent or poorly developed; (1) Present, less developed than or subequal to stylar cuspule “D”; (2) Present and better developed than cuspule “D”.

***Notoryctes*: ?.**

119. Position of the stylar cuspule “E” relative to cusp “D” or “D-position”:

(0) “E” more lingual to “D” or “D-position”; (1) “E” distal to or at same level as “D” or “D-position”.

***Notoryctes*: ?, not applicable.**

120. Upper molar interlock:

(0) Absent; (1) Tongue-in-groove interlock; (2) Parastylar lobe of a succeeding molar lumbricated with the metastylar region of a preceding molar.

Notoryctes: 0, absent.

121. Size and labial extent of the metastylar lobe and parastylar lobe (based on the upper first molar if available; if not, then based on upper second):

(0) Metastylar lobe smaller than the parastylar lobe; (1) Metastylar lobe of similar size and labial extent to the parastylar lobe; (2) Metastylar lobe much larger than the parastylar lobe; (3) Metastylar lobe absent.

***Notoryctes*: 1, similar size.**

122. Salient postmetacrista on the upper molars (applicable to taxa with reversed triangulation):

(0) Absent or weakly developed; (1) Well-developed but no longer than the metacone-protocone distance; (2) Hypertrophied and longer than the metacone-protocone distance.

***Notoryctes*: 0, absent.**

123. Selenodont molar pattern:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

124. Outline of the lower first molar crown (in crown view):

(0) Laterally compressed; (1) Oblong with slight labial bulge; (2) Triangular or tear-drop shaped; (3) Rectangular (or rhomboidal); (4) circular.

PeerJ PrePrints

***Notoryctes*: 2, triangular.**

125. Aspect ratio and outline of the upper first molar:

(0) Laterally compressed; (1) Longer than transversely wide (oval-shaped or spindle shaped); (2) Transversely wider than long (triangular outline); (3) Rectangular or nearly so; (4) circular.

***Notoryctes*: 2, transversely wider than long.**

126. Carnassial shearing blades on last upper premolar and first lower molar:

(0) Absent; (1) Present.

***Notoryctes*: 0, Absent.**

MOLAR WEAR PATTERN

127. Functional development of occlusal facets on individual molar cusps:

(0) Absent; (1) Absent at eruption but developed later by crown wear; (2) Wear facets match upon tooth eruption (inferred from the flat contact surface upon eruption).

***Notoryctes*: 2, wear facets match upon tooth eruption.**

128. Topographic relationships of wear facets to the main cusps:

PeerJ PrePrints

(0) Wear pattern across the entire crown; (1) Lower cusps a, c support two different wear facets (facets 1 and 4) that contact the upper primary cusp A; (2) Lower cusps a, c support a single wear facet (facet 4) that contacts the upper primary cusp B (this facet extends onto cusp A as wear continues, but 1 and 4 do not develop simultaneous in these taxa); (3) Multicuspate series, each cusp may support 2 wear facets.

***Notoryctes*: 2.**

129. Development and orientation of prevallum/postvallid shearing (based on either upper or the lower molar structures):

(0) Absent; (1) Present and obtuse; (2) Present, hypertrophied and transverse.

***Necrolestes*: 1, present.**

***Notoryctes*: 1, present.**

130. Wear facet 1 (a single facet supported by cusp a and cusp c) and facet 2 (a single facet supported by cusp a and cusp b):

(0) Absent; (1) Present.

***Notoryctes*: 1, present.**

131. Upper molars - development of facet 1 and the preprotocrista:

PeerJ PrePrints

(0) Facet 1 (prevallum crest) short, not extending to the stylocone area; (1) Facet 1 extending into the hook-like area near the stylocone; (2) Preprotocrista long, extending labially beyond the paracone.

***Notoryctes*: 1.**

132. Differentiation of wear facet 3 and facet 4 (applicable to taxa with a distal cusp d or "hypoconulid"):

(0) Absent; (1) Present; (2) Facets 3 and 4 hypertrophied on the flanks of the strongly Vshaped talonid.

***Notoryctes*: 0, absent.**

133. Orientation of facet 4 (on the posterior aspect of the hypoconid):

(0) Present and oblique to the long axis of the tooth; (1) Present and forming a more transverse angle to the long axis of the tooth.

***Notoryctes*: ?, not applicable.**

134. Morphology of the posterolateral aspect of the talonid:

(0) Gently rounded; (1) Angular.

***Notoryctes*: ?, not applicable.**

PeerJ PrePrints

PeerJ PrePrints

135. Wear pattern within the talonid basin:

(0) Absent; (1) Present; (2) Present apically on the crests of the talonid; (3) Apical wear on crest and lophodont.

***Notoryctes*: 0, absent.**

136. Development of the distal metacristid:

(0) Present; (1) Absent.

***Notoryctes*: 1, absent.**

137. Differentiation of wear facets 5 and 6 on the labial face of the entoconid:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

138. Surficial features on the occluding surfaces on the talonid :

(0) Smooth surface on the talonid heel (or on cusp d); (1) Multiple ridges within the talonid basin; (2) Talonid present, but wear occurs apically on the crests of cristid obliqua and hypoconid cristid (V-shaped talonid crests).

***Notoryctes*: ?, not applicable.**

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

139. Molar wear facets pseudo-3 and pseudo-4:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

140. Molar wear facets pseudo-5 and pseudo-6:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

141. Pseudo cusp e and f hypertrophied:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

OTHER DENTAL FEATURES

142. Number of lower incisors:

(0) Five or more; (1) Four; (2) Three; (3) Two; (4) One; (5) No incisors.

***Notoryctes*: 3, two.**

143. Number of upper incisors:

PeerJ PrePrints

(0) Five; (1) Four; (2) Three; (3) Two or one; (4) No incisors.

***Notoryctes*: 2, three.**

144. Lower anterior-most incisor enamel:

(0) Covers the whole incisor; (1) Restricted anteriorly.

***Notoryctes*: 0, covers the whole incisor.**

145. Lower anterior-most incisor with open root:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

146. Upper anterior-most incisor enamel:

(0) Covers the whole incisor; (1) Restricted anteriorly.

***Notoryctes*: 0, covers the whole incisor.**

147. Upper anterior-most incisor with open root:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

PeerJ PrePrints

PeerJ PrePrints

148. Upper canine - presence vs. absence, and size:

(0) Present and enlarged; (1) Present and small; (2) Absent.

***Notoryctes*: 1, present and small.**

149. Number of upper canine roots:

(0) One; (1) Two.

***Notoryctes*: 0, one.**

150. Lower canine - presence vs. absence and size:

(0) Present and enlarged; (1) Present and small; (2) Absent.

***Notoryctes*: 2, absent.**

151. Number of lower canine roots:

(0) One; (1) Two.

***Notoryctes*: 0, one.**

152. Number of upper premolars:

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

(0) Five or more; (1) Four; (2) Three; (3) Two or less.

***Notoryctes*: ?, unknown.**

153. Number of lower premolars:

(0) Five or more; (1) Four; (2) Three; (3) Two or less.

***Notoryctes*: 3, two.**

154. Number of lower molars or molariform postcanines:

(0) Six or more; (1) Five; (2) Four; (3) Three; (4) Two or less.

***Notoryctes*: ?.**

155. Number of upper molars or molariform postcanines:

(0) Six or more; (1) Five; (2) Four; (3) Three; (4) Two or less.

***Notoryctes*: ?.**

156. Total number of upper postcanine loci:

(0) More than 8; (1) Eight; (2) Seven, (3) Six; (4) Five or less.

***Notoryctes*: 3, six.**

PeerJ PrePrints

PeerJ PrePrints

157. Number of lower postcanine loci:

(0) Eight or more; (1) Seven; (2) Six; (3) Five or less.

***Notoryctes*: 3, five.**

158. Procumbency and diastema of first (functional) upper premolar or postcanine in relation to the upper canine:

(0) Not procumbent and without diastema; (1) Procumbent and with diastema.

***Notoryctes*: 0, not procumbent.**

159. Diastema separating the lower first and second premolars (defined as the first and second functioning premolar or premolariform postcanine):

(0) Absent (gap less than one tooth root for whichever is smaller of the adjacent teeth); (1) Present, subequal to one tooth-root diameter or more; (2) Present, equal to or more than one-tooth length.

***Notoryctes*: 1, present.**

160. Ultimate premolar bladed or crenulated:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

161. Upper anterior-most incisor:

(0) Subequal to the remaining incisors, no diastema with the second incisor; (1) Anteriorly projecting, separated from the second incisor by a diastema; (2) Absent.

***Notoryctes*: 0, subequal.**

162. Ultimate and penultimate upper incisors are relatively compressed laterally:

(0) Absent; (1) Present, and spoon-shaped to rhomboid-shaped in lateral view; (2) Present, and spatulate in lateral view; (3) Ultimate and/or penultimate upper incisors bicuspate or tricuspate.

***Notoryctes*: 1, present, spoon-shaped.**

163. Staggered lower incisor:

(0) Absent; (1) Present.

***Necrolestes*: 1, present.**

***Notoryctes*: 1, present.**

164. Replacement pattern of incisors and canines:

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

(0) More than one replacement; (1) One replacement; (2) No replacement.

***Notoryctes*: ?, unknown.**

165. Replacement of at least some posterior functional molariform postcanines:

(0) Present; (1) Absent.

Notoryctes: ?, absent.

166. Procumbency and enlargement of the lower anterior-most incisor:

(0) Absent; (1) Present (at least 50% longer than the adjacent incisor).

***Peligrotherium*: 0, absent**.

***Cronopio*: 1, present.**

***Necrolestes*: 1, present.**

***Notoryctes*: 0, absent.**

167. Enlarged diastema in the lower incisor-canine region (better developed in older individuals):

(0) Absent; (1) Present and behind the canine; (2) Present and behind the posterior incisor.

***Notoryctes*: 0, absent.**

PeerJ PrePrints

168. U-shaped ridge in the lower multi-rowed molars:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

169. Single-aligned and the labial row of multi-cusp or multi-rowed lower molar – Cusp ratio:

(0) Second mesial cusp (b2) highest; (1) Mesial cusp highest.

***Notoryctes*: ?, not applicable.**

170. Multi-rowed upper premolar/molar - cusp ratio in the labial row of multi-cusp row:

(0) Distal cusp highest, with a gradient of anteriorly decreasing height; (1) Cusps in same row of equal height.

***Notoryctes*: 1, cusps in same row of equal height.**

171. Alignment of multi-cuspate upper first and second molars:

(0) Second lingually offset from the first so that the lower second molar lingual row occludes with the lingual side of the upper second labial row; (1) Lower second molar labial row occludes with the labial side of the upper second labial row.

***Notoryctes*: 1.**

PeerJ PrePrints

172. Enamel microstructure:

(0) Synapsida columnar enamel (prismless); (1) ‘Transitional’ (sheath indistinct, ‘prismatic’ crystallites inclined at less than 45o to the ‘interprismatic’ matrix); (2) Full prismatic enamel; (3) Enamel absent.

***Notoryctes*: 1, transitional.**

173. Open root end of the postcanines

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

VERTEBRAE AND RIBS

174. Fusion of the atlas neural arch and intercentrum (modified from Rougier et al., 2012):

(0) Unfused; (1) Fused.

***Notoryctes*: 1, Fused.**

175. Atlas rib:

(0) Present; (1) Absent.

***Notoryctes*: 1, absent.**

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

176. Fusion of dens to the axis:

(0) Absent; (1) Present.

***Notoryctes*: 1, present.**

177. Axis rib:

(0) Present; (1) Absent.

***Notoryctes*: 1, absent.**

178. Postaxial cervical ribs:

(0) Unfused; (1) Fused.

***Notoryctes*: 1, fused.**

179. Number of thoracic vertebrae:

(0) 13 or less; (1) 15 or more.

***Notoryctes*: 1, fifteen.**

180. Overlapping ventral costal plates:

PeerJ PrePrints

PeerJ PrePrints

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

181. Overlapping lumbar or posterior thoracic ribs:

(0) Present; (1) Absent.

***Notoryctes*: 0, absent.**

182. Anticlinal vertebra:

(0) Absent; (1) Present.

***Notoryctes*: 1, present.**

183. Mobile lumbar ribs:

(0) Present; (1) Absent.

***Notoryctes*: 1, absent.**

184. Orientation of lumbar ribs or transverse processes:

(0) Posterolaterally directed; (1) Laterally or anterolaterally directed.

***Notoryctes*: 1, anterolaterally directed.**

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014
PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)

PeerJ PrePrints

185. Xenarthrous articulation in addition to the pre- and post-zygapophyses of lumbar vertebrae:

(0) Absent; (1) Present.

***Notorycte*s: 0, absent.**

SHOULDER GIRDLE

186. Interclavicle:

(0) Present; (1) Absent.

***Notoryctes*: ?, unknown.**

187. Contact relationships between the interclavicle and the sternal manubrium:

(0) Two elements distinct from each other, posterior end of the interclavicle abuts with the anterior border of manubrium; (1) Two elements distinct from each other, the interclavicle broadly overlaps the ventral side of the manubrium; (2) Complete fusion of the embryonic membranous and endochondral elements resulting in a single and enlarged manubrium.

***Notoryctes*: ?, unknown.**

188. Inverclavicle distal expansion:

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

189. Cranial margin of the interclavicle/manubrium (assuming the interclavicle is fused to the sternal manubrium in living therians):

(0) Emarginated or flat; (1) With a median process.

***Notoryctes*: 1, median process.**

190. Interclavicle to sternal manubrium length ratio

(0) Interclavicle twice the length of manubrium; (1) Interclavicle nearly equal to manubrium in length.

***Notoryctes*: ?, unknown.**

191. Sternoclaviclular joint:

(0) Immobile; (1) Mobile.

Notoryctes: 1, mobile.

192. Sternal manubrial craniolateral process:

(0) Absent; (1) Present.

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

***Notoryctes*: 0, absent.**

193. Acromioclavicular joint:

(0) Extensive articulation; (1) Limited articulation (either pointed acromion, pointed distal end of clavicle, or both).

***Notoryctes*: 1, limited.**

194. Curvature of the clavicle:

(0) Boomerang-shaped; (1) Slightly curved.

***Notoryctes*: 1, slightly curved.**

195. Scapula - supraspinous fossa: degree of development along the length:

(0) Present only in the “acromional region” of the scapula, and on the cranial border of the scapula and positioned anterior to the glenoid; (1) Weakly developed; (2) Fully developed.

***Necrolestes*: 1, weakly developed.**

***Notoryctes*: 2, fully developed.**

196. Proportion of supraspinous vs. infraspinous fossae:

(0) Supraspinous "fossa" on the cranial aspect of the scapula and much narrower than infraspinous fossa; (1) Supraspinous width is 50% to 80% that of infraspinous fossa; (2) Fossae subequal; (3) Supraspinous over 150% that of infraspinous fossa.

***Notoryctes*: 2, fossae subequal.**

197. Scapula - acromion process:

(0) Short stump, level with or behind the glenoid; (1) Hook-like and extending below the glenoid.

***Notoryctes*: 1, extending below the glenoid.**

198. Scapula - a distinctive fossa for the teres major muscle on the lateral aspect of the scapular plate:

(0) Absent; (1) Present.

***Notoryctes*: 1, present.**

199. Procoracoid:

(0) Present; (1) Fused to the sternal apparatus.

***Notoryctes*: 1, fused.**

PeerJ PrePrints

PeerJ PrePrints

200. Procoracoid foramen:

(0) Present; (1) Absent.

***Notoryctes*: 1, absent.**

201. Coracoid:

(0) Large, with posterior process; (1) Small, without posterior process.

***Notoryctes*: 1, small.**

202. Anterior process of the coracoid:

(0) Indistinctive; (1) Distinctive; (2) Distinctive and forming a broad plate.

***Notoryctes*: 0.**

203. Coracoid process bridging over posteriorly toward the vertebral border of scapula:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

204. Size of the anterior-most element ('manubrium') relative to the subsequent sternebrae in the sternal apparatus:

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

(0) Large; (1) Small.

***Notoryctes*: 1, small.**

205. Orientation of the glenoid:

(0) Nearly parallel and facing posterolaterally; (1) Oblique and facing more posteriorly; (2) Perpendicular.

***Necrolestes*: 1, oblique.**

***Notoryctes*: 1, oblique.**

206. Shape and curvature of the glenoid:

(0) Saddle-shaped, oval and elongate; (1) Uniformly concave and more rounded in outline. ***Notoryctes*: 1, uniformly.**

207. Medial surface of the scapula:

(0) Convex; (1) Flat.

***Notoryctes*: 1, flat.**

208. Suprascapular incisure (defined as the prominent emargination on the cranial border of the supraspinus fossa):

PeerJ PrePrints

PeerJ PrePrints

(0) Absent; (1) Present.

***Notoryctes*: 1, present.**

FORELIMB AND MANUS

209. Humeral head:

(0) Subspherical, weakly inflected; (1) Spherical, strongly inflected.

***Necrolestes*: 0, subspherical, weakly inflected** (Asher et al., 2007; Rougier et al., 2012)

***Notoryctes*: 1, spherical.**

210. Intertubercular groove of the humerus:

(0) Shallow and broad; (1) Narrow and deep; (2) wide and deep

***Necrolestes*: 0, Shallow and broad** (Rougier et al., 2012).

***Notoryctes*: 2, wide and deep.**

211. Size of the lesser tubercle of the humerus relative to the greater tubercle:

(0) Wider; (1) Narrower.

