



THE FACIAL SKELETON OF THE EARLY OLIGOCENE *COLODON* (PERISSODACTYLA, TAPIROIDEA)

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ABSTRACT

Two skulls of the early Oligocene *Colodon* from the White River Group in South Dakota are much more derived than previously reported. In particular, morphologies of the facial skeleton and narial region are surprisingly modern, including a deeply retracted nasoincisive incisure, and other indicators of prehensile proboscis development. High-resolution X-ray computed tomography was used to explore the internal anatomy of these tapiroids, and revealed frontal sinuses, and an internal facial skeleton approaching that of modern tapires. This not only indicates an earlier origin for these anatomical conditions than previously recorded, but in a phylogenetic context indicates that *Colodon* is more closely related to *Tapirus* than is *Protapirus*.

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INTRODUCTION

Perhaps the most extraordinary feature of the living tapires is their prehensile proboscis. It is derived from modified muscles of the face and upper lip, and its presence is indicated by several osteological features (Witmer et al. 1999). These osteological correlates include the reduction of the bony wall of the nasal chamber (Witmer et al. 1999); the presence of processes and scars for

attachment of proboscis musculature (Witmer et al. 1999); and a posterior displacement of the dorsal facial skeleton (i.e., telescoping; see Colbert 1999). Further conditions correlated with the telescoping of the skull are the development of frontal sinuses overlying the anterior cranial cavity, the loss of contact between the premaxillae and nasals, the apparent loss of a true maxillary sinus, and the unique condition of having the maxilloturbinals, premaxillae, and maxillae embrace the cartilagi-

nous nasal septum (Witmer et al. 1999). The fossil record of the tapiroids includes crania that document less derived states for these character complexes, which provides insight into the evolution of their facial skeleton.

In this report, I present the first detailed description of the facial skeleton and some of the elements surrounding the facial skeleton of early Oligocene *Colodon* from North America. This description uses high-resolution X-ray computed tomography (HRXCT) to explore the internal anatomy of two *Colodon* skulls from South Dakota. Even though both *Colodon* specimens are sub-adult, they nonetheless preserve several indicators of prehensile proboscis development and have a derived telescoped condition. Although these remarkable skulls provide a glimpse of a facial morphology less derived than *Tapirus*, they are nevertheless more similar to *Tapirus* than to other Eocene and early Oligocene tapirs. This similarity is contrary to the observations presented in an earlier cranial description of *Colodon* (Radinsky 1963, figure 21) and supports a different phylogenetic placement for *Colodon* than previously hypothesized (e.g., Colbert and Schoch 1998; Dashzeveg and Hooker 1997; Holbrook 1999; Radinsky 1963; Schoch, 1989b).

MATERIALS AND METHODS

The Specimens

Locality Data. FAM 42891 (specimen from the Frick American mammals collection at the AMNH, hereafter referred to as the AMNH skull) is an isolated skull from the Whitneyan of Shannon County, South Dakota. Data from the original specimen label cites Skinner and Mefferd as the collectors from northeast of Indian Stronghold on the divide between west Big Corral Draw and Cottonwood Creek from a lower *Protoceras* channel. The label mentions that this would be in the upper Oreodon beds or lower Poleslide Member of the Brule Formation of Jim Bump.

SDSM 59566 (hereafter referred to as the SDSM skull) is an isolated skull from the Orellan of South Dakota, collected by Japeth Boyce, who donated it to the South Dakota School of Mines, where it has been on display in the Museum of Geology. Japeth Boyce provided the following provenance information (Boyce, personal commun., 2005): specimen collected from the 'Metamynodon sandstone,' a channel sand in the lowest Brule Formation located just below the lower nodular layer; site approximately midway between Cottonwood Pass and Stronghold Table.

Preservation and Relative Maturity. Although both are partially crushed and distorted, the two skulls described here are generally well preserved and relatively complete. The AMNH skull is horizontally flattened (Figure 1A), and the SDSM skull is compressed sagittally and sheared (Figure 1B), with the right side elevated relative to the left. The different compaction planes of these two specimens present somewhat complementary information for interpreting the degree of anatomical deformation, but precise determination of the true skull shape is not possible. Thus, for example, while the AMNH skull suggests a wide rostrum for *Colodon*, the SDSM rostrum is narrow, and the true shape is some intermediate condition.

The braincase of the SDSM skull is more completely preserved than the AMNH skull, which lacks posterior parietals and most of its occipital shield, including the basioccipital and supraoccipitals. The critical narial region, which is the focus of this description, is better preserved on the AMNH skull. The SDNH skull only preserves fragments of its nasals, and most of the narial opening margins are damaged.

