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ORIGINAL PAPER

# Rooting Around the Eutherian Family Tree: the Origin and Relations of the Taeniodonta

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**Abstract** Placing early groups into the overall phylogeny of eutherian mammals can be challenging, particularly when the group does not have extant members. We investigated the relationships of the Taeniodonta, an extinct group from the Late Cretaceous through Paleogene of North America. This group has a few purported close relatives, including *Cimolestes*, *Procerberus*, and *Alveugena*, that may form a sequence of ancestors and descendants. The leading hypothesis is that *Procerberus* gave rise to taeniodonts through *Alveugena*. We test this hypothesis and analyze relations to known stem and crown Eutheria to determine the place of taeniodonts in eutherian phylogeny. Cladistic analyses were performed using previously published characters and datasets, namely a taeniodont/cimolestid specific dataset and a reanalysis of Wible and colleagues (2009), with added taxa for both. Our studies suggest that taeniodonts arose from *Cimolestes* through *Alveugena*, that *Procerberus* is more distantly related to taeniodonts, and that taeniodonts and their relatives are stem eutherians. We diagnose the Taeniodonta based on these analyses. Other Paleogene groups, especially those allied with *Cimolestes* such as tillodonts and pantolestans, merit further study. Our findings indicate that stem eutherians such as the Taeniodonta, in addition to crown eutherians, continued to diversify during the Paleogene.

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## Introduction

Taeniodonts are especially intriguing eutherian mammals. They are a classic example of rapid evolution, having been one of the first mammalian lineages to reach large body size (Patterson 1949). Their ecology as a group ranging from small insectivores to large, digging herbivores and the morphologies associated is quite distinct. The taeniodonts are a strictly North American group, allowing their biogeographical distribution to be easily gleaned from resources such as the Paleobiology Database and their history of dispersal and radiation inferred (Weinstein, unpublished thesis). Finally, their temporal range from the Late Cretaceous (Fox and Naylor 2003) through the middle Eocene (Turnbull 2004) makes them part of the great diversification of mammals following the mass extinction at the end of the Cretaceous (Fox and Naylor 2003; Rose 2006).

Taeniodonts are one of twenty or so orders of extinct eutherians known only from fossils whose relationships to the living and other extinct groups is unknown (Kielan-Jaworowska et al. 2004; Rose 2006). Determining whether an extinct eutherian order is part of the crown or stem group has been difficult, both because few characters distinguish crown and stem eutherians and because the ancestral condition of the crown group for many characters is unknown. Extinct group placement is further complicated by molecular sequence analyses (e.g., Springer et al. 2004) that leave out any group without some living representatives. Progress in the emergence of a stable tree for extant eutherian mammals has realigned relationships among living orders but unfortunately resulted in a large number of orphaned extinct lineages, whose relationships to the extant orders and even membership in the crown group remain uncertain. Taeniodont placement within Eutheria is further hampered by their highly modified morphology, obscuring potential synapomorphies that might be shared with other groups.

The origin of Taeniodonta has been under debate for over a century. Though the group was originally allied with rodents (Cope 1888) and edentates (Wortman 1896, 1897; Matthew 1937), more recent hypotheses agree that taeniodonts are one of the many lineages descended from *Cimolestes*, an early, primitive eutherian mammal known from the Late Cretaceous and early Paleocene of North America (Lillegraven 1969; McKenna 1969). *Procerberus*, another purported descendant of *Cimolestes*, has been consistently suggested as the link between *Cimolestes* and the taeniodonts (Lillegraven 1969; McKenna 1969). The early species *P. formicarum* and the larger *P. grandis*, which has taeniodont-like tooth wear, have been suggested as the lineage that gave rise to the taeniodonts (Eberle 1999). *Alveugena*, a relatively recent find, has been well supported as the bridge between *Procerberus* and the taeniodonts (Eberle 1999; Rook et al. 2010).

Whether any given extinct eutherian taxon is part of the stem or crown group helps to constrain the time of appearance of the crown group, which further allows molecular phylogeneticists to estimate divergence times (e.g., Springer et al. 2003) and paleontologists to test those estimates (Foote et al. 1999; Hunter and Janis 2006). Differences in crown and stem members of the Paleogene diversification help resolve how the Cretaceous/Paleogene extinction event impacted the evolution of the Eutheria, a topic of ongoing discussion and debate (Savage and Russell 1983; Alroy 1999; Novacek 1999; Archibald and Deuthschmann 2001; Rose and Archibald 2005; Rose 2006; Bininda-Edmonds et al. 2007; Wible et al. 2007, 2009; Meredith et al. 2011; O'Leary et al. 2013).

Here, using cladistic analysis, we test the hypotheses that *Cimolestes, Procerberus*, and *Alveugena* are sister taxa to the taeniodonts and that the taeniodonts are monophyletic. We also test the hypothesis that taeniodonts are members of the crown group of Eutheria. In order to accomplish these goals, we adapted character sets already used to explore the relationships among taeniodonts and their presumed close relatives (Schoch 1986; Eberle 1999; Rook et al. 2010; Rook and Hunter 2011) and the best dataset available at the present time for testing crown or stem group status of extinct eutherians (Wible et al. 2007, 2009).

## Materials and Methods

### Cladistic Analyses

We performed a heuristic branch-swapping cladistic analysis using NONA (Goloboff 1999) and WinClada (Nixon 2002). NONA was used to find the most parsimonious tree(s), calculate branch length, and calculate Bremer support values, which show how many steps longer a tree would need to be before the clade in question is lost (Wenzel 2002). WinClada was used to calculate homoplasy indicators based on the NONA trees: consistency index (CI), based on the number of additional unnecessary evolutionary steps taken in a character; and retention index (RI), determined by how different the character evolution is from the maximum possible number of steps (Wenzel 2002).

### Taeniodont Relations to Basal Cimolestans

Characters follow Rook et al. (2010) and Rook and Hunter (2011), using thirty-seven characters based partly on and modified from Schoch's (1986) monograph on the taeniodonts and Eberle's (1999) analysis of *Alveugena* (see Appendix 1 for character definitions and matrix). Taxa were added to test the hypothesis of basal cimolestan origins of the taeniodonts: *Aaptoryctes*, *Acmeodon*, *Didelphodus*, and *Palaeoryctes*. *Protictis*, an early carnivoramorphan, was chosen as an outgroup because of its phylogenetic remoteness from the groups in question. Characters were scored for nineteen taxa, including all known genera of Taeniodonta, using the literature (Table 1) and observations of taeniodont and other specimens at the American Museum of Natural History and the National Museum of Natural History.