***Notoryctes*: 1, narrower.**

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

212. Torsion between the proximal and distal ends of the humerus:

(0) Strong (≥30º); (1) Moderate (30º – 15º); (2) Weak (< 15º).

***Notoryctes*: 0, strong.**

213. Ventral extension of the deltopectoral crest or the position of the deltoid tuberosity:

(0) Short and limited to the proximal part of the humeral shaft; (1) Extending ventrally (distally) at least 1/3 the length of the shaft.

***Notoryctes*: 1, extending distally.**

214. Teres tuberosity on medial side of humerus.

(0) Absent; (1) Present; (2) Hypertrophied.

***Notoryctes*: 0, absent.**

215. Ulnar articulation on the distal humerus:

(0) Bulbous ulnar condyle; (1) Cylindrical trochlea in posterior view with a vestigial ulnar condyle in anterior view; (2) Cylindrical trochlea without an ulnar condyle (cylindrical trochlea extending to the anterior/ventral side).

***Notoryctes*: 1, vestigial ulnar condyle.**

PeerJ PrePrints

216. Radial articulation on the distal humerus:

(0) Distinct and rounded radial condyle in both anterior (ventral) and posterior (dorsal) aspects (that does not form a continuous synovial surface with the ulnar articulation in the ventral/anterior view of the humerus); (1) Rounded radial condyle anteriorly but cylindrical posteriorly; (2) Capitulum (forming a continuous synovial surface with the ulnar trochlea; cylindrical in both anterior and posterior aspects).

***Necrolestes*: 2, capitulum.**

***Notoryctes*: 1.**

217. Entepicondyle (medial epicondyle) and ectepicondyle (lateral epicondyle) of the humerus:

(0) Robust; (1) Weak.

***Necrolestes*: 0, robust**, (Rougier et al., 2012).

***Notoryctes*: 0, robust.**

218. Sigmoidal shelf for the supinator ridge extending proximally from the ectepicondyle:

(0) Absent; (1) Present.

***Dryolestes*: 0, absent**, (Rougier et al., 2012).

***Necrolestes*: 1, present**, (Rougier et al., 2012).

***Notoryctes*: 1, present.**

PeerJ PrePrints

PeerJ PrePrints

219. Coronoid process of semilunar notch of ulna:

(0) Absent; (1) Present and level to olecranon process; (2) Present and higher than olecranon process.

***Notoryctes*: 1, present.**

220. Styloid process of the radius:

(0) Weak; (1) Strong.

***Notoryctes*: 0, weak.**

221. Enlargement of the scaphoid:

(0) Not enlarged (scaphoid ≤150% of the lunate); (1) Enlarged (scaphoid twice the size of the lunate); (2) Enlarged with a distolateral process.

***Notoryctes*: ?, unknown.**

222. Size and shape of the hamate (unciform):

(0) About equal size to the triquetrum, anteroposteriorly compressed; (1) Hypertrophied, much larger than the triquetrum, mediolaterally compressed.

***Notoryctes*: 0, equal size to the triquetrum and anteroposteriorly compressed**, (Szalay, 1994).

223. Trapezium morphology and proportion:

(0) Elongate to cuboidal, larger than or subequal to the trapezoid; (1) Bean-shaped or fusiform, smaller than the trapezoid.

Notoryctes: **1.**

224. Triquetrum-lunate proportion:

(0) Triquetrum nearly twice the size of the lunate; (1) Triquetrum subequal to the lunate.

***Notoryctes*: 1, subequal**, (Szalay, 1994).

PELVIC GIRDLE

225. Anterior process of the ilium:

(0) Short (less than the diameter of the acetabulum); (1) Long, 1-1.5 times the diameter of the acetabulum; (2) Elongate, more than 1.5 times the diameter of the acetabulum.

***Notoryctes*: 2, elongate**, (Warburton, 2003).

226. Posterior process of the ilium:

PeerJ PrePrints

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

(0) Present; (1) Reduced or absent.

***Notoryctes*: 1, reduced.**

227. Acetabular dorsal emargination:

(0) Open (emarginated); (1) Closed (with a complete rim).

***Necrolestes*: 0, open**, (Rougier et al., 2012).

***Notoryctes*: 0, open.**

228. Sutures of the ilium, ischium, and pubis within the acetabulum:

(0) Present; (1) Fused.

***Notoryctes*: 1, Fused.**

229. Ischiatic dorsal margin and tuberosity:

(0) Dorsal margin concave (emarginated) and ischiatic tuberosity present; (1) Dorsal margin concave and ischiatic tuberosity hypertrophied; (2) Dorsal margin straight and ischiatic tuberosity small.

***Notoryctes*: 2, dorsal margin straight and ischiatic tuberosity small.**

230. Posterior spine of the ischium:

PeerJ PrePrints

(0) Short and pointed; (1) expanded with oblique posterior spine; (2) expanded and truncated.

***Notoryctes*: 0, short.**

231. Epipubic bone:

(0) Present; (1) Absent.

***Notoryctes*: 0, present.**

232. Width of epipubis:

(0) Narrow; (1) wide.

***Notoryctes*: 0, narrow.**

233. Fusion of the sacral vertebrae with the proximal caudal vertebrae:

(0) Absent; (1) Present.

***Notoryctes*: 1, present.**

234. Fusion of the ischium with the caudal vertebrae:

(0) Absent; (1) Present.

***Notoryctes*: 1, present.**

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014
PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)

PeerJ PrePrints

235. Preacetabular tubercle on the ilium for M. rectus femoris:

(0) Absent; (1) Present.

***Necrolestes*: 1, present**, (Asher et al., 2007).

***Notoryctes*: 1, present**, (Warburton, 2003).

236. Fully encircled synovial surface inside the acetabulum:

(0) Absent; (1) Present.

***Necrolestes*: 0, absent.**

***Notoryctes*: 0, absent.**

237. Lesser psoas tuberosity or process on the pubis:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent.**

HINDLIMB AND PES

238. Inflected head of the femur set off from the shaft by a neck:

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

(0) Neck absent and head oriented dorsally; (1) Neck present, head spherical and inflected medially.

***Necrolestes*: 1, neck present and head inflected medially**, (Asher et al., 2007. Rougier et al., 2012).

***Notoryctes*: 1, neck present and head inflected medially**, (Warburton, 2003).

239. Fovea for the acetabular ligament on the femoral head:

(0) Absent; (1) Present.

***Necrolestes*: 1, present.**

***Notoryctes*: 1, present**, (Warburton, 2003).

240. Orientation of the greater trochanter:

(0) Directed dorsolaterally; (1) directed dorsally.

***Necrolestes*: 1, directed dorsally**, (Rougier et al., 2012).

***Notoryctes*: 1, directed dorsally**, (Warburton, 2003).

241. Position of the lesser trochanter:

(0) On medial side of the shaft; (1) On the ventromedial or ventral side of the shaft.

***Necrolestes*: 0, medial side of the shaft**, (Rougier et al., 2012).

PeerJ PrePrints

***Notoryctes*: 0, medial side of the shaft.**

242. Size of the lesser trochanter:

(0) Large; (1) Small to absent.

***Necrolestes*: 1, small**, (Rougier et al., 2012).

***Notoryctes*: 1, small**, (Warburton, 2003).

243. The third trochanter of femur:

(0) Absent; (1) Present; (2) Present as a continuous ridge connected to the greater trochanter.

***Necrolestes*: 2, present and connected to the greater trochanter.**

***Notoryctes*: 2, present and connected to the greater trochanter**, (Warburton, 2003).

244. Patellar facet (‘groove’) of the femur:

(0) Absent; (1) Shallow and weakly developed; (2) Well-developed.

***Necrolestes*: 1, weakly developed.**

Notoryctes: 1, weakly developed, (Warburton, 2003).

Comments: Rougier et al. (2012) codified *Necrolestes* as lacking a patellar groove o distal femus (Character 201-0). However, Asher et al., (2007) indicate the presence of a “…slight fossa

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.715v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

that may correspond to a patellar trochlea…”. Following this, *Necrolestes* is here codified in the present work as having a weakly developed patellar groove (state 1).

245. Proximo-lateral tubercle or tuberosity of the tibia:

(0) Large and hook-like; (1) Indistinct.

***Notoryctes*: 1, indistinct.**

246. Distal tibial malleolus:

(0) Weak; (1) Distinctive.

***Notoryctes*: 0, weak.**

247. Fibula contacting the distal end of the femur:

(0) Present; (1) Absent; (2) Fibula fused with the tibia.

***Notoryctes*: 0, present.**

248. Fused distal portions of the tibia and fibula:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent**, (Warburton, 2003).

PeerJ PrePrints

249. Parafibular process of the fibula:

(0) Absent or unfused to the fibular; (1) fused to fibula and enlarged:

***Notoryctes*: 0, absent.**

250. Distal fibular styloid process:

(0) Weak or absent; (1) Distinct.

***Notoryctes*: 0, absent.**

251. Fibula contacting the calcaneus:

(0) Extensive contact; (1) Reduced; (2) Absent.

***Notoryctes*: 2, absent.**

252. Superposition of the astragalus over the calcaneus:

(0) Little or absent; (1) Weakly developed; (2) Present.

***Notoryctes*: 2, present.**

253. Astragalo-navicular articulation:

(0) articulating facet indistinctive; (1) Weakly developed.

***Notoryctes*: 0, indistinctive.**

254. Astragalar neck basal width:

(0) Neck narrower than the head; (1) Neck about same width as the head; (2) Widest point of neck at mid-length; (3) Astragalar neck widest at the base.

***Notoryctes*: 1, Neck about same width as the head.**

255. Astragalonavicular contact aspect ratio:

(0) Navicular contact transversely wider than dorsoventrally thick; (1) Navicular contact dorsoventrally thicker than transversely wide.

***Notoryctes*: 0, contact transversely wide**.

256. Expansion of navicular contact in the astragalar head region:

(0) Restricted anteriorly; (1) Asymmetrical spread only to the medial side of the astragalar “headneck region”; (2) Astragalar head supersedes navicular so the navicular facet shifted ventrally; (3) Symmetrical spread of the navicular facet to both the lateral and the medial sides of the neck.

***Notoryctes*: 3, symmetrical**.

PeerJ PrePrints

PeerJ PrePrints

257. Astragalar trochlea (defined as a saddle-shaped upper ankle joint):

(0) Absent; (1) Present, but weak (defining crest on the medial astragalo-tibial facet weakly developed); (2) Present, with clear separation of the medial and lateral tibial facets.

***Notoryctes*: 1, present, but weak**.

258. Well-defined medio-tibial crest (more or less parallel to the tibio-fibular crest) on the astragalus:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent**.

259. Astragalar medial plantar tuberosity:

(0) Absent; (1) Present, but weakly developed; (2) Present, and ventrally flaring or protruding.

***Notoryctes*: 2, present and ventrally flaring**.

260. Distal end of the calcaneal tubercle:

(0) Short, dorso-ventrally compressed, without a terminal swelling; (1) dorso-ventrally compressed, with a terminal swelling; (2) Elongate, vertically deep, and mediolaterally compressed, with terminal swelling.

***Notoryctes*: 0, dorso-ventrally compressed without a terminal swelling**.

PeerJ PrePrints

261. Morphology of the peroneal process of the calcaneus:

(0) Laterally expanded shelf, larger than the combined length of the sustentacular and astragalar facets, lateral to the astragalar facet; (1) With a distinct and long peroneal process, laterally projecting; (2) With a distinct peroneal process, demarcated by a deep peroneal groove at the base; (3) Laterally directed, small peroneal shelf demarcated from the anterior (cuboidal) edge of the calcaneus; (4) Anterolaterally directed, hypertrophied peroneal process/shelf; (5) Peroneal structure laterally reduced (lateral surface is straight from the calcaneal tubercle).

***Notoryctes*: 5, reduced**.

262. Placement of the base of the peroneal process relative to the level of the cuboid facet of the calcaneus:

(0) Peroneal structure posterior to the level of the cuboid facet; (1) Peroneal structure developed anteriorly at the same level as the cuboid facet; (2) Peroneal structure hypertrophied, extending anteriorly beyond the level of the cuboid facet.

Notoryctes: 2.

263. Peroneal groove of the calcaneus:

(0) Indistinct, on the anterolateral aspect of the lateral shelf; (1) Distinct, deep separation of the peroneal process; (2) Weakly developed, with shallow groove on the lateral side of the process; (3) Distinct, on the anterolateral corner of the peroneal process.

PeerJ PrePrints

Notoryctes: 3.

264. Alignment of the cuboid to the main axis of the calcaneus (horizontal plane):

(0) On the anterior end of the calcaneus; (1) On the anteromedial aspect of the calcaneus:

***Notoryctes*: 0, on the anterior end of the calcaneus.**

265. Orientation of the calcaneocuboid joint in dorso-ventral plane:

(0) Calcaneocuboid facet on the calcaneus oriented ventrally (more visible in the plantar view than in dorsal view); (1) Calcaneocuboid facet oriented anteriorly (distally); (2) Calcaneocuboid facet oriented ventromedially or medio-obliquely.

***Notoryctes*: 1, oriented anteriorly.**

266. Saddle-shaped calcaneocuboid joint:

(0) Calcaneocuboid facet on the calcaneus relatively flat to slightly concave; (1) Saddle-shaped.

***Notoryctes*: 0, flat**.

267. Lower ankle joint - orientation of the sustentacular facet of the calcaneus in relation to the horizontal plane:

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

(0) Nearly vertical; (1) Oblique (≤70o) to nearly horizontal.

Notoryctes: 1.

268. Antero-posterior placement of the sustentacular facet relative to the astragalar facet on the calcaneus:

(0) Directly anterior to the astragalar facet and vertically oriented on the medial edge of the calcaneus; (1) On the dorsal aspect and positioned anteromedial to the astragalar facet on the calcaneus; (2) On the dorsal aspect, medial to the astragalar facet; (3) On the dorsal aspect, anterior to the astragalar facet.

Notoryctes: 2.

269. Confluence of the sustentacular facet and the astragalar facet on the calcaneus:

(0) Absent; (1) Present.

***Notoryctes*: 1, present**.

270. Ventral outline of the sustentacular process of the calcaneus:

(0) Indistinctive; (1) Medially directed shelf, with rounded outline; (2) Protruding triangle, posteromedially directed.

***Notoryctes*: 0, indistinctive**.

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

271. Antero-posterior position of the sustentacular facet/process (using the most salient point of the facet/process in ventral view as landmark) relative to the length of the calcaneus:

(0) Near the mid-point; (1) Near the anterior (proximal) one-third.

Notoryctes: 1.

272. Shape of posterior calcaneo-astragalar process/protuberance and its contiguous fibular contact on the calcaneus:

(0) Confluent with fibular contact and indistinctive; (1) Oblong to ellipsoidal; (2) Nearly spherical and bulbous, more transversely developed than character state 1; (3) Transversely confluent with the sustentacular facet.

Notoryctes**: 0, indistinctive**.

273. Placement of the calcaneoastragalar structure:

(0) On the medial side of the body of the calcaneus; (1) On the dorsal side of the body of the calcaneus, but bordering on the body's medial margin (without a protruding outline); (2) On the dorsal side of the body of the calcanues and protruding beyond the body's medial margin; (3) Withdrawn and separated from the medial margin and placed along the lateral margin of the body of the calcaneus.

Notoryctes**: 0, medial side of the body of the calcaneus**.

274. Anterior ventral (plantar) tubercle of the calcaneus:

(0) Absent; (1) Present, at the anterior edge (just lateral to the cuboid facet); (2) Present, set back from the anterior edge.

***Notoryctes*: 1, present**.

275. Anteroventral groove or depression of the calcaneus:

(0) Absent; (1) Present.

Notoryctes: 1.

276. Cross-sectional shape of the body of the calcaneus at the level of the posterior calcaneoastragalar facet:

(0) Dorso-ventrally compressed; (1) Mediolaterally compressed.

***Notoryctes*: 0, dorso-ventrally compressed**.

277. Ventral curvature of the calcaneal tubercle:

(0) Present; (1) Absent.

***Notoryctes*: 1, absent**.

278. Proportion of the navicular and cuboid (transverse width measured in dorsal view):

PeerJ PrePrints

(0) Navicular narrower than or subequal to cuboid; (1) Navicular wider than cuboid.

***Notoryctes*: 0, equal**.

279. Proportion of the entocuneiform, mesocuneiform, and ectocuneiform (in ventral view):

(0) Mesocuneiform and ectocuneiform small, their combined width smaller than the width of the entocuneiform; (1) Mesocuneiform and ectocuneiform large, their combined width (in dorsal view) exceeding the width of the entocuneiform.

***Notoryctes*: 0, small**.

280. Medio-plantar aspect of the cuboid deeply notched by the peroneus longus tendon:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent**.

281. Prehallux:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent**.

282. Side-by-side contact of metatarsal V and the peroneal process of the calcaneus:

(0) Absent; (1) Present.

PeerJ PrePrints

***Notoryctes*: 1, present**.

283. Relationships of the proximal end of metatarsal V to the cuboid:

(0) Metatarsal V is off-set to the medial side of the cuboid; (1) Metatarsal V is so far offset to the side of the cuboid that it contacts the calcaneus; (2) Metatarsal V is level with the anterior end of the cuboid.