Based on dental eruption and suture closures, the AMNH skull is less mature than the SDSM specimen, and neither represents an adult condition. The immaturity of the AMNH skull is indicated by the incomplete eruption of its permanent premolars and molars; M3 is still within its crypt, and it retains deciduous premolars. The dental formula differs on the left and right sides, most likely a consequence of dP3-4 having been prepared away on the left side. The dental stage is as follows: right side, P1 missing (adult roots intact), P2, P3-4 in crypts, M1-2, M3 in crypt; left side, P1-2, dP3-4 (P3-4 in crypts), M1-2, M3 in crypt (Figure 2). This arrangement is consistent with an eruption sequence pattern observed in recent tapirs (Colbert 1999). The presence of incisors is inferred from alveoli, but canines are lacking. The AMNH specimen's immaturity is also indicated by the largely open cranial sutures. For example, the basioccipital is missing, having separated along the open sphenoccipital synchondrosis.

All the adult premolars and M1-2 are in place on the SDSM skull, but M3 lies within its crypt. I1-2 are preserved on the left premaxilla, and I1 and I3 on the right premaxilla (Figure 3). As on the AMNH skull, canines are lacking. Additional indicators of the immaturity of this specimen are the lack of fusion of the exoccipitals to the supraoccipitals, and of the basioccipital to the basisphenoid.

The Referral of these Specimens to *Colodon*. The monophyly of *Colodon* is suspect, as indicated by a series of phylogenetic analyses performed by



Figure 1. Illustration of the horizontal compaction of the AMNH skull, and sagittal compression of the SDSM skull. A. AMNH 42891 in lateral view. B. SDSM 59566 in ventral view. Scale bar equals 10 mm.

Colbert (1999). This condition is largely a consequence of the limited material, particularly nondental material that has been referred to *Colodon*. Traditionally, *Colodon* has been identified by its distinctive teeth (e.g., Colbert and Schoch 1998; Radinsky 1963). Radinsky (1963) recognized three North American species of *Colodon* (*C. kayi*, *C. woodi*, and *C. occidentalis*).

Dental characters are the basis for the referral of the skulls described here to *Colodon*. These similarities include both the degree of molarization of their premolars, and their lingually displaced and reduced molar metacones (Figures 1, 2; Radinsky 1963). The AMNH skull cannot be unquestionably referred to any particular species of *Colodon*, but the SDSM skull falls comfortably within the range of *C. occidentalis*. Species of *Colodon* were discriminated by Radinsky (1963) based on size differences in their teeth. The dentition of the AMNH skull was compared favorably to *Colodon occidentalis* by Radinsky (1963) who noted, however, that it was generally larger than other *C. occidentalis*, and would also represent a chronostratigraphic range extension from the Chadronian and Orellan into the Whitneyan North American Land Mammal 'Age'. Radinsky (1963) suggested that this speci-

men might record an evolutionary increase in size within the *C. occidentalis* lineage over time.

The slightly smaller dentition of the Orellan SDSM skull falls within the size range for *C. occidentalis*, to which it is referred (compare measurements presented in Radinsky 1963 and dental measurements for the two skulls provided in Table 1). Although it cannot be assumed that the two *Colodon* skulls described here belong to a single species, it is clear that they were closely related based on overall morphological similarities.

HRXCT Scanning and Image Processing

Both *Colodon* skulls were scanned at the University of Texas High-Resolution X-ray CT Facility (UTCT) using the high-energy subsystem as described by Ketcham and Carlson (2001). The original data sets for both are saved as 1024 by 1024 pixel TIFF images with a 16-bit gray scale depth. The slice thickness for the AMNH skull was 0.50 mm, and the inter-slice spacing 0.40 mm. The field of reconstruction was 125 mm, yielding an in-plane resolution of 0.122 mm/pixel and 556 slices in the original coronal plane. The original data set for the SDSM skull comprises 576 slices in the coronal plane, each slice having a thickness of 0.50 mm and an inter-slice spacing of 0.45 mm. An



Figure 2. The dentition of AMNH 42891. Scale bar equals 10 mm.

animation of the original CT data of the AMNH skull, reduced from their original image size for web viewing, can be seen in Appendix 1. The field of reconstruction was 112 mm, yielding an in-plane resolution of 0.109 mm per pixel. An animation of the original CT data of the SDSM skull, reduced from their original image size for web viewing, can be seen in Appendix 2.