### Stem Versus Crown Eutheria

For investigation into the stem or crown group membership of the Taeniodonta, we used the published character matrix of Wible et al. (2009). *Schowalteria*, the most basal taeniodont (according to Rook et al. 2010; Rook and Hunter 2011) and *Alveugena*, the purported sister taxon (Eberle 1999; Rook et al. 2010) were added (see Appendix 2 for character definitions and codes of added taxa).

## Results

### Taeniodont Relations to Basal Cimolestans

A single most parsimonious tree was returned from 4,458,560 trees searched in the cladistic analysis, with a length of 187, CI of 0.41 and RI of 0.63. Bremer support values were also calculated (see Fig. 1). In the most parsimonious tree, *Alveugena* is the sister group of taeniodonts, with *Cimolestes* as the sister group to the clade *Alveugena* + Taeniodonta. The two *Procerberus* species produce a single clade, unlike in Eberle's (1999) analysis. *Alveugena* is supported as the sister taxon with Bremer value of 3, but the *Cimolestes* connection is less well supported.

### Stem Versus Crown Eutheria

Figure 2 shows the stem portion of the strict consensus of the three most parsimonious trees, from 1,704,982,120 examined,

**Table 1** Literature used for character coding

| Taxa | Literature |
|---|---|
| *Aaptoryctes* | Gingerich (1982) |
| *Acmeodon* | Van Valen (1966); Wilson (1985) |
| *Alveugena* | Eberle (1999); Rook et al. (2010) |
| *Cimolestes* | Lillegraven (1969) |
| *Conoryctella* | Schoch and Lucas (1981a) |
| *Conoryctes* | Schoch (1986) |
| *Didelphodus* | Van Valen (1966) |
| *Ectoganus* | Schoch (1986) |
| *Huerfanodon* | Schoch and Lucas (1981b) |
| *Onychodectes* | Schoch (1986) |
| *Palaeoryctes* | Bloch et al. (2004) |
| *Procerberus formicarum* | Sloan and Van Valen (1965) |
| *Procerberus grandis* | Middleton and Dewar (2004) |
| *Protictis* | Krause and Gingerich (1983) |
| *Psittacotherium* | Schoch (1986) |
| *Schochia* | Lucas and Williamson (1993) |
| *Schowalteria* | Fox and Naylor (2003) |
| *Stylinodon* | Schoch (1986) and Turnbull (2004) |
| *Wortmania* | Schoch (1986) |

found in the eutherian analysis. All three trees have a length of 2328 steps, CI 0.25, and RI 0.5. Bremer support values were also calculated (see Fig. 2). *Schowalteria* and *Alveugena* fall as stem eutherians, within the Cimolestidae. The unambiguous characters that hold together this cimolestid clade are the presence of a single p1 root, the absence of P5 paraconid, precingula on upper molars, postcingula on upper molars, upper molars with prominent paraconule midway or closer to the paracone, and the posterior edge of the anterior zygomatic root is aligned with M1.

## Discussion

### Taeniodont Monophyly

The monophyly of the Taeniodonta has recently been called into question by the discovery of an ancient taeniodont from the Late Cretaceous of Canada, *Schowalteria*. Fox and Naylor (2003) speculated that *Schowalteria* was a stylinodontid, the younger family of taeniodonts, based on certain characters but not on a cladistic analysis. They argued that its early appearance caused Taeniodonta to be a para- or even polyphyletic grouping. This concern has been disputed recently, but is still likely a cause for debate (Rook and Hunter 2011).

Here, the monophyly of Taeniodonta is supported by a Bremer support of 3 (Fig. 1). *Schowalteria* is the sister group to the rest of the taeniodonts (as also in Rook and Hunter 2011), no longer contradicting its early appearance in the fossil record. There are also no autapomorphic characters in this analysis precluding *Schowalteria* from being the ancestral taeniodont (Rook and Hunter 2011). Accordingly, we rediagnose the monophyletic Taeniodonta in the final section of this paper to include *Schowalteria* and all other taeniodonts.

### Taeniodont Relations to Basal Cimolestans

The basal cimolestan tree reported here differs from the phylogenies of Eberle (1999) and Rook et al. (2010). Although *Alveugena* is still the sister taxon to the taeniodonts (Eberle 1999; Rook et al. 2010), *Cimolestes* is the sister taxon to *Alveugena* + Taeniodonta, not *Procerberus*. The *Procerberus* species do not appear as a lineage leading to *Alveugena* and the taeniodonts, contrary to Eberle (1999) and Rook et al. (2010), but are a monophyletic clade (see also Rook et al. 2010). *Alveugena* as a sister taxon to the taeniodonts is again supported (Eberle 1999; Rook et al. 2010), with a Bremer support value of 3.

The original placement of *Cimolestes* as basal to *Procerberus* and *Alveugena* was likely due to its use as an outgroup in those earlier studies (Eberle 1999; Rook et al. 2010). *Cimolestes* is only slightly more primitive in character than *Alveugena*, and using it as an outgroup may have failed to fully polarize characters in the earlier analyses. *Protictis* as the outgroup in this study, chosen because it is completely removed from the problem, allowed *Cimolestes* to fall closer to the taeniodonts than *Procerberus*. In the earlier studies of Eberle (1999) and Rook et al. (2010), *Cimolestes* was constrained to the base of the tree. Although this study agrees with Eberle (1999) and Rook et al. (2010) in supporting the hypothesis of a cimolestid origin of the taeniodonts, it disagrees over which cimolestid (*Cimolestes* or *Procerberus*) is more closely related.

Another pattern that emerges is the paraphyly of McKenna and Bell's (1997) Cimolestidae, which includes *Cimolestes* and *Procerberus* as well as *Didelphodus* and *Acmeodon*. The latter two taxa are here allied with the widely recognized palaeoryctids, *Aaptoryctes* and *Palaeoryctes*. These two "cimolestid" taxa are disputed in their familial placement. Though the paraphyly of the cimolestids is apparent in this analysis, other inferences about the palaeoryctid and cimolestid taxa are beyond the scope of the current study. As for the taeniodonts, they are still more closely related to the cimolestids, particularly *Cimolestes*, than to the palaeoryctids.