***Notoryctes*: 1, metatarsal V is so far offset to the side of the cuboid.**

284. Ventrolateral tubercle at the proximal end of metatarsal V:

(0) Absent; (1) Present, at the anterior edge of the calcaneus; (2) Present, off-set posteriorly from the anterior edge of the calcaneus.

***Notoryctes*: 0, absent**.

285. Angle of metatarsal III to the calcaneus (which indicates how much the sole of the foot is 'bent' from the long axis of the ankle):

(0) Metatarsal III aligned with (or parallel to) the long axis of the calcaneus; (1) Metatarsal III arranged obliquely from the long axis of the calcaneus.

***Notoryctes*: 0, aligned**.

286. Metatarsal II and metatarsal III proximal ends:

PeerJ PrePrints

PeerJ PrePrints

(0) II and III even or II more proximal than III; (1) III more proximal than II.

***Notoryctes*: 0**.

287. Opposable hallux:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent**.

OTHER POSTCRANIAL CHARACTERS

288. Ossified patella:

(0) Absent; (1) Present.

***Notoryctes*: 1, present**.

289. Sesamoid bones in the digital flexor tendons:

(0) Absent; (1) Present, unpaired; (2) Present, paired.

***Notoryctes*: 1, present, unpaired**.

290. External pedal (tarsal) spur:

(0) Absent; (1) Present.

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

***Notoryctes*: 0, absent**.

291. Pes digital grouping:

(0) Didactylous; (1) Syndactylous.

***Notoryctes*: 0, didactylous.**

292. Epiphyses in long bones:

(0) Absent; (1) Present.

***Notoryctes*: 1, present**.

BASICRANIUM

293. External size of the cranial moiety of the squamosal:

(0) Narrow; (1) Broad; (2) Expanded posteriorly to form the skull roof table.

***Notoryctes*: 1, broad**.

294. Participation of the cranial moiety of the squamosal in the endocranial wall of the braincase:

(0) Absent; (1) Present.

Notoryctes: ?.

295. Multiple vascular foramina (for rami temporales) in the squamosal and parietal:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent**.

296. Multiple vascular foramina (for branches of external ethmoidal artery) in the dorsal surface of the frontal:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent**.

297. Topographic relationships of the dentary-squamosal contact (or glenoid) and the cranial moiety of the squamosal (only applicable to taxa with the dentary-squamosal joint; this character is best seen in ventral view):

(0) Contact on the internal aspect of the zygoma, without a constricted neck; (1) Contact on the zygoma, with a constricted neck; (2) Contact on the cranial moiety of squama; (3) On zygoma, without a constricted neck.

***Peligrotherium*: 0, without a constricted neck**, (Rougier et al., 2012).

***Necrolestes*: 0, without a constricted neck**, (Rougier et al., 2012).

***Notoryctes*: 0, without a constricted neck**.

PeerJ PrePrints

298. Cross-section profile of the squamosal anterior to its zygomatic root:

(0) Rounded or triangular and tapering anteriorly; (1) Dorsoventral expanded and mediolaterally compressed, and not tapering anteriorly.

***Notoryctes*: 0, rounded**.

299. Postglenoid depression on the squamosal:

(0) Present as the post-craniomandibular joint sulcus (“external auditory meatus” on the zygoma); (1) Absent; (2) Present on the skull base.

***Necrolestes*: 2, present**.

***Notoryctes*: 1, absent**.

300. Squamosal - entoglenoid process:

(0) Absent or vestigial; (1) Present, but separated from the postglenoid process; (2) Present, enlarged and connected to the postglenoid process.

***Necrolestes*: 1, present**.

***Notoryctes*: 1, present**.

301. Position of the craniomandibular joint:

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

(0) Posterior or lateral to the level of the fenestra vestibuli; (1) Anterior to the level of the fenestra vestibuli.

Necrolestes**: 1, anterior**.

Notoryctes**: 1, anterior**.

302. Orientation of the glenoid on the squamosal:

(0) On the inner side of the zygoma and facing ventromedially; (1) On the platform of the zygoma and facing ventrally.

Necrolestes**: 1, on the platform of the zygoma**.

Notoryctes**: 1, on the platform of the zygoma**.

303. Postglenoid process of the squamosal:

(0) Absent; (1) Postglenoid crest raised below the fossa, but without a distinctive process; (2) Distinctive process; (3) Distinctive process buttressed by ectotympanic.

Necrolestes**: 1, without a distinctive process.**

Notoryctes**: 1, without a distinctive process.**

304. Postglenoid foramen position:

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

(0) Posterior to the glenoid area; (1) Medial to the postglenoid process; (2) Anterior to the postglenoid process.

***Cronopio*: 0, posterior**.

***Necrolestes*: 0, posterior**.

***Notoryctes*: ?, not applicable**.

305. Postglenoid foramen presence vs. absence and composition:

(0) Absent; (1) Present, in the squamosal; (2) Present, between the squamosal and petrosal; (3) Present, between the squamosal and ectotympanic.

***Necrolestes*: 2, between the squamosal and petrosal**.

***Notoryctes*: 0, absent**.

306. Medial margin of the glenoid fossa:

(0) Formed by the squamosal; (1) Formed by the alisphenoid.

***Necrolestes*: 0, formed by the squamosal**.

***Notoryctes*: 0, formed by the squamosal**.

307. Squamosal - epitympanic recess (this character may be ordered):

PeerJ PrePrints

(0) No contribution to the “epitympanic area” of the petrosal; (1) Small contribution to the posterolateral wall of the epitympanic recess; (2) Large contribution to the lateral wall of the epitympanic recess; (3) Squamosal forming a large part of enlarged epitympanic sinus.

***Peligrotherium*: 1, small contribution**, (Páez Arango, 2008).

***Notoryctes*: 1, small contribution**.

308. Contribution of the basisphenoid wing (parasphenoid ala) to the external bony housing of the cochlea:

(0) Participates in the rim of the fenestra vestibuli; (1) Does not reach the rim of the fenestra vestibuli; (2) Absent or excluded from the cochlear housing.

***Peligrotherium*: 2, absent**, (Rougier et al., 2012).

***Necrolestes*: 2, absent**, (Rougier et al., 2012).

***Notoryctes*: 2, absent**.

309. Relationship of the cochlear housing to the lateral lappet of the basioccipital:

(0) Entirely covered by the basioccipital; (1) Medial aspect covered by the basioccipital; (2) Partially covered by the basioccipital; (3) Fully exposed as the promontorium.

***Peligrotherium*: 3, fully exposed**, (Rougier et al., 2012).

***Necrolestes*: 3, fully exposed**, (Rougier et al., 2012).

PeerJ PrePrints

***Notoryctes*: 3, fully exposed.**

310. Thickened rim of the fenestra vestibuli:

(0) Present; (1) Absent.

***Peligrotherium*: 0, present.**

***Necrolestes*: 0, present**.

***Notoryctes*: 1, absent**.

311. Cochlear housing fully formed by the petrosal:

(0) Absent; (1) Present.

***Reigitherium*: 1, present**.

***Notoryctes*: 1, present**.

312. Ventromedial surface of the promontorium:

(0) Flat; (1) Inflated and convex.

***Reigitherium*: 1, inflated and convex.**

***Peligrotherium*: 1, inflated and convex.**

***Necrolestes*: 1, inflated and convex.**

PeerJ PrePrints

***Notoryctes*: 1, inflated and convex**.

313. Lateral wall and overall external outline of the promontorium:

(0) Triangular, with a steep and slightly concave lateral wall; (1) Elongate and cylindrical; (2) Bulbous and oval shaped.

***Necrolestes*: 2: bulbous and oval shaped**.

***Notoryctes*: 2: bulbous and oval shaped**.

314. Cochlea:

(0) Cochlear recess (without a canal); (1) Short canal; (2) Elongate canal, to the fullest extent of the promontorium; (3) slightly curved; (4) Elongate and partly coiled; (5) Elongate and coiled to at least 360°.

***Dryolestes*: 4, elongate and partly coiled**, (Luo et al., 2012).

***Notoryctes*: 5, coiled to a least 360º**, (Ladèveze et al., 2008).

315. Internal acoustic meatus - cribriform plate:

(0) Absent; (1) Present.

***Dryolestes*: 1, present.**

***Coloniatherium*: 0, absent.**

PeerJ PrePrints

PeerJ PrePrints

***Reigitherium*: 0, absent.**

***Peligrotherium*: 1, present.**

***Necrolestes*: 1, present.**

***Notoryctes*: 1, present.**

316. Internal acoustic meatus depth:

(0) Deep with thick prefacial commissure; (1) Shallow with thin prefacial commissure.

***Henkelotherium*: 1, shallow**.

***Coloniatherium*: 0, deep.**

***Reigitherium*: 0, deep.**

***Cronopio*: 0, deep.**

***Necrolestes*: 1, shallow.**

***Notoryctes*: 1, shallow.**

317. Primary bony lamina within the cochlear canal:

(0) Absent; (1) Present.

***Necrolestes*: 1, present**, (Rougier et al., 2012).

***Notoryctes*: 1, present.**

PeerJ PrePrints

318. Secondary bony lamina for the basilar membrane within the cochlear canal:

(0) Absent; (1) Present.

***Necrolestes*: 1, present**, (Rougier et al., 2012).

***Notoryctes*: 1, present.**

319. Crista interfenestralis:

(0) Horizontal, broad, and extending to the base of the paroccipital process; (1) Vertical, delimiting the back of the promontorium; (2) Horizontal, narrow, and connecting to the caudal tympanic process.

***Necrolestes*: 1, vertical**, (Rougier et al., 2012).

***Notoryctes*: ?, unknown**.

320. Post-promontorial tympanic recess:

(0) Absent; (1) Present.

***Dryolestes*: 1, present**, (Luo et al., 2012).

***Notoryctes*: 1, present**.

321. Rostral tympanic process of the petrosal:

(0) Absent or low ridge; (1) Tall ridge, but restricted to the posterior half of the promontorium; (2) Well-developed ridge reaching the anterior pole of the promontorium.

***Dryolestes*: 0, absent**, (Luo et al., 2012).

***Coloniatherium*: 0, absent**, (Rougier et al., 2009).

***Peligrotherium*: 0, absent**, (Páez Arango, 2008).

***Necrolestes*: 2, well-developed ridge**, (Ladevèze et al., 2008).

***Notoryctes*: 2, well-developed ridge**, (Ladevèze et al., 2008).

322. Caudal tympanic process of the petrosal:

(0) Absent; (1) Present as a continuos crest; (2) Present, notched; (3) Present, hypertrophied and buttressed against the exoccipital paracondylar process.

***Dryolestes*: 1, present**, (Luo et al., 2012).

***Peligrotherium*: 1, present.**

***Necrolestes*: 1, present.**

***Notoryctes*: 1, present**, (Ladevèze et al., 2008).

Comentaries: Rougier et al. (2012) codified this character as absent (state 0) for *Peligrotherium*. However, Páez Arango (2008) remarks the presence of the caudal tympanic process, delimiting posteriorly to the post-promontorial tympanic recess. Conseuqently, *Peligrotherium* is here coded as present (state 1).

PeerJ PrePrints

Asher et al. (2007) indicated that in *Necrolestes* the caudal tympanic process was absent. However, most recently Ladevèze et al. (2008) and Rougier et al. (2012) described and figured such structure in *Necrolestes*. For instance, in this work the caudal tympanic process is here codified as present (state 1).

323. Petrosal - tympanic process:

(0) Absent; (1) Present.

***Necrolestes*: 0, absent**, (Rougier et al., 2012).

***Notoryctes*: 0, absent**, (Ladevèze et al., 2008).

324. Rear margin of the auditory region:

(0) Marked by a steep wall; (1) Extended onto a flat surface.

***Necrolestes*: 1, flat surface**, (Rougier et al., 2012).

***Notoryctes*: 1, flat surface**.

325. Prootic canal (modified state 2):

(0) Absent; (1) Present, vertical; (2) Present, horizontal.

***Dryolestes*: 2, present**, (Luo et al., 2012).

***Necrolestes*: 0, absent.**

***Notoryctes*: 0, absent**, (Ladevèze et al., 2008).

PeerJ PrePrints

PeerJ PrePrints

Comentaries: In contrast to Asher et al. (2007) Ladevèze et al. (2008) indicates the presence of a small tympanic opening of the prootic canal in *Necrolestes*. However, Rougier et al. (2012) codified this opening as absent (state 0) due to a reexamination of the available middle ear material of *Necrolestes* (Rougier, 2012 *pers. com.*).

326. Position of the sulcus for the anterior distributary of the transverse sinus relative to the subarcuate fossa.

(0) Anterolateral; (1) Posterolateral.

Dryolestes**: 0, anterolateral**, (Luo et al., 2012).

Necrolestes**: 0, anterolateral**, (Ladevèze et al., 2008).

Notoryctes**: 0, anterolateral**, (Ladevèze et al., 2008).

327. Lateral trough floor anterior to the tympanic aperture of the prootic canal and/or the primary facial foramen:

(0) Open lateral trough, no bony floor; (1) Bony floor present; (2) Lateral trough absent.

Dryolestes**: 1, bony floor present**, (Luo et al., 2012).

Reigitherium**: 1, bony floor present**, (Rougier et al., 2012).

Peligrotherium**: 1, bony floor present**, (Rougier et al., 2012)..

Necrolestes**: 1, bony floor present**, (Rougier et al., 2012).

Notoryctes**: 1, bony floor present**.

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.735v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014
PeerJ reviewing PDF | (v2014:12:3598:1:1:NEW 20 Dec 2014)

PeerJ PrePrints

328. Anteroventral opening of the cavum epiptericum:

(0) Present; (1) Present, with reduced size (due to the anterior expansion of the lateral trough floor); (2) Present, partially enclosed by the petrosal; (3) Present, enclosed by the alisphenoid and petrosal; (4) Present, as large piriform fenestra.

***Dryolestes*: 2, partially enclosed by the petrosal**, (Luo et al., 2012).

***Henkelotherium*: 2, partially enclosed by the petrosal**, (Rougier et al., 2012).

***Reigitherium*: 2, partially enclosed by the petrosal**, (Rougier et al., 2012).

***Coloniatherium*: 2, partially enclosed by the petrosal**, (Rougier et al., 2009).

***Peligrotherium*: 2, 3, partially enclosed by the petrosal and alisphenoid**, (Rougier et al., 2012).

***Cronopio*: 2, partially enclosed by the petrosal**, (Rougier et al., 2012).

***Necrolestes*: 2, partially enclosed by the petrosal**, (Rougier et al., 2012).

***Notoryctes*: 3, enclosed by the alisphenoid and petrosal**, (Archer, 1976).

329. Enclosure of the geniculate ganglion by the bony floor of the petrosal in the cavum supracochleare:

(0) Absent; (1) Present.

***Notoryctes*: 1, present**, (Archer, 1976).

PeerJ PrePrints

330. Hiatus Fallopii:

(0) Present, in the petrosal roof of the middle ear; (1) Present, at the anterior end of the petrosal; (2) Absent (applicable only to those taxa with a cavum supracochleare).

***Dryolestes*: 0, present, in the petrosal roof**, (Luo et al., 2012).

***Henkelotherium*: 0, present, in the petrosal roof**, (Luo et al., 2012. Ruf et al., 2009).

***Coloniatherium*: 1, present, at the anterior end**, (Rougier et al., 2009).

***Peligrotherium*: 0, present, in the petrosal roof**, (Páez-Arango, 2008).

***Necrolestes*: 0, present, in the petrosal roof**, (Ladevèze et al., 2008).

***Notoryctes*: 0, present, in the petrosal roof**, (Archer, 1976).

331. Foramen ovale - composition:

(0) Between the petrosal and alisphenoid; (1) Secondary foramen partially or fully enclosed by the alisphenoid, in addition to the primary foramen between the petrosal and alisphenoid; (2) In the petrosal (anterior lamina); (3) Between the alisphenoid and squamosal; (4) Within the alisphenoid.

***Notoryctes*: 1**, (Archer, 1976).

332. Foramen ovale - position:

PeerJ PrePrints

(0) On the lateral wall of the braincase; (1) On the ventral surface of the skull.

***Notoryctes*: 1, ventral surface**, (Archer, 1976).

333. Number of exit(s) for the mandibular branch of the trigeminal nerve (V3):

(0) One; (1) Two.

***Peligrotherium*: 1, two**, (Rougier et al., 2012).

***Notoryctes*: 1, two**, (Archer, 1976).

334. Quadrate ramus of the alisphenoid:

(0) Forming a rod underlying the anterior part of the lateral flange; (1) Absent.

Peligrotherium: 1, absent, (Rougier et al., 2012).

***Notoryctes*: 1, absent**.

335. Alisphenoid canal (for the ramus inferior and/or ramus infraorbitalis):

(0) Absent; (1) Present.

***Peligrotherium*: 1, present**, (Páez Arango, 2008).

***Notoryctes*: 0, absent**.

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.715v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

336. Anterior lamina exposure on the lateral braincase wall:

(0) Present; (1) Reduced or absent.

***Henkelotherium*: 0, present**, (Ruf et al., 2009).

***Coloniatherium*: 0, present**, (Rougier et al., 2009).

***Peligrotherium*: 0, present**, (Páez Arango, 2008).

***Cronopio*: 0, present**, (Rougier et al., 2011).

***Necrolestes*: 0, present**, (Rougier et al., 2012).

***Notoryctes*: ?, unknown**.

337. Orientation of the anterior part of the lateral flange:

(0) Horizontal shelf; (1) Ventrally directed; (2) Medially directed and contacting the promontorium; (3) Vestigial or absent.