Animated three-dimensional (3D) renderings, and ‘dynamic cutaway’ views of the skulls (see DigiMorph: Colodon AMNH and DigiMorph: Colodon AMNH) were produced using VGStudioMax software. Comparative CT Data and Terminology.

http://digimorph.org/specimens/Colodon_cf_occidentalis/AMNH/
http://digimorph.org/specimens/Colodon_cf_occidentalis/SDSM/

The descriptions presented here make reference to an HRXCT dataset for *Protapirus* (SDSM 2829; see [http:// DigiMorph.org/ specimens/ protapirus_simplex/](http://DigiMorph.org/specimens/protapirus_simplex/)), a White River contemporary of *Colodon*, whose cranial anatomy is generally much less derived than *Tapirus*. The original data sets for *Protapirus* are saved as 1024 by 1024 pixel TIFF images with a 16-bit gray scale depth. The slice thickness was 0.50 mm, and the inter-slice spacing 0.50 mm. The field of reconstruction was 140 mm, yielding an in-plane resolution of 0.1637

Table 1. Dental measurements for the described specimens.

	AMNH 42891		SDSM 59566	
	left	right	left	right
dP2 Length				
dP2 Width				
dP3 Length		12.3		
dP3 Width		13.9		
dP4 Length		13.2		
dP4 Width		16.6		
P1 Length		9.5	9.1	9
P1 Width		9.2	9.5	7.6
P2 Length	12.3	12	10.18	10.5
P2 Width	13.7	12.9	13.1	13.1
P3 Length	12.8	12.9	11.4	11.8
P3 Width	16.7	16.2	15.8	15.7
P4 Length	13.4	13.2	11.6	11.3
P4 Width	15.1	17	16.4	15.8
M1 Length	15.6	15.5	14.61	14.57
M1 Width	18.7	18.6	17.31	17.31
M2 Length	18.6	17.7	16.84	16.84
M2 Width	21.7	21	19.03	19.75
M3 Length	21.2	20.5		
M3 Width	20.8	23.1		



Figure 3. The dentition of SDSM 59566. Scale bar equals 10 mm.

mm/pixel and 602 slices in the original coronal plane. An animation of the original CT data of *Protapirus*, reduced from their original image size for web viewing, can be seen in Appendix 3. Anatomical terminology generally follows Witmer et al. (1999).

Phylogenetic Analysis

The evolutionary position of *Colodon* within Ceratomorpha (exclusive of all but the most basal rhinocerotoids) was estimated using character data derived from both literature descriptions and observed specimens (Appendices 4, 5). The analyzed data matrix includes 22 in-group taxa and 89 cranial and dental characters (Appendices 4, 5) that were largely developed from the literature. The matrix includes specimens referred to a 'new San Diego taxon,' described by Colbert (1999). The data matrix (Appendix 5) was analyzed with PAUP v4.08b (Swofford 2003), using a heuristic search option, characters unordered, and keeping only the most parsimonious trees. Outgroups include *Homogalax protapirinus*, *Isectolophus latidens*, and *I. annectens*. Diagnoses assume 'Deltrans' character optimization.

DEFINITION OF SUPRASPECIFIC TAXA

Formal ancestry-based definitions (sensu Rowe and Gauthier 1992; de Queiroz and Gauthier 1990, 1994; Bryant 1996) are presented here for emended taxonomic concepts for *Tapirus* and Tapiridae. Definitions for Ceratomorpha and Tapiromorpha are modified from Froehlich (1999)

and Holbrook (1999), and definitions for Tapiroidea from Holbrook (1999). All definitions refer to either a type species, species, or a particular specimen as specifiers. Figure 4 illustrates the phylogenetic framework for these names and their specifiers.

Tapirus Brünnich 1772. Redefined here as the clade stemming from the most recent common ancestor of *Tapirus indicus* Desmarest 1819, *Tapirus bairdii* (Gill 1865), *Tapirus pinchaque* Roulin