### Stem Versus Crown Eutheria

The main result of our large-scale analysis is that the taeniodonts unite with the Cimolestidae, placing them among

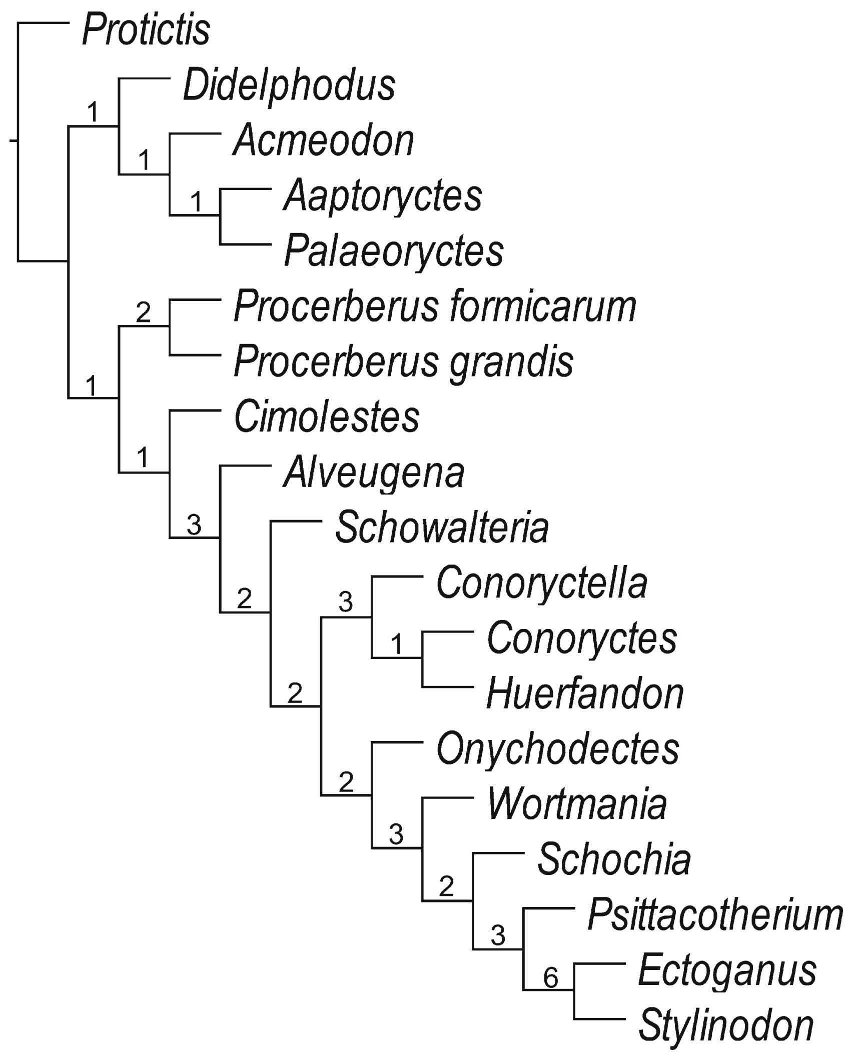


**Fig. 1** Cimolestid tree from cladistic analysis. Single most parsimonious tree found in NONA, with a length of 187, CI of 0.41, and RI of 0.63. Bremer supports from NONA added

stem Eutheria. This study is the first time a taeniodont has been identified as a stem or crown member of the Eutheria, and this analysis places them with the former, along with *Alveugena*. This placement is supported by Bremer supports of 4 for *Alveugena* + *Schowalteria*, and does not change the original Bremer support values of the Wible et al. (2009) Cimolestidae clade. The basal taeniodont is separated from the other cimolestids in this analysis by a number of features: two greatly enlarged lower incisors; a one-tooth-root-width diastema between p1 and p2; double-rooted P4; p5 talonid width equal to the trigonid; lower molars with vestigial paraconids, protoconids subequal in height to the para- and/or metaconids, and m3 smaller than m2; anterior mental foramen below p2, masseteric fossa extending anteriorly onto the dentary body, and a mandibular symphysis extending to p1 or more anteriorly.

The characters listed below emerge as potentially diagnostic for crown Eutheria. Though this study did not explicitly seek out such characters, this list could be a jumping-off point for future research and placement of eutherian groups. The vast majority of the characters separating the stem and crown eutherians in this analysis were dental. Several were molar characters, only three were cranial, and one was a premolar character— a diastema present between the first and second lower premolars. The characters of the upper molars included a strongly reduced or absent ectoflexus, a metacone and paracone that are subequal with bases separated, and weak or absent postmetacrista. The characters of the lower molars were trigonids less than twice or subequal in height and subequal or narrower in width than talonids, and possessing a protoconid that is subequal to the paraconid and/or metaconid. Finally, the cranial characters, all from the dentary, were the absence of a condyloid crest, a condylar process lacking a posteriorly directed peduncle, and a condyle that lies above the tooth row by more than a molar length. These characters show once again that the taeniodonts belong with the stem eutherian mammals and not with any later-appearing clade. This list also gives researchers specific characters that may be used to distinguish extinct stem from crown eutherians in the future.