***Coloniatherium*: 1, ventrally directed**, (Rougier et al., 2009).

***Peligrotherium*: 1, ventrally directed**, (Páez Arango, 2008).

***Necrolestes*: 1, ventrally directed**, (Rougier et al., 2012).

***Notoryctes*: ?, unknown**.

338. Vertical component of the lateral flange:

(0) Present; (1) Absent.

PeerJ PrePrints

***Notoryctes*: ?, unknown**.

339. Vascular foramen in the posterior part of the lateral flange (and anterior to the pterygoparoccipital foramen):

(0) Present; (1) Absent.

***Henkelotherium*: 1, absent**, (Rougier et al., 2012).

***Coloniatherium*: 1, absent**, (Rougier et al., 2012).

***Peligrotherium*: 1, absent**, (Rougier et al., 2012).

***Necrolestes*: 0, present**, (Rougier et al., 2012).

***Notoryctes*: ?, unknown.**

340. Relationship of the lateral flange to the crista parotica (or the anterior paroccipital process that bears the crista):

(0) Widely separated; (1) Narrowly separated; (2) Continuous.

***Dryolestes*: 2, continuos**, (Luo et al., 2012).

***Henkelotherium*: 2, continuous**, (Rougier et al., 2012).

***Coloniatherium*: 1, narrowly separated**, (Rougier et al., 2009).

***Peligrotherium*: 0, widely separated**, (Páez Arango, 2008).

***Necrolestes*: 1, narrowly separated**, (Rougier et al., 2012).

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

***Notoryctes*: ?, unknown**.

341. Pterygoparoccipital foramen (for the ramus superior of the stapedial artery):

(0) Laterally open notch; (1) Foramen enclosed by the petrosal or squamosal; (2) Absent.

***Dryolestes*: 1, enclosed by the petrosal**, (Luo et al., 2012).

***Henkelotherium*: 1, enclosed by the petrosal**, (Rougier et al., 2012).

***Coloniatherium*: 1, enclosed by the petrosal**, (Rougier et al., 2009).

Peligrotherium: 1, enclosed by the petrosal, (Páez Arango, 2008).

***Necrolestes*: 1, enclosed by the petrosal**, (Rougier et al., 2012).

***Notoryctes*: ?, unknown.**

342. Position of the pterygoparoccipital foramen relative to the level of the fenestra vestibuli:

(0) Posterior or lateral; (1) Anterior.

***Coloniatherium*: 0, posterior**, (Rougier et al., 2012).

***Peligrotherium*: 0, posterior**, (Rougier et al., 2012).

***Necrolestes*: 0, posterior**, (Rougier et al., 2012).

***Notoryctes*: ?, unknown.**

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

343. “Bifurcation of the paroccipital process” - presence vs. absence:

(0) Absent; (1) Present.

***Dryolestes*: 0, present**, (Luo et al., 2012).

***Henkelotherium*: 0, absent**, (Rougier et al., 2012).

***Coloniatherium*: 1, present**, (Rougier et al., 2012).

***Peligrotherium*: 1, present**, (Rougier et al., 2012).

***Cronopio*: 1, present**, (Rougier et al., 2012).

***Necrolestes*: 1, present**, (Rougier et al., 2012).

***Notoryctes*: ?, unknown**.

344. Posterior paroccipital process of the petrosal:

(0) No ventral projection below the level of the surrounding structures; (1) Projecting below the surrounding structures.

***Dryolestes*: 1, projecting below the surrounding structures**, (Luo et al., 2012).

***Henkelotherium*: 0, no ventral projection**, (Rougier et al., 2012).

***Coloniatherium*: 0, no ventral projection**, (Rougier et al., 2012).

***Peligrotherium*: 1, projecting below the surrounding structures**, (Rougier et al., 2012).

***Necrolestes*: 1, projecting below the surrounding structures**, (Rougier et al., 2012).

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

***Notoryctes*: 1, projecting below the surrounding structures.**

345. Morphological differentiation of the anterior paroccipital region:

(0) Anterior paroccipital is bulbous and distinctive from the surrounding structures; (1) Anterior paroccipital region has a distinct crista parotica.

***Dryolestes*: 1, distinct crista parotica**, (Luo et al., 2012).

***Henkelotherium*: 1, distinct crista parotica**, (Rougier et al., 2012).

***Peligrotherium*: 0, 1**, (Rougier et al., 2012).

***Notoryctes*: 1, distinct crista parotica**.

346. Epitympanic recess lateral to the crista parotica:

(0) Absent; (1) Present.

***Notoryctes*: 1, present**, (Ladevèze et al., 2008).

347. Tympanohyal contact with the cochlear housing:

(0) Absent; (1) Present.

***Henkelotherium*: 0, absent**, (Ruf et al., 2009).

***Peligrotherium*: 0, absent**, (Páez Arango, 2008).

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

***Necrolestes*: 0, absent**, (Rougier et al., 2012).

***Notoryctes*: 0, absent**.

348. Relationship of the squamosal to the paroccipital process:

(0) Squamosal covers the entire paroccipital region; (1) No squamosal cover on the anterior paroccipital region; (2) Squamosal covers a part of the paroccipital region, but not the crista parotica (the squamosal wall and the crista parotica are separated by the epitympanic recess).

***Coloniatherium*: 2**, (Rougier et al., 2012).

***Peligrotherium*: 2**, (Rougier et al., 2012).

***Notoryctes*: 2**, (Ladevèze et al., 2008).

349. Medial process of the squamosal reaching toward the tympanic cavity:

(0) Absent; (1) Present (near or bordering on the foramen ovale).

***Henkelotherium*: 0, absent**, (Rougier et al., 2012).

***Necrolestes*: 0, absent**, (Rougier et al., 2012).

***Notoryctes*: 0, absent**, (Archer, 1976).

350. Stapedial artery sulcus on the petrosal:

(0) Absent; (1) Present.

PeerJ PrePrints

PeerJ PrePrints

***Cronopio*: 1, present**, (Rougier et al., 2012).

***Necrolestes*: 1, present.**

***Notoryctes*: ?, unknown**.

Comentaries: Asher et al. (2007) and Ladevèze et al. (2008) indicate for *Necrolestes* the absence of the stapedial artery, denoted by the loss of the stapedial artery sulcus. However, Rougier et al. (2012) codified this character as present (state 1) due to a reexamination of available material (Rougier, 2012 *pers. com.*).

351. Transpromontorial sulcus for the internal carotid artery on the cochlear housing:

(0) Absent; (1) Present.

***Dryolestes*: 1, present**, (Luo et al., 2012).

***Peligrotherium*: 1, present**, (Rougier et al., 2012).

***Necrolestes*: 1, present**, (Rougier et al., 2012).

***Notoryctes*: 0, absent**, (Ladevèze et al., 2008).

352. Deep groove on the anterior pole of the promontorium:

(0) Absent; (1) Present.

***Dryolestes*: 1, present**, (Luo et al., 2012).

***Coloniatherium*: 0, absent**, (Rougier et al., 2009).

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

***Peligrotherium*: 0, absent**, (Páez Arango, 2008).
***Necrolestes*: 1, present**, (Ladevèze et al., 2012).
***Notoryctes*: 0, absent**.

353. Perbullar canal or sulcus for the internal carotid artery (SICA).
(0) Absent; (1) Present.
***Dryolestes*: 1, present**, (Luo et al., 2012).
***Henkelotherium*: 1, present**, (Ruf et al., 2009).
***Peligrotherium*: 1, present**, (Páez Arango, 2008).
***Notoryctes*: ?, unknown**.

354. Epitympanic wing medial to the promontorium:
(0) Absent; (1) Present.
***Necrolestes*: 1, present**, (Ladevèze et al., 2008).
***Notoryctes*: ?, unknown**.

355. Ectopterygoid process of the alisphenoid:
(0) Absent; (1) Present.

PeerJ PrePrints

***Necrolestes*: 0, absent**, (Rougier et al., 2012).

***Notoryctes*: 0, absent**.

356. Tympanic process of the alisphenoid:

(0) Absent; (1) Present, but limited to the “piriform” region of the basicranium; (2) Intermediate; (3) Well-developed, extending to near the jugular foramen.

***Notoryctes*: 2, intermediate**, (Archer, 1976).

357. Hypotympanic recess in the junction of the alisphenoid, squamosal, and petrosal:

(0) Absent; (1) Present.

***Coloniatherium*: 0, absent**, (Rougier et al., 2012).

***Peligrotherium*: 0, absent**, (Rougier et al., 2012).

***Necrolestes*: 0, absent**, (Rougier et al., 2012).

***Notoryctes*: 1, present**, (Archer, 1976).

358. Separation of the fenestra cochleae from the jugular foramen:

(0) Absent; (1) Separate but within the same depression; (2) Separate (not within the same depression).

***Dryolestes*: 2, separate**, (Luo et al., 2012).

PeerJ PrePrints

***Coloniatherium*: 2, separate**, (Rougier et al., 2009).

***Peligrotherium*: 2, separate**, (Páez Arango, 2008).

***Necrolestes*: 2, separate**, (Rougier et al., 2012).

***Notoryctes*: 2, separate**, (Ladevèze et al., 2008).

359. Channel of the perilymphatic duct:

(0) Open channel and sulcus; (1) At least partially enclosed channel.

***Dryolestes*: 1, partially enclosed**, (Luo et al., 2012).

***Coloniatherium*: 1, partially enclosed**, (Rougier et al., 2009).

***Peligrotherium*: 1, partially enclosed**, (Páez Arango, 2008).

***Notoryctes*: 1, partially enclosed**, (Ladevèze et al., 2008).

360. Jugular foramen size relative to the fenestra cochleae (applicable only to those taxa with a jugular foramen fully separated from the fenestra cochleae):

(0) Jugular subequal to the fenestra cochleae; (1) Jugular larger than the fenestra cochleae.

***Dryolestes*: 0, subequal**, (Luo et al., 2012).

***Henkelotherium*: ?, unknown**, (Ruf et al., 2012).

***Coloniatherum*: 0, subequal**, (Rougier et al., 2009).

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

***Peligrotherium*: 0, subequal**, (Páez Arango, 2008).

***Notoryctes*: 0, subequal**, (Ladevèze et al., 2008).

361. Relationship of the jugular foramen to the opening of the inferior petrosal sinus:

(0) Confluent; (1) Separate.

***Dryolestes*: 1, separate**, (Luo et al., 2012).

***Henkelotherium*: 1, separate**, (Ruf et al., 2009).

***Coloniatherium*: ?, unknown**, (Rougier et al., 2009).

***Notoryctes*: 1, separate**, (Ladevèze et al., 2008).

362. Stapedial muscle fossa size:

(0) Absent; (1) Present, small; (2) Present, large (twice the size of the fenestra vestibuli).

***Dryolestes*: 1, present, small**, (Luo et al., 2012).

***Peligrotherium*: 1, present, small**, (Páez Arango, 2008).

***Notoryctes*: 2, present, large**, (Ladevèze et al., 2008).

363. Alignment of the stapedial fossa relative to the crista interfenestralis:

(0) aligned with crista interfenestralis; (1) lateral to the crista interfenestralis.

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

***Dryolestes*: 0, aligned**, (Luo et al., 2012).

***Coloniatherium*: 1, lateral**, (Rougier et al., 2012).

***Peligrotherium*: 1, lateral**, (Páez Arango, 2008).

***Cronopio*: 1, lateral**, (Rougier et al., 2012).

***Necrolestes*: 1, lateral**, (Rougier et al., 2012).

***Notoryctes*: ?, unknown**.

364. Hypoglossal foramen:

(0) Indistinct, either confluent with the jugular foramen or sharing a depression with the jugular foramen; (1) Separated from the jugular foramen; (2) Separated from the jugular foramen; the latter has a circular, raised external rim.

***Necrolestes*: 1, separate**, (Rougier et al., 2012).

***Notoryctes*: 1, separate**.

365. Number of separate hypoglossal foramina:

(0) Single; (1) Double.

***Necrolestes*: 0, single**, (Rougier et al., 2012).

***Notoryctes*: 0, single**.

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

MIDDLE EAR OSSICLE CHARACTERS

366. Geometry (shape) of the incudo-mallear contact:

(0) Trochlear (convex and cylindrical) surface of the incus; (1) Trough; (2) Saddleshaped contact on the incus; (3) Flat surface.

***Notoryctes*: 3, flat**, (Segall, 1970).

367. Alignment of the incus and the malleus:

(0) Posterior-anterior; (1) Posteromedial to anterolateral; (2) Dorsoventral.

***Notoryctes*: 1, posteromedial to anterolateral**, (Segall, 1970).

368. Twisting of the dorsal plate relative to the trochlea on the quadrate:

(0) Dorsal plate aligned with the trochlea; (1) Dorsal plate twisted relative to the trochlea, (2) Dorsal plate twisted and elevated from the trochlea; (3) Dorsal plate reduced to a conical process (crus longum).

***Notoryctes*: 2, twisted and elevated from the trochlea**, (Segall, 1970).

369. Presence of a quadrate/incus neck (slightly constricted region separating the dorsal plate or crus brevis from the trochlea; this represents the differentiation between the ‘body’ and crus brevis of the incus):

(0) Absent; (1) Present.

PeerJ PrePrints

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

***Notoryctes*: 1, present**, (Segall, 1970).

370. Dorsal plate (= crus brevis) of the quadrate/incus:

(0) Broad plate; (1) Pointed triangle; (2) Reduced.

***Notoryctes*: 2, reduced**, (Mason, 2001).

371. Incus - angle of the crus brevis to crus longum of the incus (this is equivalent to the angle between the dorsal plate and the stapedial process of the quadrate):

(0) Alignment of the stapedial process (crus longum) and the dorsal plate (crus brevis) (or an obtuse angle between the two structure) (distinctive process is lacking, stapes/incus contact is on the medial side of the quadrate trochlea); (1) Perpendicular or acute angle of the crus brevis and crus longum ("A-shaped" incus).

***Notoryctes*: 0, alignment**, (Segall, 1970).

372. Primary suspension of the incus/quadrate on the basicranium:

(0) By quadratojugal in addition to at least one other basicranial bone; (1) By squamosal only; (2) By petrosal (either by the preserved direct contact of the incus or by inference from the presence of a well-defined crista parotica).

***Coloniatherium*: 2, by petrosal**, (Rougier et al., 2012).

***Peligrotherium*: 2, by petrosal**, (Rougier et al., 2012).

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

***Necrolestes*: ?, unknown**, (Rougier et al., 2012).

***Notoryctes*: 2, by petrosal**.

373. Quadratojugal:

(0) Present; (1) Absent.

***Notoryctes*: 1, absent**.

374. Morphology of the stapes:

(0) Columelliform–macroperforate; (1) Columelliform–imperforate (or microperforate); (2) Bicrurate–perforate.

***Notoryctes*: 1, columnelliform-imperforate**, (Segall, 1970; Mason, 2001).

375. Stapedial ratio:

(0) Less than 1.4; (1) 1.4-1.8; (2) ≥1.8.

***Dryolestes*: 0, ratio = 1.3**, (Luo et al., 2012).

***Coloniatherium*: 1, ratio = 1.5**, (Rougier et al., 2009).

***Notoryctes*: 1, ratio > 1.4**, (Segall, 1970; Ladevèze et al., 2008).

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.715v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

376. Bullate stapedial footplate:

(0) Absent; (1) Present.

***Notorycte*s: ?, unknown**.

377. Malleolar neck:

(0) Absent; (1) Present.

***Notoryctes*: 1, present**, (Segall, 1970).

378. Length of the malleus manubrium:

(0) Shorter than the combined width of the surangular and prearticular anterior to the incudomalleolar joint; (1) longer than the combinted width of surangular and prearticular.

***Notoryctes*: 1, longer**, (Segall, 1970).

379. Thickness of malleolar manubrium:

(0) robust; (1) gracile.

***Notoryctes*: 1, gracile**, (Mason, 2001).

380. Distinctive angle or bending of Meckel's bone (=anterior portion of postdentary rod) anterior to the level of ectotympanic (angular) bone:

(0) Absent; (1) Present.

***Notoryctes*: ?, unknown**.

381. Medio-lateral contact vs. separation of Meckel's element (either independent or as an ossified component of the "postdentary rod") from the posterior (pterygoid) region of mandible:

(0) Presence of medio-lateral contact either in adult or in embryonic stage until Meckel's cartilage re-absorption; (1) Embryonic Meckel's cartilage medio-laterally separated from the posterior part of mandible; (2) Ossified Meckel's cartilage medio-laterally separated from the posterior part of mandible:

***Notoryctes*: ?, unknown**.

382. Ectotympanic size/shape (may be ordered):

(0) Plate-like; (1) Curved and rod-like; (2) Ring-shaped; (3) Slightly expanded (fusiform); (4) Expanded; (5) Tube-like.

***Notoryctes*: 4, expanded**, (Segall, 1970).

383. Ectotympanic arc

(0) about 70 degrees: (1) ≤ 90 – 135 degrees; (2) ≥ 135 degrees.

***Notoryctes*: ?, unknown**.

PeerJ PrePrints

PeerJ PrePrints

384. Anterior process of the ectotympanic (angular):

(0) Present; (1) Absent.