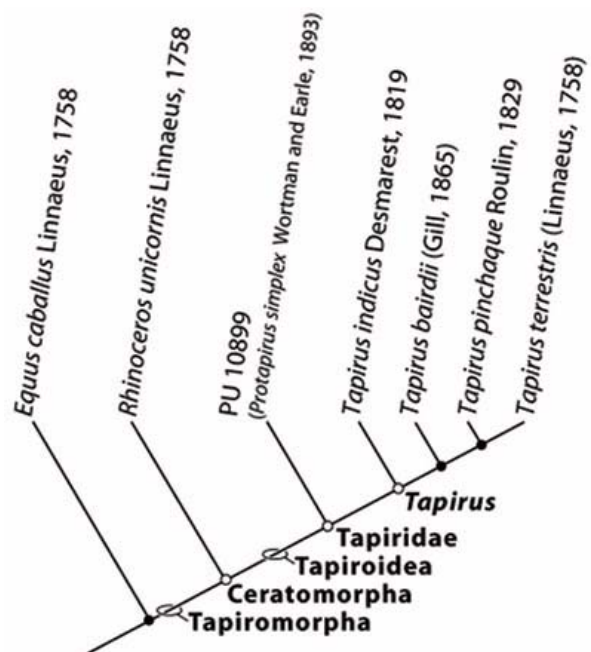


Figure 4. Phylogenetic framework for the taxa defined in the text.

1829, and the type species, *Tapirus terrestris* (Linnaeus 1758).

This crown-group definition codifies the general view that all living tapiroids belong to *Tapirus* (e.g., Colbert and Schoch 1998; Hershkovitz 1954; Nowak 1999; Prothero and Schoch 1989a, 1989b; Simpson 1945; Ray and Sanders 1984; Wilson and Reeder 1993). Eisenberg et al.'s (1990) referral of *T. indicus* to the genus *Acrocodia* is not followed here.

Tapiridae Burnett 1830. Redefined here as the clade stemming from the most recent common ancestor of PU 10899 (the type of *Protapirus validus* Hatcher 1896, here referred to *P. simplex* Wortman and Earle 1893, following Albright 1998) and *Tapirus terrestris* (Linnaeus 1758).

This node-based definition reflects the general consideration of North American *Protapirus* as a basal tapiroid (e.g., Scott 1941; Radinsky 1963; Schoch 1989b; Hooker, 1989). Because the status of North American species of *Protapirus* is unclear (see Albright 1998), the articulated cranium of PU 10899, rather than a particular species, is used as a specifier. PU 10899 is the first described *Protapirus* in the literature with the distinctive, deep nasoincisive incisure (Hatcher 1896). Note that Scott's (1941, plate 79) illustration of this specimen is a reconstruction based in part upon SDSM 2829. Although PU 10899 is currently referred to *P. simplex* (a species considered to include *P. validus*; Albright 1998), it is potentially a junior subjective synonym of *P. obliquidens* Wortman and Earle 1893 (see Albright 1998). It is also possible that New and Old World *Protapirus* are not monophyletic (Colbert and Schoch 1998; Colbert 1993), requiring the removal of North American '*Protapirus*' from *Protapirus* sensu stricto. This definition differs from Holbrook (1999, p. 345), who generally defined tapiromorph 'families', including Tapiridae, as stem-based groups comprising "the type genus and all genera which are more closely related to it than to any other type genus."

Tapiroidea Burnett 1830. Redefined here as the clade consisting of *Tapirus terrestris* (Linnaeus 1758) and all organisms that share a more recent common ancestor with *Tapirus terrestris* than with *Rhinoceros unicornis* Linnaeus 1758 (definition modified from Colbert and Schoch 1998).

The redefinition of the traditional, paraphyletic Tapiroidea (e.g., see Radinsky 1963), relegates many Eocene perissodactyls formerly considered tapiroids (e.g., *Homogalax*, *Cardioloophus*, *Isectolophus*, and apparently the Asian lophialetids, breviodontids, and rhodopagids) to the more inclusive Tapiromorpha (Hooker 1984, 1989; Schoch 1989b;

Dashzeveg and Hooker 1997; Colbert and Schoch 1998; Holbrook 1999). Although *Heptodon* is generally considered the most basally diverging tapiroid (see Dashzeveg and Hooker 1997), it has also been hypothesized to fall outside this clade (e.g., Hooker 1989). This definition is in keeping with Dashzeveg and Hooker's (1997) consideration of the Tapiroidea as the group "comprising the extant family Tapiridae plus its more immediate extinct relatives," and refines the similar stem-based definition of Holbrook (1999).

Ceratomorpha Wood 1937. Redefined here as the clade stemming from the most recent common ancestor of *Rhinoceros unicornis* Linnaeus 1758, and *Tapirus terrestris* (Linnaeus 1758). This reformulates Holbrook's (1999) Ceratomorpha by explicitly identifying specifying species.

Tapiromorpha Haeckel 1873. Redefined here as the clade consisting of *Tapirus terrestris* Linnaeus 1758 and all organisms that share a more recent common ancestor with *Tapirus terrestris* than with *Equus caballus* Linnaeus 1758.