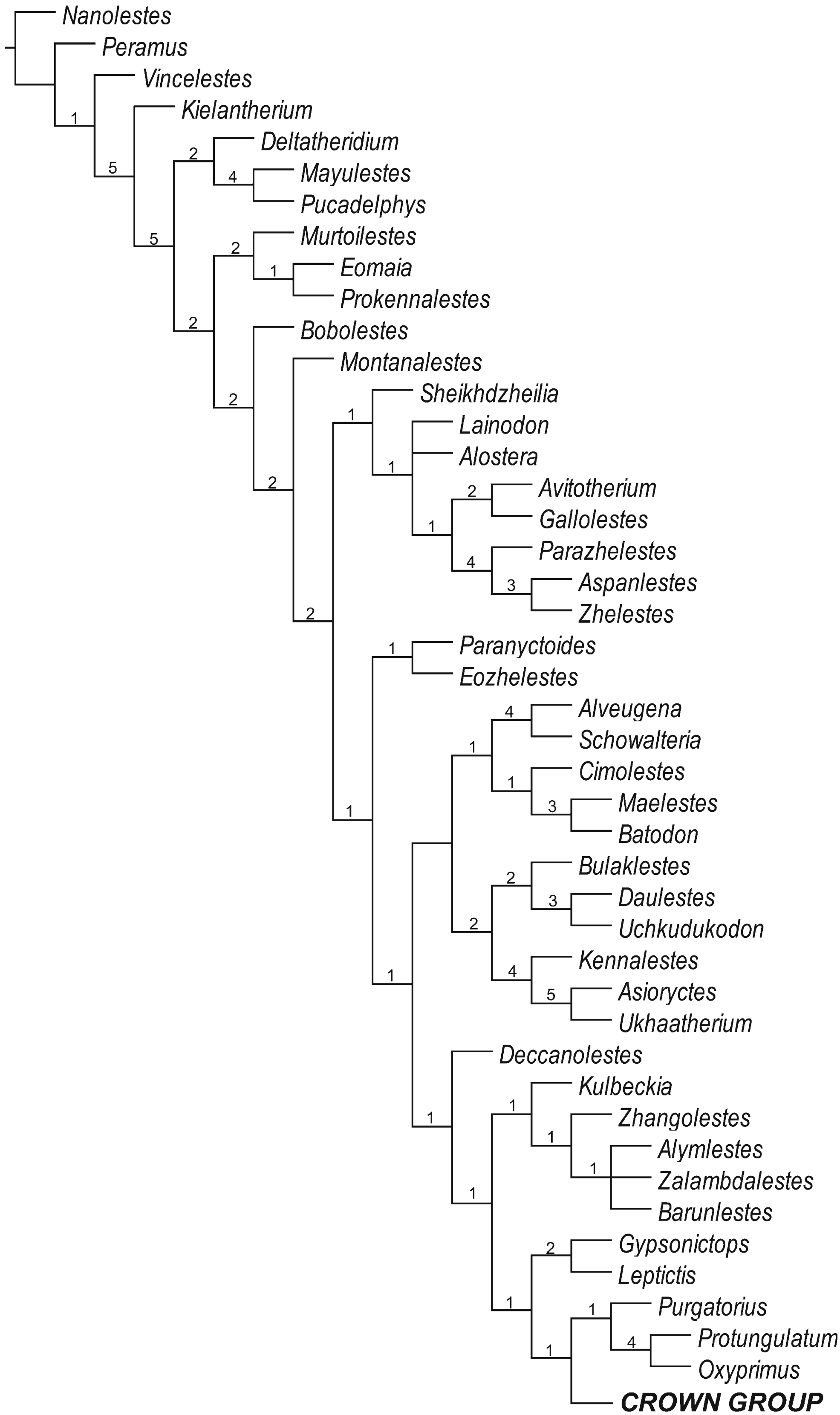


**Fig. 2** External relations among Eutheria from cladistic analysis. Strict consensus of three most parsimonious trees found in NONA, each with length 2328, CI 0.25, and RI 0.54. Bremer supports from NONA added. Crown group node collapsed to focus on stem placement of our taxa and for space. Full tree figure can be found in Appendix 2

Character states that place the taeniodonts among the stem eutherians are best seen in the oldest, most basal members of the group. More derived, later taeniodonts appear to converge on some crown eutherian states, such as reduced upper molar stylar shelves and nearly equal lower molar trigonid and talonid heights. This distribution of character states hints at possible future avenues of study involving the parallel and convergent evolution of some traits in crown and stem eutherians in the Paleogene.

## Conclusions

It has been suggested that taeniodont origins lie within the basal cimolestids (including *Cimolestes*) (McKenna 1975). In these analyses, it is evident that *Alveugena* is the sister group of taeniodonts, but *Cimolestes* may be more closely related to the taeniodonts than *Procerberus*, as opposed to *Procerberus* being more closely related to taeniodonts in the studies of Eberle (1999) and Rook et al. (2010). *Cimolestes* and *Alveugena* are the closest sister groups to the taeniodonts, and quite possibly form an ancestral sequence. No other cimolestan genus included is more closely related. Taeniodonta to all evidence is also monophyletic (Rook and Hunter 2011; Rook et al. 2010), and we present a revised diagnosis of the clade in the following section.

Taeniodonts and *Alveugena* are placed as stem eutherians along with *Cimolestes*. Their placement as stem eutherians and use in the current analysis have helped to determine several characters that could be used to distinguish stem from crown eutherians in the future. These analyses show once again that crown and stem eutherians were diversifying together through the Paleogene.

## Systematic Paleontology

MAMMALIA Linnaeus, 1758
EUTHERIA Gill, 1872
**Taeniodonta** Cope, 1876

*Included Genera. Onychodectes* Cope, 1888, *Wortmania* Hay, 1899, *Conoryctes* Cope, 1881, *Conoryctella* Gazin, 1939, *Huerfanodon* Schoch and Lucas, 1981a, *Psittacotherium* Cope, 1882, *Ectoganus* Cope, 1874, *Stylinodon* Marsh, 1874, *Schochia* Lucas and Williamson, 1993 (now *Robertschochia* Lucas, 2011), and *Schowalteria* Fox and Naylor, 2003.

*Distribution.* Lancian (Late Cretaceous) to Uintan (middle Eocene) of western North America, Tiffanian (middle to late Paleocene) and Uintan of Texas, and Tiffanian of South Carolina.

*Diagnosis*. Larger than cimolestids and differs from *Cimolestes* and *Alveugena* in the following ways: upper and lower canines moderate to large, stout, and recurved; P1/p1 single rooted, P2/p2 double rooted, P4 triangular, p4 premolariform, P5 with well-developed paracone and protocone, lacking a metacone, with cuspate stylar shelf, and p5 nonmolariform with a well-developed talonid heel, more so than the cimolestids; upper molars molariform with small, lingually placed protocone and conules, paracone and metacone moderate and placed far labial, small stylar shelf, no pre- or post-cingula, ectocingula present and well developed; lower molars with variable relative trigonid/talonid widths, trigonid/talonid heights generally subequal and where different never as different as with the cimolestids, protoconids and metaconids subequal with smaller paraconid placed more labial than the metaconid, and lacking the accessory talonid notch cusp and expanded m3 talonid of *Cimolestes* and *Alveugena*; hypsodonty found in all cheek teeth, with early animals showing more crown hypsodonty and later showing more root hypsodonty to hypselodonty; and the wear pattern generally over entire surface of cheek teeth and often deep enough to expose pulp cavity.

*Comments on Diagnosis.* We numbered premolars assuming an ancestral count of five of which the third upper and lower premolars are lost in crown eutherians and some stem eutherians (e.g., Wible et al. 2009). Although the Taeniodonta has not been formally diagnosed, Schoch (1986) provided a detailed list of taeniodont characteristics. The diagnosis above has been modified from Schoch's (1986) list. Premolar, canine, and wear characters were added, and also lower molar paraconid characters. Characters removed or modified include subequal talonid and trigonid on the lower molars and decreasing molar size posteriorly.

*Discussion.* Taeniodonta is here referred to as a monophyletic clade as demonstrated above in the phylogenetic analysis. The new discovery of *Schowalteria* has modified the diagnosis the most, as it is the earliest and most basal taeniodont, whereas *Onychodectes* had been claimed as most basal at the time of Schoch (1986). Although the monophyly of this group has been debated, these parsimony analyses, the first undertaken of the entire group along with non-taeniodonts among both crown and stem eutherians, show that the Taeniodonta is a monophyletic stem eutherian group.

A recently published study of eutherian relationships (O'Leary et al. 2013) reported a single most parsimonious tree in which *Protungulatum donnae* occurs within the eutherian crown group and an assumption that *Purgatorius* does as well. Using the character matrix of Wible et al. (2009), we recovered *Protungulatum* and *Purgatorius* as part of the sister taxon to the crown group (Figs. 2 and 3; see also Wible et al. 2009). Enlarging the crown group in our tree to include *Protungulatum* and *Purgatorius*, but also to exclude taxa that O'Leary et al. (2013) found to be stem eutherians (*Maelestes*, *Ukhaatherium* and *Zalambdalestes*) would not change our main inference that cimolestids and taeniodonts are stem eutherians.