***Notoryctes*: 1, absent**, (Archer, 1976).

385. Position/orientation of the incisura tympanica:

(0) Posteroventral; (1) Posterior; (2) Postero-dorsal; (3) Dorsal.

***Notoryctes*: 2, postero-dorsal**, (Segall, 1970).

386. Fusion of the ectotympanic to other bones:

(0) Absent; (1) Fused to other bones.

***Notoryctes*: 1, fused to alisphenoid and periotic tympanic wing**, (Archer, 1976).

387. Entotympanic and its contribution to the bullar structure:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent**, (Segall, 1970).

OTHER CRANIAL CHARACTERS

388. Posterior extent of the bony secondary palate:

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.715v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

(0) Anterior to the posterior end of the tooth row; (1) Level with the posterior end of the tooth row; (2) Extending posterior to the tooth row; (3) Extending to the basisphenoid-basioccipital suture.

***Notoryctes*: 1, level with the posterior end of the tooth row.**

389. Posterior median spine (or torus) on the palate:

(0) Absent; (1) Present.

***Necrolestes*: 0, absent**, (Rougier et al., 2012).

***Notoryctes*: 0, absent**.

390. Pterygopalatine ridges:

(0) Present; (1) Absent.

***Necrolestes*: 1, absent**, (Rougier et al., 2012).

***Notoryctes*: 1, absent**.

391. Transverse process of the pterygoid:

(0) Present and massive; (1) Present but reduced (as the hamulus); (2) Greatly reduced (with a vestigial crest on pterygoid) or absent.

***Peligrotherium*, 2, greatly reduced**, (Páez Arango, 2008).

PeerJ PrePrints

Necrolestes**: 1, 2**, (Rougier et al., 2012).

Notoryctes**: 2, absent**.

392. Pterygoids contact on midline on pharyngeal roof:

(0) Present; (1) Absent.

Notoryctes**: 1, absent**.

393. Ventral opening of the minor palatine foramen:

(0) Encircled by the pterygoid (and ectopterygoid if present) in addition to the palatine; (1) Encircled by the palatine and maxilla, separated widely from the subtemporal margin; (2) Encircled completely by the palatine (or between palatine and maxilla), large, with thin bony bridge from the subtemporal margin; (3) Large, posterior fenestration; (4) Notch.

Notoryctes**: ?, unknown**.

394. Transverse canal foramen:

(0) Absent; (1) Present.

Peligrotherium: 1, present, (Páez Arango, 2008).

Notoryctes: 1, present, (Archer, 1976).

PeerJ PrePrints

395. Carotid foramen position:

(0) Within the basisphenoid; (1) Within the basisphenoid/basioccipital suture; (2) Within the basisphenoid/petrosal suture; (3) Through the opening of the cavum epiptericum.

***Peligrotherium*: 3, through the opening of the cavum epiptericum, (Paéz Arango, 2008)**.

***Necrolestes*: 0, within the basisphenoid**, (Rougier et al., 2012).

***Notoryctes*: 2, within the basisphenoid/petrosal suture.**

396. Overhanging roof of the orbit:

(0) Absent; (1) Present, formed by the frontal.

***Necrolestes*: 0, absent**, (Rougier et al., 2012).

***Notoryctes*: 0, absent**.

397. Exit(s) of the infraorbital canal:

(0) Single; (1) Multiple.

***Peligrotherium*: 0, single**, (Páez Arango, 2008).

***Notoryctes*: 0, single**.

398. Composition of the posterior opening of the infraorbital canal (maxillary foramen):

PeerJ PrePrints

(0) Between the lacrimal, palatine, and maxilla; (1) Exclusively enclosed by the maxilla; (2) Enclosed by the maxilla, frontal and palatine.

***Notoryctes*: 1, enclosed by the maxilla**.

399. Size and shape of the lacrimal:

(0) Small, oblong-shaped on the facial part of the rostrum; (1) Large, triangle-shaped on the facial portion of rostrum; (2) Crescent shaped on the facial portion of the rostrum; (3) Reduced to a narrow strap; (4) Absent from the facial portion of the rostrum.

***Peligrotherium*: 1, triangle-shaped**, (Páez Arango, 2008).

***Notoryctes*: 1, triangle-shaped on the facial portion of rostrum**.

400. Location of the lacrimal foramen:

(0) Within the orbit; (1) On the facial side of the lacrimal (anterior to or on the anterior orbital margin).

***Cronopio*: 0, whitin the orbit**, (Rougier et al., 2012).

***Notoryctes*: 1, on the facial side**.

401. Number of lacrimal foramina:

(0) One; (1) Two.

***Cronopio*: 0, one**, (Rougier et al., 2012).

***Notoryctes*: 0, one**.

402. Lacrimal foramen composition:

(0) Within the lacrimal; (1) Bordered by or within the maxilla.

***Notoryctes*: 0, within the lacrimal**.

403. Maximum vertical depth of the zygomatic arch relative to the length of the skull (this character is designed to indicate the robust vs. gracile nature of the zygomatic arch):

(0) Between 10-20%; (1) Between 5-7%; (2) Zygoma incomplete.

***Peligrotherium*: 0, between 10-20%**, (Rougier et al., 2012).

***Necrolestes*: 0, between 10-20%**, (Rougier et al., 2012).

***Notoryctes*: 0, between 10-20%**.

404. Ultimate upper molar implanted in the anterior root of zygoma.

(0) Absent. (1) Present.

***Notoryctes*: 0, absent**.

PeerJ PrePrints

PeerJ PrePrints

405. Frontal/alisphenoid contact:

(0) Dorsal plate of the alisphenoid contacting the frontal at the anterior corner; (1) Dorsal plate of the alisphenoid with more extensive contact with the frontal (~50% of its dorsal border); (2) Absent.

***Cronopio*: 1**, (Rougier et al., 2012).

***Notoryctes*: 0**.

406. Frontal-maxilla facial contact:

(0) Absent; (1) Present.

***Notoryctes*: 1, present**.

407. Nasal-frontal suture - medial process of the frontals wedged between the two nasals:

(0) Absent; (1) Present.

***Peligrotherium*: 1, present**, (Páez Arango, 2008).

***Notoryctes*: 1, present**.

408. Posterior width of the nasal bones:

(0) Narrow; (1) broader than the width at the mid-length of the nasal.

***Notoryctes*: 1, broader**.

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

409. Pila antotica:

(0) Present; (1) Absent.

***Henkelotherium*: 1, absent**, (Rougier et al., 2012).

***Notoryctes*: ?, unknown.**

410. Fully ossified medial orbital wall of the orbitosphenoid:

(0) Absent; (1) Present, forming the ventral floor of the braincase but not the entire orbital wall; (2) Present, forming both the braincase floor and the medial orbital wall.

***Notoryctes*: ?, unknown**.

411. Separation of the optic foramen from the sphenorbital fissure:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent**, (Archer, 1976).

412. Exit for maxillary nerve:

(0) Separate from sphenorbital fissure, behind alisphenoid; (1) Separate from sphenorbital fissure, within alisphenoid; (2) Confluent with sphenorbital fissure.

***Notoryctes*: ?, unknown**.

PeerJ PrePrints

413. Separate anterior opening of orbitotemporal canal:

(0) Absent; (1) Present.

***Notoryctes*: ?, unknown**.

414. Orbital opening for the minor palatine nerve:

(0) Absent; (1) Present.

***Notoryctes*: ?, unknown**.

415. Anterior part of the jugal on the zygoma:

(0) Anterior part of the jugal extends to the facial part of the maxilla and forms a part of the anterior orbit; (1) Anterior part of the jugal does not reach the facial part of the maxilla and is excluded from the anterior orbit margin.

***Henkelotherium*: 0**, (Rougier et al., 2012).

***Peligrotherium*: 0**, (Páez Arango, 2008).

***Notoryctes*: 0**.

416. Posterior part of the jugal:

(0) Contributes to the squamosal glenoid; (1) Borders on but does not contribute to the squamosal glenoid; (2) Terminates anterior to the squamosal glenoid.

***Henkelotherium*: 0, contributes**, (Páez Arango, 2008).

***Peligrotherium*: 0, contributes**, (Páez Arango, 2008).

***Notoryctes*: 1, borders on but does not contribute**.

417. Maxillary in the sub-temporal margin of the orbit:

(0) Absent; (1) Present; (2) Present and extensive.

***Henkelotherium*: 2, present and extensive**, (Rougier et al., 2012).

***Peligrotherium*: 2, present and extensive**, (Rougier et al., 2012).

***Cronopio*: 2, present and extensive**, (Rougier et al., 2012).

***Necrolestes*: 2, present and extensive**, (Rougier et al., 2012).

***Notoryctes*: 2, present and extensive**.

418. Orbital process of the frontal borders on the maxilla within orbit:

(0) Absent; (1) Present.

***Notoryctes*: ?, unknown**.

PeerJ PrePrints

PeerJ PrePrints

419. Anterior ascending vascular channel in the temporal region:

(0) Open groove; (1) Partially enclosed in a canal; (2) Completely enclosed in a canal or endocranial; (3) Absent.

Dryolestes**: 0, open groove**, (Luo et al., 2012).

Peligrotherium**: 2, completely enclosed**, (Rougier et al., 2012).

Necrolestes**: 1,2**, (Rougier et al., 2012).

Notoryctes**: ?, unknown.**

420. Posttemporal canal for the arteria and vena diploëtica:

(0) Present, large; (1) Small; (2) Absent.

Dryolestes**: 0, present, large**, (Luo et al., 2012).

Peligrotherium**: 0, present, large**, (Páez Arango, 2008).

Notoryctes**: ?, unknown**.

421. Nuchal crest:

(0) Overhanging the concave or straight supraoccipital; (1) Weakly developed with convex supraoccipital.

Peligrotherium**: 0**, (Páez Arango, 2008).

Necrolestes**: 1, weakly developed**, (Rougier et al., 2012).

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

***Notoryctes*: 1, weakly developed**.

422. Sagittal crest:

(0) Prominently developed; (1) Weakly developed; (2) Absent.

***Peligrotherium*: 0**, (Páez Arango, 2008).

***Notoryctes*: 2, absent**.

423. Tabular bone:

(0) Present; (1) Absent.

***Peligrotherium*: 1, absent**, (Rougier et al., 2012).

***Notoryctes*: 1, absent**.

424. Occipital slope:

(0) Occiput sloping posterodorsally (or vertically oriented) from the occipital condyle; (1) Occiput sloping anterodorsally from the occipital condyle (such that the lambdoidal crest is leveled anterior to the occipital condyle and condyle is fully visible in dorsal view of the skull).

***Peligrotherium*: 1, sloping anterodorsally**, (Rougier et al., 2012).

***Necrolestes*: 1, sloping anterodorsally**, (Rougier et al., 2012).

***Notoryctes*: 1, sloping anterodorsally**.

PeerJ PrePrints

425. Occipital artery groove on the occiput extending dorsal to the posttemporal foramen:

(0) Absent; (1) Present.

***Notoryctes*: ?, unknown**.

426. Foramina on the dorsal surface of the nasals:

(0) Absent; (1) Present.

***Peligrotherium*: 0, absent**, (Rougier et al., 2012).

***Cronopio*: 0, absent**, (Rougier et al., 2012).

***Necrolestes*: 0, absent**, (Rougier et al., 2012).

***Notoryctes*: 0, absent**.

427. Septomaxilla:

(0) Present, with the ventromedial shelf; (1) Present, without the ventromedial shelf; (2) Absent.

***Peligrotherium*: 0, 1**, (Páez Arango, 2008; Rougier et al., 2012).

***Cronopio*: 0, 1**, (Páez Arango, 2008; Rougier et al., 2012).

***Notoryctes*: 1, present, whitout the ventromedial shelf**.

PeerJ PrePrints

428. Internarial process of the premaxilla:

(0) Present; (1) Absent.

***Peligrotherium*: 1, absent**, (Rougier et al., 2012).

***Cronopio*: 1, absent**, (Rougier et al., 2012).

***Necrolestes*: 0, present**, (Rougier et al., 2012).

***Notoryctes*: ?, unknown**.

429. Posterodorsal process of the premaxilla:

(0) Does not extend beyond canine ("short or absent"); (1) Extends beyond canine ("intermediate"); (2) Contacts frontal posteriorly (“long”).

***Peligrotherium*: 1, intermediate**, (Páez Arango, 2008).

***Cronopio*, 0, short**, (Rougier et al., 2011).

***Notoryctes*: 0, short**.

430. Facial part of the premaxilla borders on the nasal:

(0) Absent; (1) Present.

***Necrolestes*: 1, present**, (Rougier et al., 2012).

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)
PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

***Notoryctes*: 0, absent**.

431. Premaxilla - palatal process relative to the canine alveolus:

(0) Does not reach to the level of the canine alveolus; (1) Reaches the level of the canine alveolus.

***Peligrotherium*: 0, does not reach to the level of the canines**, (Páez Arango, 2008).

***Necrolestes*: 0, does not reach to the level of the canines**, (Rougier et al., 2012).

***Notoryctes*: 0, does not reach to the level of the canines**.

432. Incisive foramina size:

(0) Small (one or two incisors); (1) Intermediate (three or four incisors); (2) Large (more than half the palatal length).

***Necrolestes*: 1, intermediate**, (Asher et al., 2007).

***Notoryctes*: 0, small**.

433. Palatal vacuities:

(0) Absent; (1) Present, near palatomaxillary border; (2) Present, either positioned near or extended to the posterior edge of bony palate.

***Peligrotherium*: 0, absent**, (Páez Arango, 2008).

PeerJ PrePrints

***Necrolestes*: 0, absent**, (Rougier et al., 2012).

***Notoryctes*: 0, absent**.

434. Major palatine foramina:

(0) Absent; (1) Present.

***Peligrotherium*: 0, absent**, (Páez Arango, 2008).

***Necrolestes*: 0, absent**, (Rougier et al., 2012).

***Notoryctes*: 0, absent**.

435. Ossified ethmoidal cribriform plate of the nasal cavity:

(0) Absent; (1) Present.

***Notoryctes*: 1, present**, (Macrini, 2012).

436. Posterior excavation of the nasal cavity into the bony sphenoid complex:

(0) Absent; (1) Present; (2) Present and partitioned from the nasal cavity.

***Peligrotherium*: 1,2**, (Rougier et al., 2012).

***Notoryctes*: ?, unknown**.

PeerJ PrePrints

PeerJ PrePrints

Cranial Vault and Brain Endocast Characters (7 characters)

437. External bulging of the braincase in the parietal region:

(0) Absent; (1) Expanded (the parietal part of the cranial vault is wider than the frontal part, but the expansion does not extend to the lambdoidal region); (2) Greatly expanded (expansion of the cranial vault extends to the lambdoidal region).

***Peligrotherium*: 1, expanded**, (Rougier et al., 2012).

***Cronopio*: 2, greatly expanded**, (Rougier et al., 2012).

***Necrolestes*: 2, greatly expanded**, (Rougier et al., 2012).

***Notoryctes*: 2, greatly expanded**.

438. Anterior expansion of the vermis (central lobe of the cerebellum):

(0) Absent; (1) Present.

***Notoryctes*: 0, absent**.

439. Overall size of the vermis:

(0) Small; (1) Enlarged.

***Notoryctes*: 1, small**.

440. Lateral cerebellar hemisphere (excluding the paraflocculus):

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

(0) Absent; (1) Present.

***Notoryctes*: 0, absent**.

441. External division on the endocast between the olfactory lobe and the cerebral hemisphere (well-defined transverse sulcus separating the olfactory lobes from the cerebrum):

(0) Absence of external separation of the olfactory lobe from cerebral hemisphere; (1) Enlarged olfactory lobes; (2) Clear division of transverse sulcus.

***Peligrotherium*: 2, clear division**, (Rougier et al., 2012).

***Cronopio*: 2, clear division**, (Rougier et al., 2012).

***Necrolestes*: 2, clear division**, (Rougier et al., 2012).

***Notoryctes*: 2, clear division**.

442. Encephalization quotient

(0) Below 0.13; (1) Between 0.15-0.25, (2) Above 0.26.

***Notoryctes*: ?, unknown**.

443. Expansion of the posterior cerebral hemisphere (for each hemisphere, not the combined width of the posterior hemispheres):

(0) Absent; (1) Present.

***Cronopio*: 1, present**, (Rougier et al., 2012).

***Notoryctes*: 1, present**.

SOFT-TISSUE CHARACTERS

444. Trophoblasts in the placenta:

(0) Absent; (1) Present.

***Notoryctes*: ?, unknown**.

445. Mullerian ducts (oviduct and uterus) pass in between the ureters:

(0) Absent; (1) Present.

***Notoryctes*: 0, absent**.

MISCELANEOUS TRAITS

446. Proximal end of femur:

(0) craniocaudally flattened; (1) subcircular in cross-section.

***Notoryctes*: 0, craniocaudally flattened**.

447. Trochanteric fossa:

PeerJ PrePrints

PeerJ PrePrints

(0) absent; (1) present.

***Notoryctes*: 0, absent**.

448. Coronoid ridge on dentary:

(0) subhorizontal or oblique; (1) close to vertical.

***Notoryctes*: 0, oblique**.

449. Upper molar series:

(0) sub-parallel; (1) labially convex and anteriorly convergent.