This stem-based definition uses specifying species to refine Froehlich's (1999) and Holbrook's (1999) definitions of Tapiromorpha. Although Tapiromorpha has been applied to several different taxonomic assemblages in the past (see Schoch 1989a), is commonly considered to be the sister-taxon to Hippomorpha.

DESCRIPTION OF THE FACIAL SKELETON

The bauplan of the facial skeleton is surprisingly modern, including several indicators suggesting prehensile proboscis development similar to that of extant tapirs. Among the most obvious of these indicators is a deeply retracted nasoincisive incisure (narial incision), which reaches, or is close to, the level of the anterior orbit (Figure 5). On the horizontally flattened AMNH skull, the incisure lies well over the orbit and on the sagittally compressed SDSM skull at the level of the anterior orbit. This retraction is correlated with the posterior telescoping of the dorsal facial skeleton, and with the lack of a postorbital constriction (Radinsky 1965). The premaxilla does not contact the nasal, and the ascending process of the maxilla is marked by a distinctive trough that terminates posteriorly in a shallow fossa that curls onto the posterodorsal nasals and anterodorsal frontals. This trough and fossa accommodates a cartilaginous meatal diverticulum in *Tapirus*, and following Witmer et al. (1999) are called the meatal diverticulum fossa and trough (Figure 5). A similar trough on the ascending process of the maxilla in *Protapirus* differs by extending posteriorly over the supraorbital process

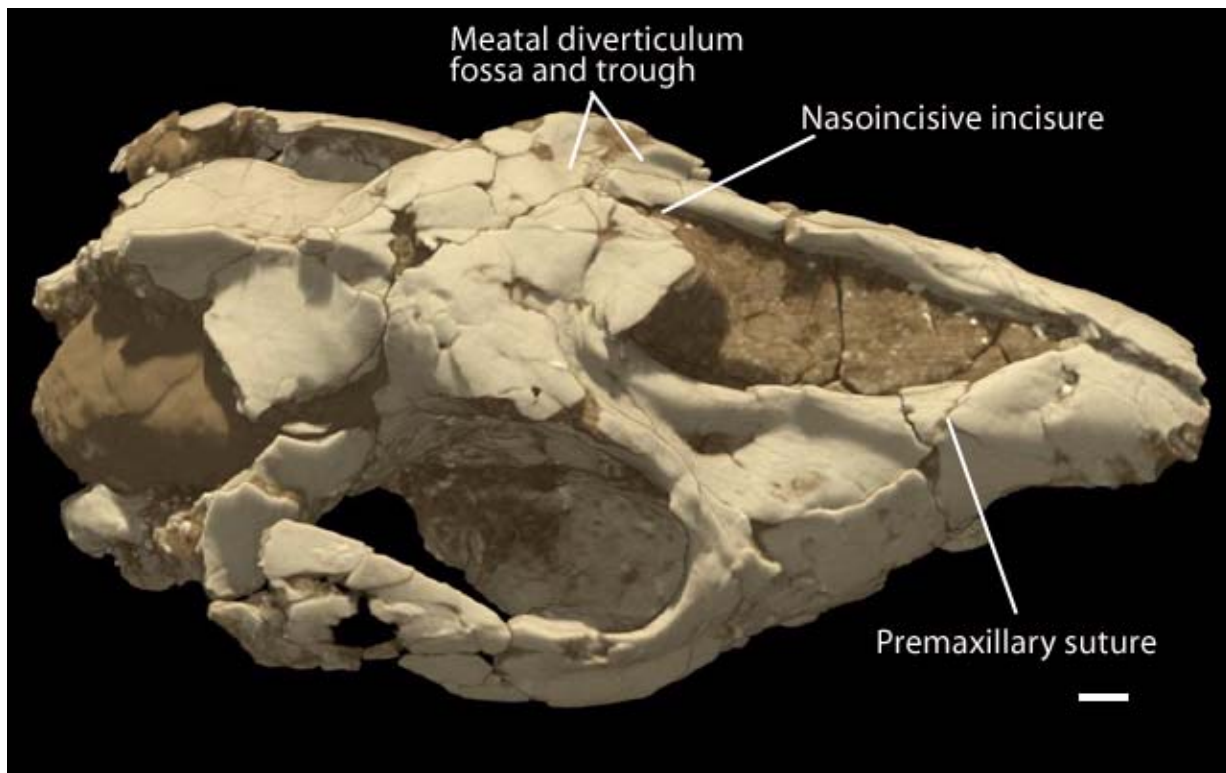


Figure 5. Oblique dorsal view of AMNH 42891 showing several features discussed in the text. Scale bar equals 10 mm.

of the frontal rather than terminating in a fossa. The lateral border of this meatal diverticulum trough anterodorsal to the orbit, comprises the lacrimo-frontal ridge, which served as the attachment area for the levator labii superioris muscle.