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## Appendix 1: Cimolestid Versus Palaeoryctid Analysis-Characters and Matrix from Analysis

### Characters

These characters are the same as those used in Rook et al. (2010) and Rook and Hunter (2011). The characters appeared originally either in Schoch (1986) as uncoded lists or in Eberle (1999) coded for *Cimolestes, Procerberus formicarum, P. grandis, Alveugena,* and *Onychodectes* only. We cite below the source for each character. All taxa were coded by the senior author for characters modified from Schoch (1986). Similarly, all taxa, other than those listed above, were coded by the senior author for the characters from Eberle (1999). Additive characters are marked below with an asterix (*) and follow Eberle (1999), Rook et al. (2010), and Rook and Hunter (2011) in treating these characters as additive, based on the character states needing to progress through the central state (for instance, "medium") before being either extreme. Premolars again are numbered assuming an ancestral count of five (e.g., Wible et al. 2009).

1. Upper molar protocone size (Schoch 1986) *

   0 = small
   1 = moderate
   2 = large

2. Upper molar conule size (Schoch 1986)

   0 = small
   1 = large
   2 = absent

3. Placement of conules on upper molars (modified from Eberle 1999)

   0 = labial
   1 = lingual

4. Upper molar paracone size (Schoch 1986) *

   0 = small
   1 = moderate
   2 = large

5. Stylar margin on upper molars (Eberle 1999) *

   0 = large, inflated stylar lobes; forward-projecting, parastylar lobe extends labially beyond, and often hooks around, metastylar lobe on tooth directly in front of it; stylar lobes appear largest on M2
   1 = para- and metastylar lobes relatively smaller than those of *Cimolestes* and *Procerberus formicarum,* but still relatively inflated; parastylar lobe is not hook-like, does not project anteriorly, and projects only slightly more labially (if at all) beyond metastylar lobe of tooth directly anterior to it
   2 = small, weak, uninflated stylar lobes; stylar shelves very narrow to absent; M2 stylar lobes subequal in size to those of other molars

6. Upper molar metacone size (Schoch 1986) *

   0 = small
   1 = moderate
   2 = large

7. Lingual cingula on upper molars (Eberle 1999)

   0 = present
   1 = absent

8. Lower molar trigonid height (modified from Eberle 1999) *

   0 = trigonid noticeably higher than talonid
   1 = trigonid only slightly higher than talonid
   2 = trigonid equal in height to talonid

9. Lower first molar trigonid width (modified from Eberle 1999)

   0 = trigonid wider than talonid
   1 = trigonid equal in width to talonid
   2 = width variable within taxon

10. Lower second molar trigonid width (modified from Eberle 1999)

    0 = trigonid wider than talonid
    1 = trigonid equal in width to talonid
    2 = width variable in taxon

11. Lower third molar trigonid width (modified from Eberle 1999)

    0 = trigonid wider than talonid
    1 = trigonid equal in width to talonid
    2 = width variable in taxon

12. Lower molar paraconids versus metaconids (Schoch 1986)

    0 = not equal
    1 = subequal

13. Molar hypsodonty (modified from Eberle 1999) *
    0 = absent
    1 = present
    2 = hypselodonty
14. P4 morphology (modified from Eberle 1999) *
    0 = triangular
    1 = submolariform
    2 = molariform
15. P5 morphology (modified from Eberle 1999) *
    0 = triangular
    1 = submolariform
    2 = molariform
16. p5 talonid heel (Schoch 1986) *
    0 = small
    1 = moderate
    2 = well developed
17. P5 parastyle (modified from Eberle 1999) *
    0 = absent
    1 = incipient
    2 = small
    3 = well developed
18. P5 stylocone (modified from Eberle 1999) *
    0 = absent
    1 = incipient
    2 = small
    3 = well developed
19. P5 metastyle (modified from Eberle 1999) *
    0 = absent
    1 = incipient
    2 = small
    3 = well developed
20. Lower molar paraconids (Schoch 1986) *
    0 = small
    1 = moderate
    2 = large
21. P1 (Schoch 1986)
    0 = present
    1 = absent
22. p5 morphology (Schoch 1986) *
    0 = nonmolariform
    1 = submolariform
    2 = molariform
23. M1 and M2 mesostyle (Schoch 1986)
    0 = absent
    1 = small
    2 = moderate
    3 = well developed
24. Premolars set obliquely (Schoch 1986)
    0 = no
    1 = yes
25. Lower canines (Schoch 1986) *
    0 = small
    1 = moderate
    2 = large
26. Upper incisor number (Schoch 1986) *
    0 = 3
    1 = 2
    2 = 1
27. Lower incisor number (Schoch 1986) *
    0 = 3
    1 = 2
    2 = 1
28. p4 morphology (Schoch 1986) *
    0 = nonmolariform
    1 = submolariform
    2 = molariform
29. Lower canine root (Schoch 1986) *
    0 = shallow
    1 = deep
    2 = tending towards rootlessness
    3 = rootless
30. Bilophodont molars (Schoch 1986)
    0 = absent
    1 = present
31. Transverseness of upper molars (Eberle 1999) *
    Relative Transverse Width (RTW) = Maximum Transverse Width/Anteroposterior length
    0 = transverse (RTW of M1 > 1.30)
    1 = less transverse (1.30 > RTW of M1 > 1.20)
    2 = weakly to nontransverse (RTW of M1 < 1.20)
32. Development of molar ectoflexus (Eberle 1999) *
    0 = pronounced and deep, particularly on M2
    1 = small, shallow indentation
    2 = virtually absent, resulting in a relatively straight stylar shelf
33. Size of M2 relative to M1 (Eberle 1999) *
    0 = M2 noticeably larger than M1
    1 = M2 shorter but more transverse than M1
    2 = M2 subequal in size to, or slightly smaller than, M1

34. Upper molar lingual length (modified from Eberle 1999)

    0 = not pronounced
    1 = pronounced

35. Metacrista on upper molars (modified from Eberle 1999) *

    0 = well developed
    1 = reduced
    2 = absent

36. Lower molar cingulids (Eberle 1999)

    0 = present
    1 = absent

37. Wear pattern on upper molars and premolars (Eberle 1999)

    0 = not pronounced over entire occlusal surface
    1 = pronounced over entire occlusal surface