***Peligrotherium*: 0, sub-parallel**, (Páez Arango, 2008).

***Cronopio*: 1, labially convex and anteriorly convergent**, (Rougier et al., 2011).

***Notoryctes*: 1, labially convex and anteriorly convergent**.

450. Bulbous check-teeth with low and blunt cusps:

(0) cusps thin and acute; (1) present.

***Notoryctes*: 1, present.**

451. Molars:

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

(0) brachyodont; (1) hypsodont-like.

***Necrolestes*: 1, hypsodont-like**, (Asher et al., 2007)**.**

***Notoryctes*: 1, hypsodont-like**.

452. Upper molar root number (Rougier et al., 2012):

(0) one; (1) two; (2) three; (3) with extra roots, more than three.

***Dryolestes*: 2, three**, (Rougier et al., 2012).

***Henkelotherium*: 2, three**, (Rougier et al., 2012).

***Mesungulatum*: 2, three**, (Rougier et al., 2012).

***Coloniatherium*: 2, three**, (Rougier et al., 2009).

***Reigitherium*: 2, three**, (Rougier et al., 2012).

***Peligrotherium*: 2, three**, (Páez Arango, 2008).

***Groebertherium*: 2, three**, (Rougier et al., 2012).

***Leonardus*: 1, two**, (Rougier et al., 2012).

***Notoryctes*: 1, two roots.**

453. Lower molar root contour:

PeerJ PrePrints

(0) subcilindrical in cross-section; (1) mesiodistally compressed and transversely wide, supporting the whole width of the crown.

***Notoryctes*: 1, mesiodistally compressed.**

454. Upper molars with posterior cingulum, stylocone, and posterior stylar cusp connected:

(0) separated; (1) present.

***Notoryctes*: ?, unknown**.

455. Upper molars anterior and posterior cingula:

(0) reduced; (1) forming very wide platforms.

Notoryctes: 0, reduced.

456. Upper molar cingula:

(0) located at the base of the crown; (1) elevated and continuous with occlusal planes.

***Notoryctes*: ?, not applicable**.

457. Upper molars parastyle:

(0) straight or slightly curved; (1) hooked; (2) Absent or poorly developed.

PeerJ PrePrints

***Notoryctes*: ?, unknown.**

458. Peculiar junction between the lateral and posterior semicircular canals at the point at which the latter passes under the former:

(0) absent; (1) present.

***Notoryctes*: 1, present**, (Ladevèze et al., 2008).

PeerJ PrePrints

PeerJ PrePrints

Appendix 2. Data matrix.

Thrinaxodon 0000000000000000000000000000?0?0?0?01000??????0?00000???00????00?????0000000??0????????????????00????????????????????????0??000?????????????0000000000????00?0?0000001?0??0000000010000000000?0?00000?0000000000000000000000????000000??0000000000000000000000?0000000000000?0000000011000000??000000000?00????????0000??000??00?0?00?000?0000010?1000000??0????0?00?00??0?0?000000000000000000000000000000000000000000000000?0000000000000001000000000000??0000000000000

Massetognathus 000001000000000001000000000?0?0?0001000????????20000???20????00?????0000000??????????????????00????????????????????????0??011?????????????0000000000????00?0?000000100??00??????000000??0?0?????0????00????0000000000000????10???0??00000?????0????00??????????????????????????????????????0???0??00?00????????1000??000??00?0?00?000?0000010010000000??0????0?00?00??0?0?10100000000000000100000000000030000000000000100000?0000000000?0000000000000010??0000000000000

Probainognathus 0000000000000000001000000000?000?0001000????????00000???00????00?????0000000??0????????????????00????????????????????????0??000?????????????0000000000????00?0?000000??0??00??????010000??0?0?0???0????00??????????0????0?????10???0??000?0?????0????00??0??00?00?????0??1000??000??00?0?00?000?0000010011000000??0????0?00?00??0?0?001000000?00000010000000000000000000000000000100000?000000000?0000000000000101??0000000000000

PeerJ PrePrints

```
Tritylodontids	0000010000000000000000000010?000?3000200???????20?00??2?21????
24?????0000000??????????????????00?00???????????1??????0??033023?????????????
3300002?2???0000?2?10??11201000000000?
01000000000000000000000000000000[01]1000000????200001 0?000000000000000000000?
0000000000000000000000001?000?0?00000000000?00?0???0?01111??1000000?00000000?
0000010000000100??000000?00000?0100?
0021000000000000100000000[01]01030100000000000000200100?
1000000000000[01]00000100?0111??0000000000000
```

```
Pachygenelus	0000000000000100000000000000000?2000010??????1?00000???00????
00?????0000000?000???????????????00????????????????????????0??000?????????????
3300001000??0000?1?2000001?1??00000?0??10??0000100?00000?
000000000000000100000010002100011???00?000000????
00???????????????????????????????????????0000000100?0?0?01111??1?00000?0000?000?
0000010110000000??000000?00010000?1?
0021001100000000100000000010000010101010000000100000?
100000000000000000000??????0000000000000
```

```
Adelobasileus	?????????????????????????????????????????????????????0??????0?????
0000000?000?????????????????????????????????????????????
00??????????????????????????????????????????
0??????????????????????????????????????????????????????????
0??????????????????????????????????????????????????00000?????????0221100?????
0000001?11??1010000100100000???00000000010000?10?????????0???????????0??0?0?
000????????00??0200??????0001100???????????0????????????00000000?
```

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

```
	Sinoconodon	000000100000000000000000001101000000010?????0110000?00000????
00?20??0[123]000001000???0000???0????00?00???0????????0??????0??000000?0?0??????
0000000000000331122020000001????1000??0?01????
001000000000000000000000000001000000?????????????????00000?0??
00??????????????????????????????????????????000000010000?
000221100100000000001011101010000000000100?
0000000000010001010102100110000000010000010010100010100010000002000100200000000
0100000000010000102??000?000000000

	Morganucodon	00001010000000000000000000002[01]0100000001000000000100000?
00000?0??11?20??20000020000???0000???0????00?40???0????????0??????0??00001100?
0??????000[01][01]0000000000?100000000 1101????0000000??111?00??1???00100?00000?
000000000100000 0????2100010???00001000010?000?000?0000000000000000000000??
0???????0??00000010100[01][01]?
00023111120100000000101110101000110100111001000000000100010100021002100000000 1
0000010010100010101010000000200010020000110011000000000100001 12??0000000000000

	Megazostrodon	000010000000000000000000002002001000010000000000000?00000?
0??12?20??20000020000???0000???0????00?40???0????????0??????0??00001100?0??????
0001100000000000110000000001001????2?00000?011100???????0?100000000?
0000000001000000??0??2100010?00000010000?000000000?00000000000?00??0??0?0?1?
0000000000000?0010100???000231101201 0?00000010111010000011?1001110?
1000000000100010 1?00210?21???0??001?000010?1??00010101010 0000?2?00100200001?
00???????00??0????????0000000000000

	Haldanodon	00000110001000100010000000210100100001000000000100001?10000?0??
11?20??20032000000???0000???0????00?11???0????????0??????0??03201100?0??????
```

```
0001000000001220000000000001100???00???????????????????100001000?00?00000120000?
0???????????????000?0000?0??0??????????????????????????????????????0???000001020011?
00023110020100000001?1210100?001????01010010000000001000101000????21000???00??
00002011?1000101010100000020001002010011101100000000000???2??????00001000000

        Castorocauda     00?00110001???1?000000000021010010000100???0??10000?010000?0??
11?2???20032000?00????000???0????????????????????????????????0?01100?0??????0001?
00????01?00??0??0??01100?????0??????000000??????????????????????
000012000000000011000000000000000001010000000????0000000000000000??00?0?0?
0000001100???
010??????????????????????????????????????????????????????????????????????????
1100010000?????????0??????10?000?2????0?2????1???11?00???????????????000?00000000?

        Hadrocodium      1??2?130010?402110000000000200100200?0100000101000000?0?000?0??
12?20???0000000000???0000???0????00?00???0????????0??????0??00001100?0??????
00000000001003344430000001101?????0???????????????????????????????????????????
0?????????????????????????????????????????????????????????????????????10000020101?
00023111230100000001?111010?1001102101011010000000000100?1010??????21?0??????
1????02012?103010100010000012?2?10020101211001?00??000?2??1213????0?00000000?

        Shuotherium      0010110??0000021??000?00?0????0?0001010??????111111??0013?
200120100?132321001110003100???0????11?110220100?0??0000000?0100120221100??
0100111????????????3?????0????????????
0????????????????????????????????????????????????????????????????????????????????
?????????????????????????????????????????????????????????????????????????????????
?????????????????????????????????????????????????????????????????????????????????
???????????0??0?0?????
```

PeerJ PrePrints

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.755v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

Pseudotribos 0?10011000?0001???00??????2101010001110?0???011111?1110013?
200120100?132321001110003100???0???11?110220100?0??0000000?0100120221100??
01001111??0??1010003310000??01100?????0?????101?0000010001??????????0????0???
12000000????2110??00000?10?000010?001??????????????????????????????????????0???
0???
????????????????????????0????????????2???1????????????????????????000?00000000?

Asfaltomylos 0012112110000021??0022000021310120010????????11011????013?2??
13??13?0210001?111022141100011112??????????????????????????01?02211?11021?
0000??????????????????
0???
??
??
????????????????????????0??0?0?????

Ambondro ?????1???00????1????????0?????0???0?0????????12131110??013?2??130?
1330012100?111022241120?11112??????????????????????????01?02211?
1102010000??????????????????
0???
??
??
???????????????????????????0?0?????

Ausktribosphenos 0010012010000021??002200002??1012001010??????1213111011013?2??
130213300121000221022141220032123???????????????????????????03?02221?
1112111000????????????3????
00??

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.755v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

```
???????????????????????????????????????????????????????????????????????????????????????
???????????????????????????????????????????????????????????????????????????????????????
?????????????????????????0??0?0?????

    Bishops      01?10120100?0021??0022000021310120010?0??????12131?1011013?2??
13021330012100122102214122003212 3???????????????????????????03?02221?
1112111000???????????03??0?00????????????
0??????????????????????????????????????????????????????????????????????????????????????
???????????????????????????????????????????????????????????????????????????????????????
???????????????????????????????????????????????????????????????????????????????????????
???????????0??0?0?????

    Teinolophos      1100212010013021??0022000?21310120010????????????????????3?2??
13111120012010?222042231210?02?23????????????????????????????3?02221?
2113002000????????????????????????????????????????????????????????????????????????????
???????????????????????????????????????????????????????????????????????????????????????
???????????????????????????????????????????????????????????????????????????????????????
?????????????????????????????????????????????????????0??0?0?????

    Steropodon      011001???0??00?1???????????????????10??????????????????013?2??
131111200121100222042231210?02?23???????????????????????????03?02221?
2113002000????????????3??
3??????????????????????????????????????????????????????????????????????????????????????
???????????????????????????????????????????????????????????????????????????????????????
???????????????????????????????????????????????????????????????????????????????????????
???????????????????????????0?00000000?
```

Obdurodon 11?2?1201001302110112200012131112111010??????1013100???013?2??
131111200120100222042231210?02?2320?1??????????????0????????03302221?
211310200054????2?2?333443??0????1???????
0???21???1????
11???100002110110?000231111?????
0000001?111?1101001112101110?100000000000?00?0????????1?0???????????03012?10000?
40?110211?120201122?0012110011?0??00002????2?????00100?1000?

Ornithorhynchus 11?2?1001001302110112200012131112111[123]10?????????????????13?
2??1?1?1?????20100222042231210??2?2320?1????????????????????0??0330?????2?1?1?2???
54????2?2?334443??0????1??????0?
1110111100000010001000000101000000000000001200000010012111110000111000002201001000
0?00000010110000000000000110001101001 1[01]0100002110010?
000231111411000000000101110110100111210111011000000000000?00?0?
323121211001110121010030110100002400110211212020112210012110011?0?
100002111223000000????????0

Tachyglossus 11?2?10??0014021100000000000213111??1?
010???
?????????????????54????2?2?334443????????????????
1110111100000010001000000101000000000000001200000010012111110100111000002201001000
0?00000010110000000000000110001101001 1[01]0100002110010?
0002311114110000000001011101101001112101110110000000000 10?00?0?
323121211001110121010030121102002400 11?211212021112210012110011?0?
1001021112230000 0?????????0

PeerJ PrePrints

PeerJ PrePrints

Fruitafossor 11?0014000000021??1100001121010110011?1000000010?0000?0?0??????
10?????0??00000?????????????????00?0???????????????????0???4400??????????????2??0??
1010223332000?001100????31??????010001???????0?000011000?
0010000012000100100121??????0000???0??01001000?0???????000000000000?
00000??????????01??0????10???
11???
??????????????0????????????2?1???????????????????????????000??0?0?????

Gobiconodon 11?1010??00010211012210011211400100101000000010010100000000?0??
12?10??10100010?00???0000???0????00?10???0????????0??????0??00101201?0??????
000320000101011120000000001010????20????010100000000?
101121111111001110000010100000000?
2100210000000000000100000000000000000001000000000000000????????
0010000001020011?00023111130100000001?121120000011110011100200000000011??
1011???????1?1????12????00200211000011000000001120011122121011000 1?000001??0??0?
00??001?00000000?

Repenomamus 11?1010??001102110122100112114001001010000000110101000000 0?
0??12?10??10100010?00????000???0????00?10???0????????0??????0??00101101?0??????
0003200001010112200000000 1010?????
00000010100000000110112111111001110000010100000 0???
2100210000000000000100000000000000000001000000000000000??0??0??00?
1000000102001 1?00023111130100000001?12112000001111001110020000?000011??
101???????21?1????12?????0200211000011000000001120011122121011000 1?000001010??
0100??0010000000000?

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.715v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

```
        Amphilestes     11?11?0??001102???122??0??211400200201??????110100000000?0??12?
10??10100010?00???0000???0????00????????????????????????00?01201?0??????000???????
00?21??0000??????0?????
0???????????????????????????????????????????????????????????????????????????????????????
????????????????????????????????????????????????????????????????????????????????????????
???????????????????????????????????????????????????????
1????????????????????????????????????????????000000000?

        Yanoconodon     11?1010??0011021101221001?2214001000010000000000000000000000?0??
11?10??02000031?00????000???0????00?00???0????????0??????0??00001100?0??????
000330000000003333430001001110?????
0000001010000000001101121111111001110000010101000000012100210000000000000010000000
000000000000100000000000000??0?00??000000000001020?11??00???????????????????????
0?????????????????????????????32312121???11012210100?00?????0??????11?????2????
122????????????0???????????????0000?0?0?????

        Jeholodens      11?1010??00?10211012??001?22140010000100000000101000000000?0??
11?10??02000011?00???0000???0????00?00???0????????0??????0??00001100?0??????
00011000010103322320000001111?????00000010100000000110112111111110011100??
01010100000001210021000000000000001000000000000000000010000000000000000000010000
000000102?011?0002311?130100??0???10??1?????????????????????0??0?0???????????????
21????????1221????????????00?10??11???00?????122???011??01??0??????1????????
0000000000000

        Trioracodon     11?10?0??0011021??122100102214001000010000000?0101000100000?0??
11?10??1[123]000031?00???0000???0????00?10????????????1??????1??00001100?0??????
0003?00??0000123321000??01100?????
```

PeerJ PrePrints

0???0??????????????02311?????????0??0?0??1010???0???????????????0??0???1??10???????????0???????????0???????0????????1???????????????0???????????????????????????0?00000000?

Priacodon 11?1010??0011021??1221001022140010000100000000001010100000?0??11?10??12000031?00???0000???0????00?10???0????????1??????1??00001100?0??????0003?00??0000122221000??01101????10?????????????0??0?????0????1??00231111301??000000101?12100??0111100??100??000??0??1100101???????2??0???????????020?????000??????1???????1??122?10??????????0??0??1??????????0?00000000?

Haramiyavia 0100110??000002???000000002?010?100021?????????2?000??2021????24?????0??0?000???????????????????0?00????????????1??????0??033023?????????????1?00001?1?1133?1?00??0??121000?0???0????????????2??????????????????????????????1?10000000?

Plagiaulacidans 11?2?10??00[01]302110102110102224001000210?????0??2?000??2021????24?????0??0?000???????????????????0?00????????????1??????0??033023?????????????420000102?[12][12]44[12]202103?1112100100??????01111000001101111101111001100100200001011000121?1110000000111100?01001001??00?002211120?1000110011000001010012?01?0001010110?000231111301??

PeerJ PrePrints

000000101211101100211???1111?10?000000010001111??????21?0???????2???

00000201001002000100?0000202?112202000100[01]11010000?21????????0111100000000

Cimolodontans 11?2?10??0013021101021101022140[01]1000210?????0??2?000??

2021???24?????0??0?000???????????????????0?00????????????1??????0??

033023?????????????4300002?2?33444302123?

11120111200010000111100000110111110111100110010010000[01]01100??

21011100000001111002010000010?

0000022111200100[01]110011000001010012101000001010[01]10?

00023111130100100[01]0010121110110021121[01]111[01]010[01]

[01]0000001[01]0011103231212110011 1??

211100000101001002000102000002[01]21112202001100121010000021110223??0111100000000

Tinodon 1??11?????001021??121?00???104?130?00????????0101000?0001201??12?

100010100010?110000100???00??010?10???00???0???0????0?00002102211?0???0??

000????????1??22??1??

0???

??

??

????????????????????????0?00000000?

Akidolestes 1????10??00?20????12210010211401100111000000?