The relatively robust premaxilla is slightly downcurved (see Radinsky 1965) and has three incisors. These conditions are shared with both *Tapirus* and *Protapirus*, although the premaxilla of *Tapirus* is more robust than the others. The nasal process of the premaxilla does not reach the nasal, extending posterodorsally to the level of the posterior diastema, immediately anterior to the level of the first premolar. At this point it lies just lateral to the margin of the narial opening, resting on the dorsal edge of the facial maxilla. The CT data show the posterior margin of the premaxilla extending as a wedge-shaped intrusion between the nasal and facial surfaces of the maxilla. This relationship extends the entire sutural length, from dorsal margin to the alveolar margin. Unlike *Tapirus*, the third incisors are not caniniform. The interpremaxillary suture is open on the AMNH skull, and the left and right sides are slightly displaced. Although crushed, the flattened medial premaxillary margins of the nasoincisive incisure suggest that the cartilaginous nasal septum was clasped by the premaxillae, or possibly a maxilloturbinate that lined the

narial face of the premaxillae (Figure 6). Both elements embrace the nasal septum in *Tapirus*. This contact with the cartilaginous nasal septum is situated immediately posterior to the dorsal symphysis (see Witmer et al. 1999). A single confluent palatine fissure notches the palatal premaxilla.

The maxilla lacks a canine, canine alveolus, and the corresponding alveolar ridge on its facial surface. Otherwise, the maxilla generally resembles that of *Protapirus* and *Tapirus*. *Colodon* is similar to *Tapirus* in having a large conchal sinus recess and apparently no maxillary sinus. The dorsal free edge of the facial maxilla is thickened and bears a variably developed crista conchalis on its ventromedial margin. Only fragments of the maxilloturbinate, which sutures to this crista, remain. Viewed laterally, the profile of the narial margin is marked by two broad scallops, which meet at the midpoint of the incisure margin as a low peaked eminence (Figure 7). This arrangement is similar to *Protapirus*, although the peak is more pronounced in *Protapirus*. *Protapirus* also differs in having the peak associated with a shallow fossa on the facial maxilla. The flattened and expanded medial surface of the peaked area of *Colodon* and *Protapirus* is interpreted to be a sutural contact surface for the septal portion of the maxilloturbinate. The septal maxilloturbinate of *Tapirus* is a medially directed