Matrix

| | |
|---|---|
| *Protictis* | 1102000000010111303101101000100111110 |
| *Cimolestes* | ?100000000000000133300000???0000000000 |
| *Acmeodon* | 020210100000012???111101??0?00010000 |
| *Aaptoryctes* | 2110001000000011000011000?00000010100 |
| *Palaeoryctes* | 22?200100000011133 00?0001?00000010000 |
| *Didelphodus* | 0202000000000011202101001001000000000 |
| *Procerberus formicarum* | 0100000000000022?333?0000???0001000100 |
| *Procerberus grandis* | 01001001000?0222333200001??0001000101 |
| *Alveugena* | 0?01110000?000002320000011?0001111101 |
| *Schowalteria* | ????0?11100?1002232000?021?1000001?11 |
| *Onychodectes* | 0101211122011011121200001000002221111 |
| *Conoryctella* | 2202221122201011232201102000201121111 |
| *Conoryctes* | 2202221120001121232011202110100221111 |
| *Huerfanodon* | 021222112001 11?2???111302??0102221011 |
| *Schochia* | 1102201?????102?010???01??????02211?1 |
| *Wortmania* | 10-2201000?1100211110001222001021 1111 |
| *Psittacotherium* | 2212201220001112010001012221210221111 |
| *Ectoganus* | 2212221220211222010002012222312221211 |
| *Stylinodon* | ????2?12111?2222010?02?12122312221?11 |

## Appendix 2: Stem/Crown Analysis- Characters, Matrix, and Full Figure from Analysis

Characters

Dental and cranial characters used from Wible et al. (2007, 2009). As in the original study, there are 408 dental, cranial, and postcranial characters. Characters coded here for *Alveugena* (A) and *Schowalteria* (S); all others can be found in Wible et al. (2009).

1. Teeth (A, S)

    0 = present
    1 = absent

2. Teeth (A, S)

    0 = differentiated into classes (incisors, canines, premolars, and molars) with enamel
    1 = simple peg-like without enamel

3. Number of postcanine tooth loci (A, S)

    0 = eight or more
    1 = seven
    2 = six
    3 = five or less

4. Upper diastema (A)

    0 = small, between incisors and canine
    1 = small, between canine and premolars
    2 = enlarged
    3 = absent

5. Lower diastema behind incisors (S)

    0 = absent or small
    1 = enlarged

*Dentition – Incisors*

6. Incisor shape (A)

    0 = root and crown are straight and continuous in length
    1 = a continuous curve

7. Number of upper incisors (A)

    0 = five
    1 = four
    2 = three
    3 = two
    4 = one
    5 = none

8. Number of lower incisors (S)

    0 = four
    1 = three
    2 = two, anterior position
    3 = one
    4 = none or posterior position(s) only

10. Anteriormost upper incisor size (S)

    0 = small, subequal to subsequent
    1 = enlarged
    2 = smaller than subsequent

14. Ultimate upper incisor (A, S)
    0 = in premaxilla
    1 = between maxilla and premaxilla
    2 = in maxilla
15. Anteriormost lower incisor size (S)
    0 = small, subequal to subsequent incisors
    1 = greatly enlarged
    2 = or tiny, smaller than subsequent
17. Procumbent anteriormost lower incisor (S)
    0 = absent
    1 = present
18. Anteriormost lower incisor root (S)
    0 = closed
    1 = open
21. Procumbent posterior lower incisor(s) (S)
    0 = absent
    1 = present
22. Staggered lower incisor (S)
    0 = absent
    1 = present

*Dentition – Canine*

23. Upper canine (A, S)
    0 = present, large
    1 = present, small
    2 = absent
24. Number of upper canine roots (A, S)
    0 = two
    1 = one
25. Lower canine (A, S)
    0 = present, large
    1 = present, small
    2 = absent
26. Number of lower canine roots (A, S)
    0 = two
    1 = one
27. Procumbent lower canine (A, S)
    0 = absent
    1 = present

*Dentition – Premolars*

29. Number of premolars (A, S)
    0 = five or more
    1 = four
    2 = three
    3 = two
31. Tall, trenchant premolar (A, S)
    0 = ultimate premolar
    1 = penultimate premolar
    2 = absent
32. Procumbent first upper premolar (A, S)
    0 = absent
    1 = present
33. First upper premolar roots (A, S)
    0 = two
    1 = one
    2 = three
34. Diastema posterior to first upper premolar (S)
    0 = absent
    1 = present
36. Penultimate upper premolar protocone (A)
    0 = absent
    1 = small lingual bulge
    2 = with an enlarged basin
37. Penultimate upper premolar metacone (A)
    0 = absent
    1 = swelling
    2 = large
38. Penultimate upper premolar parastylar lobe (A, S)
    0 = absent or small
    1 = well developed
39. Penultimate upper premolar roots (A, S)
    0 = two
    1 = three
    2 = one
    3 = four
40. Ultimate upper premolar protocone (A)
    0 = absent or narrow cingulum
    1 = shorter than paracone
    2 = approaches paracone in height
41. Ultimate upper premolar metacone (A)
    0 = absent
    1 = swelling
    2 = large
42. Ultimate upper premolar para- and metastylar lobes (A, S)
    0 = absent or insignificant
    1 = subequal
    2 = parastylar lobe larger
    3 = metastylar lobe larger

43. Ultimate upper premolar precingulum (A)

 0 = absent
 1 = present

44. Ultimate upper premolar postcingulum (A)

 0 = absent
 1 = present, lower than protocone
 2 = present, level with protocone

46. Ultimate upper premolar size (occlusal surface) relative to first upper molar (A, S)

 0 = smaller or subequal
 1 = larger

47. First lower premolar orientation (A, S)

 0 = in line with jaw axis
 1 = oblique

48. First lower premolar roots (A, S)

 0 = two
 1 = one

49. Diastema separating first and second lower premolars (A, S)

 0 = absent (gap less than one tooth root for whichever is smaller of adjacent teeth)
 1 = present, subequal to one tooth-root diameter or more

52. Penultimate lower premolar paraconid (A, S)

 0 = indistinctive or absent
 1 = present and distinctive

53. Penultimate lower premolar metaconids (A, S)

 0 = absent
 1 = swelling
 2 = separate from protoconid

54. Penultimate lower premolar talonid cusps (A, S)

 0 = one
 1 = two
 2 = three

55. Ultimate lower premolar paraconid (A, S)

 0 = indistinctive or absent
 1 = distinctive but low
 2 = distinctive and high

56. Ultimate lower premolar metaconids (A, S)

 0 = absent
 1 = swelling
 2 = large

57. Ultimate lower premolar talonid (A, S)

 0 = narrower than anterior portion of crown
 1 = as wide as anterior portion of crown