110100012011302011201000100000401 2200?0100???00??020?11???000??0??0000000?

2000220222100??00000001100??1011000100000000 1110?????0?????

001100001001101121111111001110111110111010000121111201000011?

000021010100100000001002010010001100001000121000021010?001020??

PeerJ PrePrints

1???
?????0??????10?0???2?????12????????0???0??????????????000?00000000?

Spalacotherium 1111010??000202?????21001021140110011100000 0?
1101000100113120012010001000004011200?0100???00??020?11???000??0??0000000?
2000220222100??0000000???????10?000?0000000??10?????
0???
??
???
0???0000000000?

Maotherium 11?1010??0002020??1221001021140101011100000011101001?
0001311001201000100000401110 0?0100???00??020?11???000??0??0000000?
2000220222100??000000022?0??10102200000010000??10?????0?1?000011110??0?1?011211?
11110?1110111110111010000121112200000001?11002101000010000 00?13020100????
1100001000020000021010?00102??11?00?231111????????1????1???1????0??1?????????2?
00000???????1???????????????????????????????????22??100000???2???12????????1??
00??????????????110000000000?

Zhangheotherium 11?1010??0002020??1221001?2114010101110000001 1101001?
0001311001201000100000401110 0?0100???00??020?10???000??0??0000000?
2000220222100??00000002200??1010220000010000 1110????20?
1100001111001001101121111111001110111110111010000121112200000001?
1100210100001000000013020100100011000010000200000 2101????1020111?0012311112????
1101001?1?1?10???0??121011110200000000 01?0?1??1??????21??????0??????0??????0??
1?????10???0???2???12???2????????00???????????????110000000000?

PeerJ PrePrints

Peramus 11?1111100002021??1121010121030120011101100200002000?000130100130001000100010011[01]0002110000[01]?0121121?0?010000??00010020200011022111100000000002??????000003310?00??0???0???0000000000?

Vincelestes 11?2?111000[01]2021??1111010121130120011100000101000000?0001301001300000020000000110000210??000?0120?11?0?010000??000101200000110221100?000000003100000100333342000030??00??????0111100111101201?101?211011110011101010001110?000012101220000000011100021100 01020?001001302010110001101 00?????210??0?00111002020011?00123?112400?111010010111010010011[01]211111102011000000011002111??????21?0???????????010110100010201000001012000100202000100111000000??1????????1101100000000

Nanolestes 11?1011100002021??112?0??12103012001110??????0000000?000130100130001002100010011000021000?00?0121?11?0?0?0000??10120120200011022111100000000011?????001?02??0?00??0???0?????0???0?00000000?

Kielantherium 11?101110?002?21??111101?2????0130011?0??????0000000?0001301??13000110211001011102015110000[01]001???????????????????????????01?02221?1001000000????????0??12??0??0??????0?????

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.755v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

0???
??
??
???????????0000000000?

Aegialodon ??1?01??
13000110211001?111020151100?11001????????????????????????????1??2221?
1001000000???????????????????????????????
0???
??
??
?????????????00000000?

Montanalestes 11?2?13100004021??111201032103013001110??????1202001000013?2??
130102102110012012021151100111002???????????????????????????0??02221?
1001110000???????????03??0?
00??
??
??
??????????????1??????????0??0?0?????

Prokennalestes 11?1113100001021??1112010221030120011101[01]112?
1202000020013022013020110111001201202115110011100221022020010011001011010020001
20222121001110000???????1010033?0000?00?1?0?????
0???
???23111251111110100102?10????13?1?

PeerJ PrePrints

```
111011???11001???110?21????????2??1?????????????????????0???????????1??????????
1????????????0??????????????0?000000000

Murtoilestes	????????????????????????????????????????????????????????13022013?
20210111001?012021151100?1100?210220200?00110010110000200012?222121001?
10000???????????????????????????????
0????????????????????????????????????????????????????????????????????????????????????????
?????????????????????????????????????????????????????????????????????????????????????????
?????????????????????????????????????????????????????????????????????????????????????????
?????????????00000000?

Eomaia	11?1113100001021??
1112010221030120011101011111201000020013022013020?101110012??202?151100111??
2210220200100110010??000?20001202221210011??00010000000000003310010000?100?????
011?1100111101200?101122101111002110111200221021000121112200000001?
1110211000012210021223020101301111010000100210001200111?0?1????2??0????1??51?
11??????????1????????????????????????????11???????????????????????????0????????00??0??
10?0???2???10?20???????02??1???????1??????????0?00000000?

Kennalestes	11?2?1310000402110111200022???0?
2001110111120100200010001302201302021021100122220311511001110022102201101001101
1010000?200012022212100111000021????01011[01]33200100001101?????
001??????????????????????????????????????????????????????????????????????????????????????
??2?????????????????????????????110021221122102231112511??210211002?1?2001013?????
10110201000110011002110??????21?2??????321300?0110200000200??0?
01012121100202201110021010?00??1011223????00000000000
```

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

Asioryctes 11?2?13100004021101112000221030130011101112201102000010013022013020210211001201203115110011100221022011010011001000000?20001202221210011100001000000101113321010000?101?????001111??11110??????????????????????0?????0???0?11000?????2?0??00??????0??100001221002122302010130111101000000?0200001?0011100212211221022311125?1??2102110?241?2001013???1110110201000110011002110??????21?2??????32130020110200000200?101010?2121100202201110021010000??1011223??110000000000?

Ukhaatherium ?1???????00?40??????????022???0??00?1101112201102000020013022013020?1021100120120311511001110221022011010011001000000?20001202221210011100001000000000113321010030?101?????0?1??1?011110??0???0?1221011110?2110111200221021 00?1210?2200000001?111021100001221002122302010130111010000???200??1??01??00?1?2??221???3?????????2??21????4?0????0???????1???????0?0?1??????21?1?????????2???????21??0?0?????0????????0?010???21??0????????0??????0?????????????110000000000?

Zalambdalestes 11?2?1[023]1000[01]40211011120[01]0221030120011101112210212200120013022013120310211001022204205110001110220?1201201101100000000?20001202221210011100002?11?001101133?1010200?111?????0??1110011110??0???01?221011110?2110111200221021000121112200000001?1110211210?12210021223?201013?011300000000200001?00111003122112210223111 25?1??210211002411200101 3???11101102010001100110021 11??????21?2??????3213002011020000020 1?1010101211110[01]2021011000210100 00??1011223??1100000000000

```
    Daulestes    11?2?131000140211011120002210301200110???1??????????
00013022013020210211001?11202115110011100220?12021010011111010000?
20001202221210011100001?00??00101133200?0??0?100?????
0???????????????????????????????????????????????????????????????????????????????????????
????????????????????????????????110021201120102231112511???10?????2?????01013???????
11?201100??001????????1????2??1??????3???00?01?1??000?100?10?000?212110[01]20???1??
00??????00??2??????????0?10000000?

    Aspanlestes    ?????1????0??0?????????1??????0???0?1?011112?1?010000?
0013023113110210211001?11201215110001100220?120321110312100?0000?
2100120222121001110000???????????033?0??0????1?0?????
0???????????????????????????????????????????????????????????????????????????????????????
???????????????????????????????????????????????3?????????1?0?0?1????0?????
1?????????????00?1????????1???????????1??????????????????????
0???????????????????????????????????????????????????010000000?

    Eoungulatum    ?????1????????????????1??????0???0?1??10110???????????
013024213110310211001?11201215111001200320?12232111031210010000?
0100120222121001110000???????????1332???0????1?0?????
0???????????????????????????????????????????????????????????????????????????????????????
???????????????????????????????????????????????3?????????1???0?1????
0???????????????????000??????????1???????????
1??????????????????????????????????????????????????????????????????????????10000000?

    Cimolestes    1??2?1010?0140211?111200?22103012?0111010122?
1101000010013023113020210211001221203115110011200221012111010011110000000?
20001202221210011100002?00??0000113321?00????1?0????
```

PeerJ PrePrints

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

20??
??
??
0???
??????????0000000000?

Gypsonictops 1??2?101000140211?111200?22103012?0111011122?
1212000110013023113120210211001221204115110011200221012111010011110000000?
2000120222121001110000??????0000113320?00????1?0????
20??
??
??
????????????0?00000000?

Protungulatum 11?2?101000140211?11120002210301200111010120?
1211000010013024213110210211001211201215111001201320?12232111031000000000?
0100120222121001110000??????0000113321?00????100????
20???
2220032122312?1013011132011??????????????????????????????2311125?1??1?0?0?00??
[01]0?????1?????????????11001????1??21???????????
2??1???????????????????????????0?10000000?

Erinaceus 11?2?
1310001412110111200022103013001110101101121220010001302201311031021100101120221
5111001211220?12122111020??0000000?
010033022212111111000032000010103333420002001110????201111100111101200?
11112110111101211011120022102100012111221?

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.755v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

000001111112102101222003212251201013011132011000002001012001110031211120102231 1

1251111210211002311300111 3???

111011020110011001100211121311121220111014213002111130000020011011011 21211?

221210111002111002012201122311110000000000

Leptictis 11?2?

131000140211011120002210301300111011122112122001000130222131103102110012112041 1

5110001101220?12111110011110000000?

0100120222121111110000220000001011332100020 0?100?????0??????0111101200?101?22??

111?0121101112002210 21????2111221?

000001111112112101222003212231201013011132011 00??0200?01??

0111003121112010223111251111110201002311300111 3???

111011020110011001100211 0??????21?20?????

32130121111200000300010110112121110202101110021010000122011223??1100000000000

Canis 111??

131010140211011110002211301300111001000100110000101110230120010100000000000000 10

210?001210000?010202110110001100 00?03101212121 00?

0210000022000000002332310000000100????2111111101111012 0??

101121201111012111111200221121000021 11221?

000001101101112102221202212251001013011 1?30110??

0020000120011100302111311022311125111?11?3??0?23111101113?????

101102000010000110?

112[01]2131112122011101421311201114010013000101101121101022022121000211111001220

01223111100000000001

PeerJ PrePrints

Felis 111??1310101402110111100022113013001110010001001100001011102301200101000000000000000210?001210000?01020211000?00110000?03101212121 00?02100???22000000003443430?00000100????2111111011110120??1011212011110121111112002211210000211122 1?0000011011011121022212022122510010130111?30110??0020000120011100302111311022311125111?11?3??0?23111101113?????101102000010000110?1120213111212201110142131120111401001300010110112110102202212100021111100122001223111100000000001

Rattus 1112?111000141211011112000222?011000210????????????????013???21313?0004000000????42041100013?1400??2022211020??????????0?003102???????01?0???4311112?2?333343???1?02112????201111100111101200?101122101110001101000210221120000121112 11?0010111111121110012210032122500010110 11?310110110001000120011100201011002012311125111111010000241101011131??2?1011010100111002111111021311121220111014213002011121200140011011001212011221321210002121?20012111122311110010 0000000

Oryctolagus 1112?111000140211011111000222?011?11210001200001 00001??013???01313?0004000000????210410?00?3?1300??2012111030??????????0?013202???????01?0???4311112?2?333343??0??02112????21111110011110 1201?10112210111000200101120022102000012111201?001011111112101100?2111321225000101301013101101100010001200111002010110020?231112511111101000024110101 1131??2?

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

```
101101000011100111011102131112122011101521300001111210030011?
2111121201122132121000212 1?2001211112231111000000000000

          Bradypus          111??1310101412110111100022113013?01110????????????????0??????
15???????????03?????????????????????????????????????????????0440???????????????55????1?
2?????00??????01??????311111110111111120??
101121201112102111111200221121000021111321?
1100011011011000012212012122510010130111?30110??
00200001200111003021113110223111251 11?11?3??0?23021101013?????
1011020000[01]0000110?112021311121220111014213113011110300101001?11021211011220?
212100021011001122001223111100010000000

          Tamandua          111??1310101412110??????0?21?30???1??10????????????????
0???????????????????????????????????????????????????????????????????????????????????
55????1?2??????????????01??????3?111111011111120??
10112120111210211110120022112100002111321?
110001101101102002221201212251001 0130??1?30110??
00200001200111003121113110223111251 11?11?3??0?231?1101013?????
101102001000000110?11202131112122011101421311301111030010100 2?11021211011220?
212100021011001122001223111100010000000

          Glyptotherium     111??131010141211011110002211301310111 1????????????????0??????
15???????????03?????????????????????????????????????????????0330???????????????55????1?
2?????00??????01??????311111110111111120??
10112120111200211110120022112100002111321?
1100011011011021022212012122510010130111?30110??
0020000120011110302111311022311125111?11?3??0?230?1101013?????1011020000?
```

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

```
0000110?1120???11??22011101421311301111030010100101102121211122 0?212101021011?
01122???2231111000100000000

    Dasypus     111??131010141211011110002211301310111????????????????0??????
15???????????03?????????????????????????????????????????????0440???????????????55????1?
2?????43??????01??????31111111011111120??
1011212011120021111012002211210000211132 1?
110001101111102102221202212251001013011 1?30110??
0020000120011110302111311022311125111?11?3??0?23011101013?????
1011020000000000110?11202131112122011101421311301111130010100201101121211122 0?
21210102101100112200122311110001000000 0

    Chaetophractus   111??131010141211011110002211301310111????????????????0??????
15???????????03?????????????????????????????????????????????0440???????????????55????1?
2?????43??????01??????31111111011111120??
10112120111200211110120022112100002111321?
11000110111110210222120221225100101301 11?30110??
0020000120011111302111311022311125111?11?3??0?23021101013?????
1011020000[01]0000110?
112[01]213111212201110142131130111113001010020110212121112 20?
212101021011001122001223111100010000000

    Euphractus     11???131010141211011110002211301310111????????????????0??????
15???????????03?????????????????????????????????????????????0440???????????????55????1?
2?????43??????01??????31111111011111120??
10112120111200211110120022112100002111321?
110001101111102102221202212251001013011 1?30110??
```

0020000120011111302111311022311125111?11?3??0?23021101013?????
1011020000[01]0000110?
112[01]21311121220111014213113011111300101002011021212111220?
212101021011001122001223111100010000000

Holoclemensia ??????????????????????????????????0?1???????????????????
130210130201102110011111021151100?2100120?120111100010010011121200012?
222121001000000??????????????????0????????????
0???
??
??
?????????????00000000?

Sinodelphys 11???131010?4021??111?0??2210301300111000??11?1010?00?001302??
130101100110011111?21151100121??121122???110??????01101212100??02221?
10010000001100000000113211120?10?100?????0?????00111?0120??101123101111012?
111112?0221121111021????00000001?1??0?100000121201??1242202011021?
210001111021000020011??
0???
????????????0??????10?0???2????0?2?3??????0??????????1????????110?00000000?

Deltatheridium 11?2?14101012021??
1111000421030130011100000110001000000013021013000110[123]11001111102115110001100
121122010110001001001001022201202221210010000001100??00002222211100?12100????
20???
12???????2??????110212???00??????????????11100?020112????231112510??110100212312???

PeerJ PrePrints

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.715v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

1013???2?1011?2?00001???1101111???????2??1???????????02?11?2?000?201010?000121???
0[01]2031????002?011000?????????????0000000000

Atokatheridium ??????????????????????????????????0?????????????????????1?
021013000110011001?111021151100?0??0121?220101100010010010010222012?
222121001000000???????????????????????????????
0???
??
??
?????????????00000000?

Sulestes ??????????????????????????????????0?????????????????????13?
21013000110011001?111121151100?11102211220101100010010011110222012?
222121001010000???????????????????????????????
0???
??
??
????????????000000000?

Marsasia 11?2?14101012021??11112014??1?013?0?????????????????????13????130?
02?0011001?111121151100?22112???????????????????????????0??02???????????
000????????????2??????????????????
0???
??
??
???????????0000000000?

PeerJ PrePrints

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

```
        Asiatherium     11?1?141010140211?111100142?0?
0130011100000110001000000013022013010310211001011112215110112211221022021111121
1?000100102100120222121001110000??????00?0222221010?????0??????0????10011110??
0????11231011110?2110111200221121111021012200000001?111011010001????????
2???????????????????????????0?001110?3020112010?2311125????1111?0??23??4101013?????
10?1?2??0?0101111???11???????2??????????????02011?2?00??21??10?0?0?2????0[01]20???
11000??????10??2????????110000000000?

        Kokopellia      ?1?1?1410?012??1??1?1100??2?????3?01110????1?
0001000000013021013010210211001001112215110112210221?220201100111?
1001111021001202221210011100001?????0000?222?1?10??0?100????
20????????????????????????????????????????????????????????????????????????????????????????
??????????????????????????????????????????????????????????????????????????????????????????
??????????????????????????????????????????????????????????????????????????????????????????
?????????????00000000?

        Anchistodelphys ???????????????????????????????????0????????????????????01?
021013020310211001?011122051101132102211220221210210101011110?
200120222111001110000????????????????????????????????
0?????????????????????????????????????????????????????????????????????????????????????????
??????????????????????????????????????????????????????????????????????????????????????????
??????????????????????????????????????????????????????????????????????????????????????????
????????????00000000?

        Albertatherium  ???????????????????????????????????0????????????????????0?
3022013????????????????1???????????????2112202221102101100111112200?2?222111??????
000??????????????2?????????????????
```

```
0???????????????????????????????????????????????????????????????????????????????????????
????????????????????????????????????????????????????????????????????????????????????????
????????????????????????????????????????????????????????????????????????????????????????
?????????????00000000?

    Didelphodon    11?2?14101011021??11110014211301?001110001???
00011000000130220130003102110012111122051201?
321122112202222102010100201102210120222111001110000????????00222221?00????1?
0????20??????????????????????????????????????????????????????????????????????????????
21201101231101011021221011????????????????10?30201120102231112??0????1??0?1??
11?????1??????1?????0?00?1?????0111?????????1?1???????????
0????????????????????????????0???1????0???????1??????????????0?10000000?

    Pediomys    ???2?14101011021??11110014211301?001110???????????????
0013022013010310211001111112205120113211221122022221021100001111021001202221110
01110000????????00222221100??????0????
20??????????????????????????????????????????????????????????????????????????????
21201101242202011021221011?????????????????????????????123111???0????0??0?1???1?????
1??????1???????00?1?????0111???????????1?????????????????2???0??????????????????????
1????????????1????????????????00000000?

    Turgidodon    ???2?141010110211?111100?4?11301?001110??????
0001000000013021013010310211001111113215120113211221122022211021100001111022001
20222111001110000????????00222221?00???21?0????
20??????????????????????????????????????????????????????????????????????????????????????
??????????2????????????????????????????????????223111???0????0??0?1??11?????1??????
```

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

PeerJ PrePrints

1???????00?1?????0?11???????????1??
1?????????????????????????????00000000?