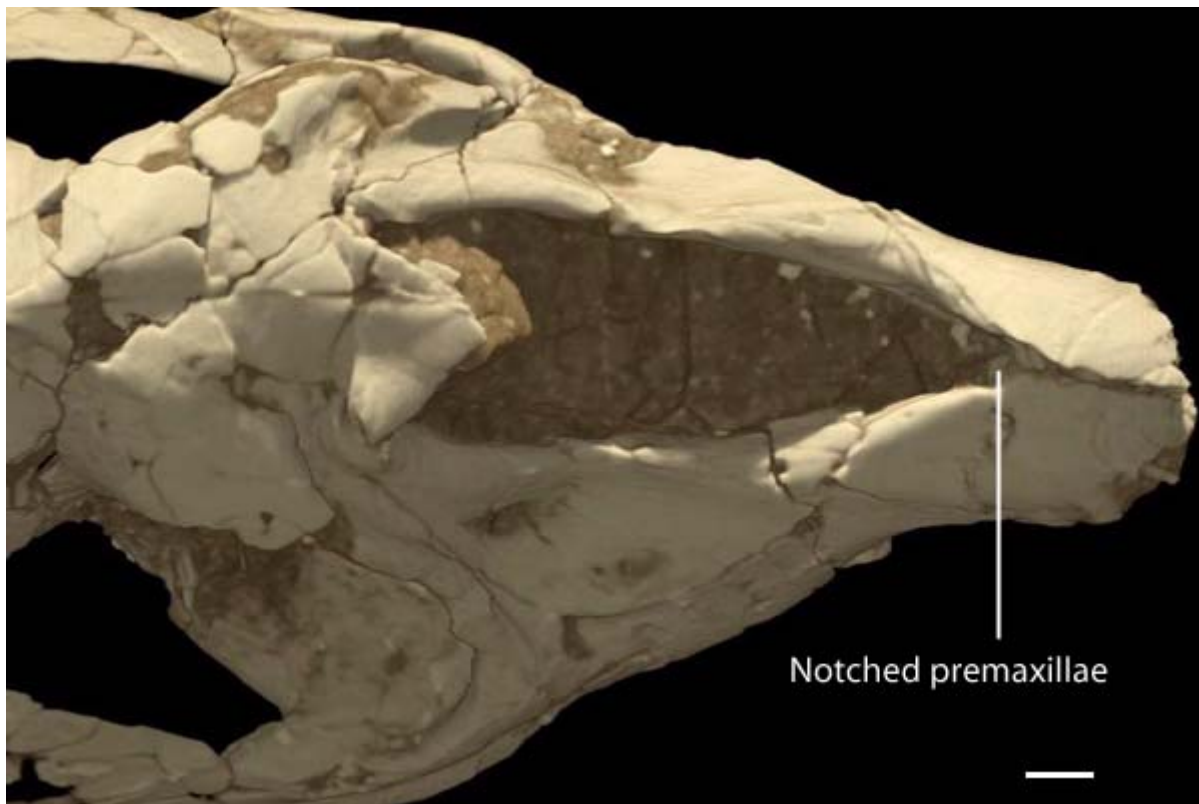


Figure 6. Dorsal view of the facial skeleton of AMNH 42891 showing the notch between the premaxillae that presumably accommodated a cartilaginous nasal septum. Scale bar equals 10 mm.

lamina that contacts the cartilaginous nasal septum (see Witmer et al. 1999). In coronal section the nasal face of the maxilla is broadly concave below the crista conchalis (Figure 8), and compares favorably with the conchal recess described for *Tapirus* by Witmer et al. (1999).

The ascending process of the maxilla extends posterior to and lateral to the descending process of the nasals. At this area the ascending maxilla is dorsally concave and contributes to the meatal diverticulum trough. The lateral margin of the maxilla is raised and contacts the frontal and lacrimals along the lacrimofrontal ridge. In *Tapirus*, this ridge serves for attachment of the levator labii superioris muscles, a prime mover of the proboscis (Witmer et al. 1999). The infraorbital foramen opens at a level above P3/P4. CT data reveal an alveolar canal arising from the infraorbital canal immediately posterior to the infraorbital foramen.

Posteroventrally, the maxillary tuber floors the orbit. The unerupted M3s of both specimens are deeply lodged within their crypts. The damaged palatal processes of the maxillae are notched anteriorly for a single palatine fissure. The perpendicular lamina of the palatines has an extended contact with the maxilla.

The horizontal laminae of the palatines are not well preserved, but their choanal margin is near the level of M1/2. Note that during the ontogeny of living tapirs the choanae migrate posteriorly with the eruption of the molar series. Rostrally the horizontal laminae intrude between the maxillae, to about P3 level. As in *Tapirus*, the posterior perpendicular lamina of the palatine extends posterior to the anterior margin of the choanae along the medial surface of the maxilla, extending to the posterior face of the maxillary tuber, where there is a small posteromedial surface for the suture with the pterygoid. The pterygoid is not preserved. Although the palatine foramina are damaged and difficult to see, the palatine canal is seen in the CT data extending along the medial margins of the maxillary tuber (e.g., Figure 9), and opening into the orbit immediately posterior to the maxillae tuber. This is similar to the palatine canal of *Tapirus*.

What is preserved of the nasals is similar to those of *Tapirus*, having an anteriorly tapering rostral process; the posteromedial margin of the rostral process with a small notch; and a short descending process resting on the posterior ascending process of the maxillae. Viewed dorsally, the rostral process is roughly triangular, widening posteriorly to the posterior nasoincisive