59. Length of ultimate lower premolar to penultimate (A, S)

 0 = longer
 1 = equal to or less

60. Ultimate lower premolar anterolingual cingulid (S)

 0 = absent
 1 = present

*Dentition – Molars*

61. Number of molars (A, S)

 0 = four or more
 1 = three
 2 = two

62. Size of molar series (A, S)

 0 = subequal
 1 = posterior increase
 2 = posterior decrease

63. Molar cusp form (A, S)

 0 = sharp, gracile
 1 = inflated, robust
 2 = crest-like

64. Upper molar shape (A, S)

 0 = as long as wide, or longer
 1 = wider than long (length more than 75 % but less than 99 % of width)
 2 = much wider than long (length less than 75 % of width)

65. Size (labiolingual width) of upper molar labial stylar shelf at maximum (A, S)

 0 = 50 % or more of total transverse width
 1 = less than 50 % but more than 25 %
 2 = less than 25 %
 2 = absent

66. Labial extent of parastylar and metastylar lobes (A, S)

 0 = parastylar lobe more labial
 1 = subequal
 2 = metastylar lobe more labial
 3 = lobes absent

67. M1 parastylar lobe relative to paracone (A, S)

 0 = parastylar lobe is anterolabial to paracone
 1 = parastylar lobe is anterior to paracone

68. Length of parastylar lobe (measured to stylocone or stylocone position) relative to total length on penultimate molar (A, S)

 0 = more than 30 %
 1 = less than 30 % but more than 20 %
 2 = 20 % or less

69. Preparastyle (A, S)
0 = absent
1 = present

70. Stylar cusp A (A, S)
0 = subequal to larger than B
1 = distinct, but smaller than B
2 = vestigial to absent

71. Stylar cusp B relative to paracone (A, S)
0 = smaller but distinctive
1 = vestigial to absent
2 = subequal

72. Stylar cusp C, mesostyle (A, S)
0 = absent
1 = present

73. Stylar cusp D (A, S)
0 = absent
1 = smaller or subequal to B
2 = larger than B

74. Stylar cusp E (A)
0 = directly lingual to D or D-position
1 = distal to D
2 = small to indistinct

75. Preparacingulum (A, S)
0 = absent
1 = interrupted between stylar margin and paraconule or paraconule position
2 = continuous

76. Deep ectoflexus (A, S)
0 = present only on penultimate molar
1 = on penultimate and preceding molars
2 = strongly reduced or absent

77. Metacone size relative to paracone (S)
0 = noticeably smaller
1 = slightly smaller
2 = subequal or larger
3 = absent or merged with paracone.

78. Metacone position relative to paracone (A)
0 = labial
1 = approximately at same level
2 = lingual

79. Metacone and paracone bases (A)
0 = adjoined
1 = separated

80. Preparacrista (A)
0 = strong, from side of paracone to stylocone
1 = weak, from base of paracone, or absent

81. Cuspate preparacrista (A)
0 = present
1 = absent

82. Centrocrista (A)
0 = straight
1 = V-shaped
2 = absent

83. Postmetacrista (A)
0 = prominent, from side of metacone to metastyle
1 = salient
2 = weak, from base of metacone, or absent

84. Cuspate postmetacrista (A)
0 = present
1 = absent

87. Development of postvallum shear (A, S)
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 = present, with second rank extending to metastylar lobe: metacingulum
3 = absent

88. Paraconule (A)
0 = weak or absent
1 = prominent, closer to protocone
2 = prominent, midway or closer to paracone

89. Metaconule (A)
0 = weak or absent
1 = prominent, closer to protocone
2 = prominent, midway or closer to metacone

92. Protocone (A)
0 = lacking
1 = small, without trigon basin
2 = with distinct trigon basin

93. Protocone antero-posterior expansion (A)
0 = none, subequal to paracone
1 = expanded, larger than paracone

94. Protocone procumbency (A, S)
0 = absent
1 = present

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

0 = no labial shift (10 %–20 %)
1 = moderate labial shift (21 %–30 %)
2 = substantial labial shift (≥ 31 %)

97. Precingulum (A, S)

0 = absent or weak
1 = present
2 = present, reaching labially passed the paraconule or paraconule position

98. Postcingulum (A, S)

0 = absent or weak
1 = present, lingual to metaconule or metaconule position
2 = present, reaching labially passed metaconule or metaconule position
3 = present, extending to labial margin

99. Hypocone on postcingulum (A, S)

0 = absent
1 = present, lower than protocone
2 = present, subequal to protocone

100. Pre- and postcingulum (A, S)

0 = separated
1 = continuous lingually

101. Number of penultimate roots (A)

0 = three
1 = four
2 = more

102. Number of roots on ultimate molar (A)

0 = three
1 = two
2 = one
4 = four or more

103. Lingual root position on upper molars (A)

0 = supporting paracone
1 = supporting trigon

104. Ultimate upper molar width relative to penultimate molar (A)

0 = subequal
1 = smaller

105. Metastylar lobe on ultimate molar (A)

0 = absent
1 = present

106. Paraconid (A, S)

0 = present
1 = absent

107. Paraconid height relative to metaconid (A, S)

0 = shorter
1 = subequal
2 = taller

108. Paraconid on lingual margin (A, S)

0 = absent
1 = present

111. Trigonid configuration (A)

0 = open, with paraconids anteromedial, paracristid-protocristid angle more than 50°
1 = more acute, with paraconid more posteriorly placed, paracristid-protocristid angle between 36 and 49°
2 = anteroposteriorly compressed, paracristid-protocristid angle 35° or less

112. Protoconid height (A, S)

0 = tallest cusp on trigonid
1 = subequal to para- and/or metaconids
2 = smaller than para- and/or metaconid

114. Anterior and labial (mesio-buccal) cingular cuspule (f) (A)

0 = present
1 = present with a distinct cingular shelf posteroventrally directed from it
2 = present with shelf continuing along buccal border
3 = absent

115. Talonid (A, S)

0 = small heel
1 = multicusped basin

117. Trigonid height relative to talonid height (A, S)

0 = twice or more
1 = less than twice
2 = subequal

118. Anteroposterior shortening at base of trigonid relative to talonid (A, S)

0 = trigonid long (more than 75 % of tooth length)
1 = some shortening (50-75 % of tooth length)
2 = anteroposterior compression of trigonid (less than 50 % of tooth length)

119. Talonid width relative to trigonid (A, S)

0 = very narrow, subequal to base of metaconids
1 = narrower
2 = subequal to wider

120. Hypoconulid (A)

0 = absent
1 = in posteromedial position (near the mid-point of transverse talonid width)
2 = lingually placed with slight approximation to entoconid
3 = close approximation to entoconid

122. Entoconid (A)

0 = absent
1 = smaller than
2 = subequal to larger than hypoconid and/or hypoconulid