Mayulestes 11?2?14101014?
2110111100142103013001110000011000100000001302101301031021100111111221512011311
0221122022220021100001011022101202221110011100001000000000222221100111?100?????
011111001111101201?10112310111101211111200221121?1??
2111220000000111110111000012???????24220201102121101 1?????210??0?
00111003020112011123111 25????110100??2411010101 3?????
10110210010100111111111??????21?????????????0201102000002110101000?201010020??
01100021111100??2????????110000000000?

Pucadelphys 11?2?
1410101402110111100142103013001110000011000100000001302101312031021100101111221
51201132102210220222211211100021111210012022211100111000010000000002222211 10111
2100?????011111001111101201?101123101111012111111210221 12?????
211122000000011111011100001213011012422020110212210 11?11?0210??0?
0011100302011201112311125 11??1101002124110101013?????
10110210010100111111111??????21?1??????2????02011?
20000211010111012010100203101100021011100?21????????1100000000000

Andinodelphys 11?2?
1410101402110111100142103013001110000011000100000001302101312031021100121111221
512010321122102202222112111000211112100120222111001110000100000000022222111 0111
?100?????0??????0???????0???0??
0????????????????2??????????????????????????0???111003?2011201122311125????1101002?

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.755v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

24110101013?????10110210010100011111111???????21?1???????????02?111?1000021?
01011001201?10020310110002101111??21??????????0?00000000?

Didelphis 11?2?
141010141211011110014210301300111000002100010000000130210130203102110010111 1221
51201032112210220222221120?
00002111122001202221110011100001000000000222221110111 2100????2011111001111 01201?
1011231011110121111112[01]02211212110211122000000011111011100001213011012422 0211
102123201111110210010200111003020112011123111251111111100212311[01]101013?????
10110200000101111011111213111212101110022120020111210000210010110012010100 20310
0100021111110121011223001100000000000

Marmosa 11?2?
141010141211011110014210301300111000002100010000000130210130203102110011111 1211
51201032122210220222221120?
000021111210012022211100111000010000000102222210001112100????011111001111 01201?
10112310111101211111120022112121102111220000000111110111000012130110124220211102
12220111111021001020011100302011201112311125111111110021231111 01013?????
10110200000101111011111213111212101110022120020111210000210010110112010100 20311
2110021111110121011223001100000000000

Caenolestes 11???14101014?2110111100142103013001110????????????????00?
3021013020310211001111113215120103212221022022221120?
00102101021001202221110011 1?000110000000002222210100202100???0?
011111001111 01201?
10112310111101211111120022112121102111220000000111110111000012130 2?
01242201011021221011110002101002001110030201120?1123111251111111 3002?

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.715v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

```
23110101013????10?102000000021110111112131??211101110032120020111310000021?
01011?0120101002032??10002111?220121???223001100000000000

    Dasyurus        11?2?
1410101402110111100142103013001110000[01]021000100000001302101302031021100111111
2215120103212221122022221120?
00102101022001202221110011100002100000000332231100011210 0?????011111001111 01201?
1011231011110121111120022112121102111220000000111110111000012131210125 10010121
213?10111100021010020011100302011201132311125111111130021231011010 13?????
10110200000102111011121?131??
2111011100421200201111200021101011011201010020320110002111111012 10112230011000
00000001

    Dromiciops      1112?
14101014021101111001421030130011100000210001000000013021013020310211001101 11320
5120103212221122022221120?
0000000112100120222111001110000100000001022222101002121 00?????
01111100111101201?
1011231011110121111120022112121102111220000000111110111000012 1302?
11251002012121 3?201111100210010200111003020112011123111251111111 3002?231?
4101013?????1011020000010211100111 02131??
212220111003213002011111000031101011 00120?
01002032121100210111101210112230011000000000 00

    Thylacomyidae   111??1410101 4?2110111100142103013001110??????????????00?
30??????????????001??11132??1????3???4????2042??1120?00100001?2?01120222101???
1100002000000???222221??0?2?210??????011111001111 01201?10112310111101211?
```

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.715v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

111200221121111021112200000001111101110000121 30????25100201212 13??11???002?0?0020111100302?112?1132311125111111130 02?2310?101013?????101102?0000102?1???11??2131??21??0?1100421?0020111?1000021?01011?012?101?020?2??1?0021?1???0121???223001100000000000

Macropus 111??1410101402110111100142103013001110???????????????00?3?25313130300200001330113204131004312400?32042211120?00100000?2300120222101110110???4200001???332232?110202112?110?01111100111101201?101123101111012111111200221121111021112200100001111101110000121312?112510010121213?10111110020000020111100302111313032311125111111113002?23114101013?????1011020000010311100111121 31??21222011100521300201111110013110101100120101003032121100210 1?020121???223001100000000000

Acrobates 111??1410101412110111100142103013001110???????????????00?3?35313130210200001010113215120004212420?32042211120?001000011210012022210100 1110???3000000010222231000020 2110?????01111100111101201?10112310111101211111120022112111102111220000000111110111000012 1302?11251002012121 3?2?11111002?0?10201111003021113130323111251111111113002?23114101013?????10110200000101111011120 2131??212?1111005213102011131000031101011001201010020321211002111112 0121???223001100000000000

Phascolarctos 111??1310101402110111100142103013001100???????????????00?3?35313130320200001330113204130004312420?32042211120?00100100?2301120222101110110???4200001???332233?20010211 1?????01111100111101201?1011231011110121111112002211211110211122001000011111011100001213 02?

PeerJ PrePrints

```
112510020121213?10111110021001020112100302111001032311125111111113002?
23114101013?????10110200000102111011111212131??
2112011100321300201113110014100101110120101003032011000211110201 21???
223001100000000000

	Vombatus	111??1410101402110111100142103013001100???????????????00?3?
353131303202000013301132041310043124 20?32032211120?00100000?
230112022210111011 0???4301012???332233?201?02112?????011111001111 01201?
101123101111012111111200221121111021112200100001111101101000121302?
112510020121213?10111110021001020112100302111 0?0032311125111111113002?
23023101013?????1011020000010111100111112131??
2112011100521300201113100014110101100120101003032021000211110011 21???
223001100100000000

	Phalanger	111??1410101402110111100142103013001110???????????????00?3?
353131303202000013300132151200043124 20?32042211120?00100100?
230012022210111011 0???320000001022222202102021 11?????011111001111 01201?
101123101111012111111200221121111021112200000000111110111000 0121302?
112510020121213?20111110021001020112100302111313032311125111111113002?
23114101013?????1011020000010311100111112131??
2122111100521310201113110013100101100120101003032021000211111201 21???
223001100000000000

	Pseudocheirus	111??1410101402110111100142103013001110????????????????0?3?
353131303202000013300132041300042124 20?32042211120?00100100?
230112022210111011 0???3200001010332232000020211 1?????011111001111 01201?
101123101111012111111200221121111021112200000000111110111000 0121302?
```

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.755v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

```
11251002012121 3?20111110021001020112100302111313032311125111111113002?
23114101013?????101102000001031110011212131??
2122111100521310201112100003110101100120101012032121000211111 20121???
223001100000000000

	Petauroides	111??1410101402110111100142103013001110???????????????0?3?
35313130320200001330013204130004212420?32042211120?00100100?
230012022210111011 0???3200000010332232000020211 1?????01111100111101201?
10112310111101211111200221121111021112200000000111110111000121312?
11251002012121 3?20111110021001020112100302111313032311125111111113002?
23114101013?????101102000001031110011212131??
2122111100521310201112100002110101100120101012032121100210111 20121???
223001100000000000

	Perameles	11???1410101412110111100142103013001110??????????????00?
302101302021021100121111321512000321222102202222112 0?
0010210102200120222111001 11?000200000000022222101002121 01?????011111001111101201?
10112310111101211111200221121211021112200000000111110110100 0121302?
11251002012121 3?10111110020010020111100302011202112311125111111113002?
23114101013?????101102000001021110111112131??
2111011100421200201112100002100101101120101002032121000211101 10121???
223001100000000000

	Dryolestes	11?1111100002020??
102100002111013001110000000101010011001130110121200004000000001100001?0??000?
0020?00???000??0??0001000?000022022111 0??0100000110 0??01011100000000301110????
```

20???????????????????????????????????????1?
110??
1???
?????????????????1???10?0?????????????????????????0???0??????????????0100000011

Henkelotherium 11?101110000202 1??102100?0211101300111000000?
0101001100113011012120000400000001100001?0??000?0020?00???000??0??0001000?
0000220221110??0100000??????010?110000000??01??0??????0?????011110??0???01121111?
110?111011?00000002100012 1?022000000011100011100010????????
1???????????????????????0???0?1011???1020?11?00?2311124??11?1?1??2?
1[12]1???????????????0????011??????21??[12]????????????????????????[12]????1?????20001?
1???????????20???????????????????????????000?00000001?

Crusafontia 11?1011100012021??
112100012113013001110000000101010011001130000121200002000000001100001?0??000??
020?00???[03]????0??0001000?0000220221110??010?0001100??0?011100000000?011?
0???
??
??
?????????????????0?00000001?

Leonardus ???2?1????????????????????????????????????0???1110100 2??01301101212?
0?0?000000?2?0?000?0???0????20?00???3????0??0001000?0100220221110??010?
000?????????????3???
1???
??

PeerJ PrePrints

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

??101010000?

Mesungulatum 1????1?????????????0?????1?????????????0000??1113?011?0013001112120000103010001100001?00?000?0020?00??03????0??0001000??000320221110??010?000??????????223342?10????1??1?10011111?

Coloniatherium 11?2?1110??1???1??1011?[01]11???3?????01100000?01113100120013001112120000403010001100001?00?000?0020?01???3????0??0001000?01003202?1110??010?000??????0101223342?10???11???311125011111?[12]00221111??????????????011?211101???121121?????????2??1?10011111?

Reigitherium 1??2?1?????1???????011???1??????2??11????0???101310000011300111121?0000403010001100001?00??00?002???????3?????????????0?0??0320220110??010?000???????????2?3????0????1???3??125??1111?[12]????2?11??10111111?

PeerJ PrePrints

```
    Paraungulatum    ???????????????????????????????????????????????1?????????
3001113???????????0??????????????????????????????????????????????0?20??1100??010?
000?????????????????????????????????????????????????????????????????????????????????????
????????????????????????????????????????????????????????????????????????????????????????
????????????????????????????????????????????????????????????????????????????????????????
???????????????????????????????????????????????101?1111?

    Groebertherium    ?????????????????????????????????????????0??????????????
23011112120000402010?01100?01?0??1???0020000???3????0??0001000?0100220221110??
010?
000?????????????????????????????????????????????????????????????????????????????????????
????????????????????????????????????????????????????????????????????????????????????????
????????????????????????????????????????????????????????????????????????????????????????
???????????????????????????????????????????????10010001?

    Peligrotherium    11?2?1110??1??11??1011?020??2[13]?13??0?10??0??
0111311022001300111212?0002030100?1?0?000?0???0??0020?00???3????0??0001000?
0100330221110??010?0001?????0101223342?10???
11?????????????????????????????????????????????????????????????10??????????????????
0?????????????????????????????????????????????????????0??????????125????11?0??1?
1[23]1???????????????1[01]????2?11??????21?12?????????2?????????????2???????????????
0??????????????????0?1??[01]??????????????????0?10111110?

    Amphitherium    11?1111100002021??11210?01210301200111011?0?00000001?
00013011013000100200000000110000210?0000??111100???000??0??0001000?
200021022111000000000001?00????0??000?0?
00??????????????????????????????????????????????????????????????????????????????????????
```

PeerJ PrePrints

??0000000000?

Cronopio 1112?1310001401110101100?021111110001??00000101130002000130110121200004000000002100000?0?0000?0020?00???3????0??0101000?0200220221110??010?000?3??0?01012233??01001?1100?????0???0000101?011?1??231112[45]010?1111012?1?1??10?011?01101011?2?110010?0210?21????????21[02]?????????????0??????????1???0?1011??????0???????????0[01]100?000??2??02?1????01001?0001

Necrolestes 1?12?1100001412110101100102113112000111000000001101002200130210121100?0400000002200?00?0?0?0????20?00???3????0??0101000?0200220222100??010?0001000000101223330010010?0000?1?100?1?1???1??0??????????1????10???11?111010101111??????10?????????00??101??0????1?2??1???????????????????????????????2??10000?01?01113?1??01115?1???111??0?2?11?????????????01112?00101?0?110121????????21?11???????????11????10100?00?11???1?0???????0???2?0??2???1000???????????0001100100??1

Notoryctes 1112?12100014121101111001121031120001100000?00110100110013011013020000400000000210000 01?0?0?00??110?00???3????0??0001000?2000220221100?001000002[23]000010202333201 0000??00????101111100111002 01?1011211111110121111101101100 21?00?2111220?000001110000110001221303?1115000201110100101102?110011011001 1?001020111???123111230111?11100011??1?101013?????1011020000010 2?11012???212000211 00??000421??02[01]1102???102100101111??????0100??1110?02?00?000??2????2??000001010000001

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

PeerJ PrePrints

Appendix 3. Diagnosis of selected clades

Theriiformes (Multituberculata + Zatheria) 60-1, 124-2, 179-0, 181-1, 182-1, 183-1, 208-1, 219-1, 228-1, 238-1, 139-1, 240-1, 244-2, 252-1, 268-1, 272-1, 273-1, 292-1, 300-1, 345-1, 363-1, 384-1, 399-2, 418-0.

Zatheria (Spalacotherioidea + derivados) 13-2, 36-1, 72-0, 175-1, 210-1, 216-1, 227-1, 230-1, 245-1, 307-1, 320-1, 322-1, 397-1, 416-1.

Dryolestoidea + Vincelestes et al. 7-1, 20-1, 33-2, 115-1, 148-0, 150-0, 177-1, 178-1, 189-1, 219-2, 254-1, 267-1, 293-1, 313-2, 350-1, 351-1, 362-2.

Vincelestes + et al. 24-1, 47-0, 64-3, 85-2, 95-1, 186-1, 213-0, 284-1, 294-1, 297-2, 342-1, 416-0, 446-1.

Theria 60-2, 82-1.

Metatheria 10-1, 40-0, 104-1, 155-2, 157-1, 158-1, 162-1, 218-1, 221-1, 222-1, 223-0, 256-1, 261-4, 262-2, 273-2, 274-1, 278-1, 279-1, 419-3.

Marsupialia 44-2, 109-0, 111-0, 321-1, 328-3, 349-0, 352-0, 360-0, 429-1.

Australidelphia 113-1, 117-0, 119-0, 161-0, 256-2, 286-1, 322-3, 420-2.

Eutheria 22-2, 42-1, 43-1, 46-1, 47-2, 68-2, 80.2, 95-2, 98-0, 108-1, 118-0, 136-1, 137-1, 143-0, 189-0, 254-1, 257-2, 258-1, 268-3, 288-1, 298-1.

Dryolestoidea 99-0, 136-1, 244-1, 325-2, 458-1

Dryolestida 33-3, 45-1, 52-1, 56-1, 153-1, 154-0, 155-0, 457-1

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014

Notoryctes + Meridiolestida 4-2, 13-4, 21-1, 31-1, 36-0, 48-1, 50-1, 104-3, 143-3, 152-2, 159-1, 172-1, 220-1

Notoryctes 7-4, 29-0, 54-1, 64-3, 95-1, 120-2, 142-2, 148-1, 150-2, 174-1, 211-0, 212-1, 244-0, 254-3, 289-1, 337-3, 350-0, 351-0, 356-2, 400-1, 406-1, 451-1

Meridiolestida 20-0, 53-2, 85-0, 121-2, 162-1, 293-0, 299-1, 301-0, 450-1, 453-1

Mesungulatoidea 60-0, 124-3, 454-1, 455-1, 456-1.

PeerJ PrePrints

PeerJ reviewing PDF | (v2014:12:3598:0:1:NEW 20 Dec 2014)

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.745v1 | CC-BY 4.0 Open Access | rec: 21 Dec 2014, publ: 21 Dec 2014