123. Postcristid (between entoconid and hypoconulid) taller than hypoconulid and nearly transverse (A)

0 = absent
1 = present

124. Mesoconid (A)

0 = absent
1 = present

125. Hypolophid (A, S)

0 = absent
1 = present

126. Labial postcingulid (A)

0 = absent
1 = present

127. Ultimate lower molar size relative to penultimate lower molar (S)

0 = subequal or larger
1 = smaller

*Mandible*

128. Number of mental foramina (A, S)

0 = two or more
1 = one

129. Anteriormost mental foramen (A, S)

0 = below incisors (or anteriormost mandible)
1 = below p1
2 = below p2
3 = more posterior

130. Posteriormost mental foramen (A, S)

0 = in canine and anterior premolar (premolariform) region (in saddle behind canine eminence of mandible)
1 = below penultimate premolar (under anterior end of functional postcanine row)
2 = below ultimate premolar
3 = at ultimate premolar and first molar junction or more posterior

131. Depth of mandibular body (A, S)

0 = slender and long
1 = deep and short

132. Space between ultimate molar and coronoid process (S)

0 = absent
1 = present

133. Coronoid process height (S)

0 = higher than condyle
1 = even with condyle

134. Coronoid process width (S)

0 = broad, roughly two molar lengths
1= narrow, subequal to or less than one molar length

138. Anteroventral extension of masseteric fossa (S)

0 = absent
1 = extending anteriorly onto mandibular body

139. Labial mandibular foramen (S)

0 = absent
1 = present

152. Mandibular symphysis posterior extent (S)

0 = p1 or more anterior
1 = p2
2 = p4 or more posterior

154. “Meckelian” groove (S)

0 = present
1 = absent

156. “Coronoid” facet (S)

0 = present
1 = absent

*Skull – Rostrum*

164. Exit(s) of infraorbital canal (S)

0 = multiple
1 = single
2 = canal absent

165. Infraorbital foramen position (S)

0 = dorsal to ultimate premolar
1 = dorsal to penultimate premolar or more anterior
2 = dorsal to first molar or more posterior

*Skull – Zygoma*

196. Posterior edge of anterior zygomatic root (S)

0 = aligned with last molar
1 = aligned with anterior molars
2 = aligned with premolars

198. Jugal (S)

0 = present
1 = absent

199. Jugal (S)

0 = contributes to anteroventral orbit and zygoma
1 = contributes to zygoma

200. Maxillary-jugal contact bifurcated (S)

0 = absent
1 = present

201. Jugal-lacrimal contact (S)

0 = present
1 = absent

202. Zygomatic arch (S)

0 = stout
1 = delicate
2 = incomplete

Matrix

Scored characters for *Alvuegena* and *Schowalteria*. All others can be found in Wible et al. (2009).

*Alveugena*

0010?13??????0????????11010?1?201?-100110100?
0010—000000?0?100120020010020001001001??322??
2101?210000110000?-00-31?0111?20000?
0120????????????????????????????????????
???????????????????????????????????????????
?????????????????????????????????????????
???????????????????????????????????????
????????????????????????????????????
?????????????????????????????????
?????????????????????????????????

*Schowalteria*

001?0??2?1???01?00??0011010?1?2010-??00??2???0011–
000001?0110012002001 00-00???????????3??????0??
1100?????100???1??1?001?????0?10220100???
10?????????????2?1-1???????11???????????????
???????????????1?00002??????????????????????
?????????????????????????????????????????????????
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Complete Eutherian tree

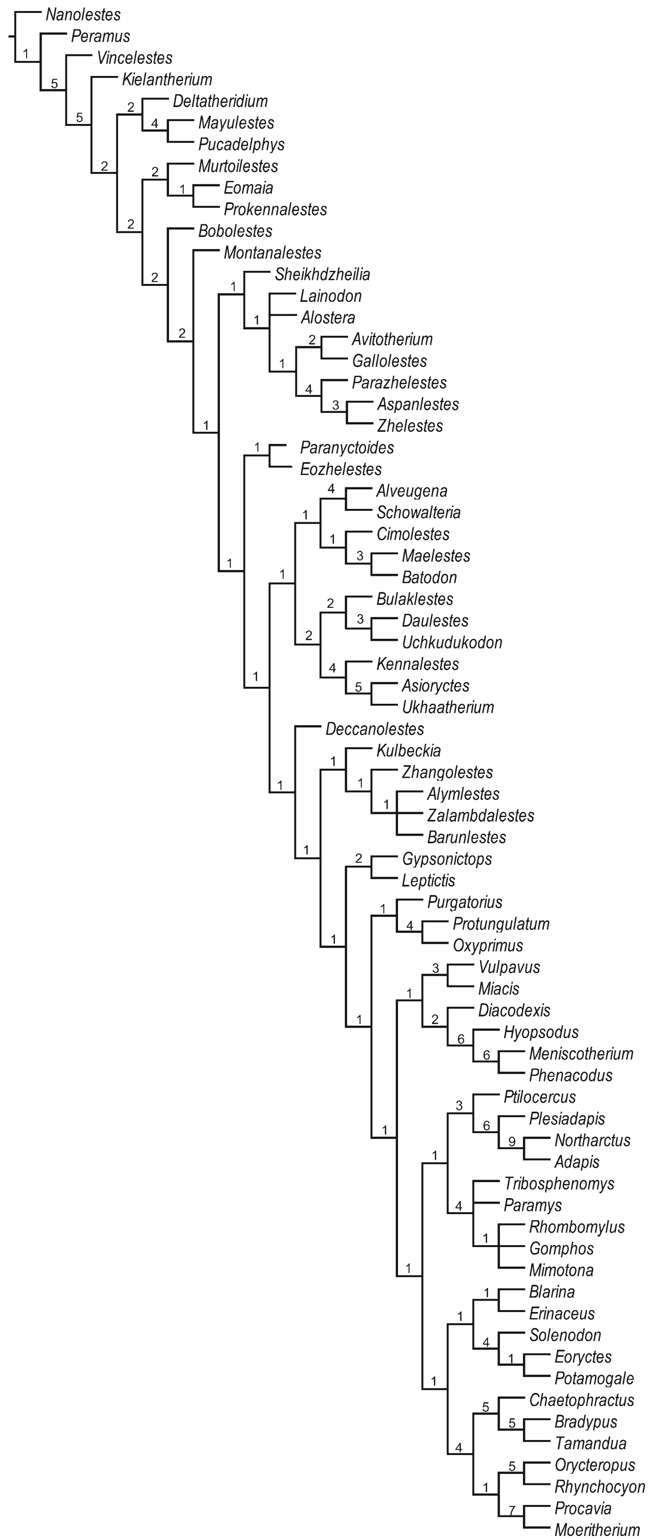


**Fig. 3** External relations among Eutheria from cladistic analysis. Entirety of tree from Fig. 2, showing both crown and stem relationships

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