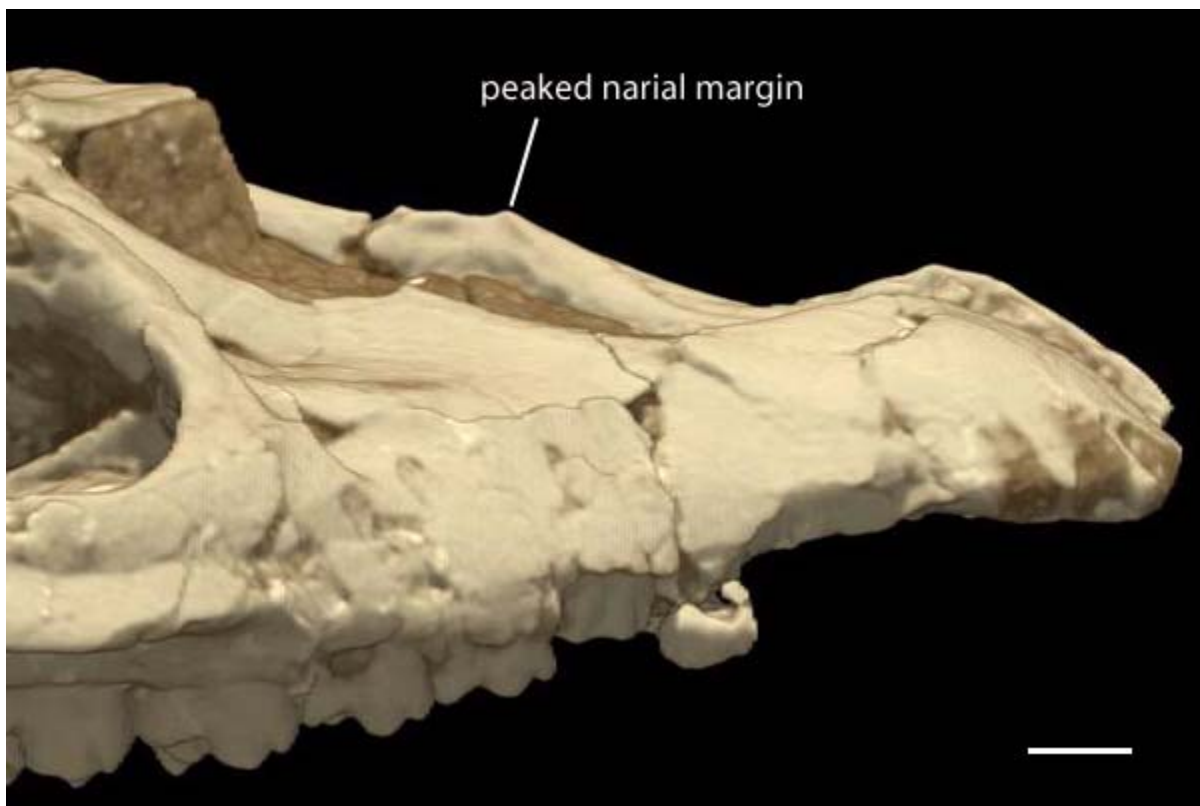


Figure 7. Lateral view of the facial skeleton of AMNH 42891 showing the peaked margin of the margin of the nasoincise incisure, and adjacent 'scalloped' areas. The peaked area is hypothesized to have articulated with a septal process of the maxilloturbinate. Scale bar equals 10 mm.

incisure. The anterior medial rostral process of the nasals is broken. A median process of the frontals intrudes between the nasals posteriorly (Figure 10). Lateral descending processes of the nasals extend rostrally along the dorsal margins of the maxillae to the level of the thickened dorsal stem of the maxilloturbinal.

The maxilloturbinals are represented by fragments. As noted above, the thickened dorsal stem is only partially preserved (Figure 10). However, considering their fragmental nature, the arrangement of the crista conchalis and of the presumed sutural contact area for the septal maxilloturbinate (Figure 7) at the peaked narial border of the maxilla indicate that the maxilloturbinals were generally similar to those of *Tapirus*. The partially preserved vomer (Figures 8, 9) has a deep septal sulcus, which lodged the cartilaginous nasal septum and the perpendicular plate of the ethmoid. Only fragments of the ethmoidal turbinals are preserved, although a delicate perpendicular plate can be seen in coronal and horizontal CT sections.

Two tubercles mark the facial face of the lacrimal, similar to the condition observed in *Tapirus*. The medial of these tubercles is continuous with the frontolacrimal ridge on the margin of the orbit.

The lacrimal foramen, or foramina, and lacrimal canal are poorly preserved, but appear similarly positioned to those of *Tapirus*.

The frontals of *Colodon* resemble *Tapirus*, being antero-posteriorly compressed, dorsally inflated, and having a median process that intrudes between the nasals anteriorly. The CT data reveal large frontal sinuses that invest almost the entire element (e.g., Figure 11). This differs from the condition in *Protapirus*, which retains elongated frontals having no sinus cavities that overlie the cranial cavity. The meatal diverticulum fossa and trough are developed on the anterior frontals, and on rostralateral processes (Witmer et al. 1999). These rostralateral processes suture with the ascending maxillae, lacrimals, and posteriorly with the posterior descending processes of the nasals. The supraorbital processes are similar to those of *Tapirus*, extending posteriorly from the frontolacrimal ridge.

RESULTS OF THE PHYLOGENETIC ANALYSIS

Phylogenetic analysis yields 189 most-parsimonious trees (treelength 311, CI excluding uninformative characters = 0.54, RI = 0.62). See

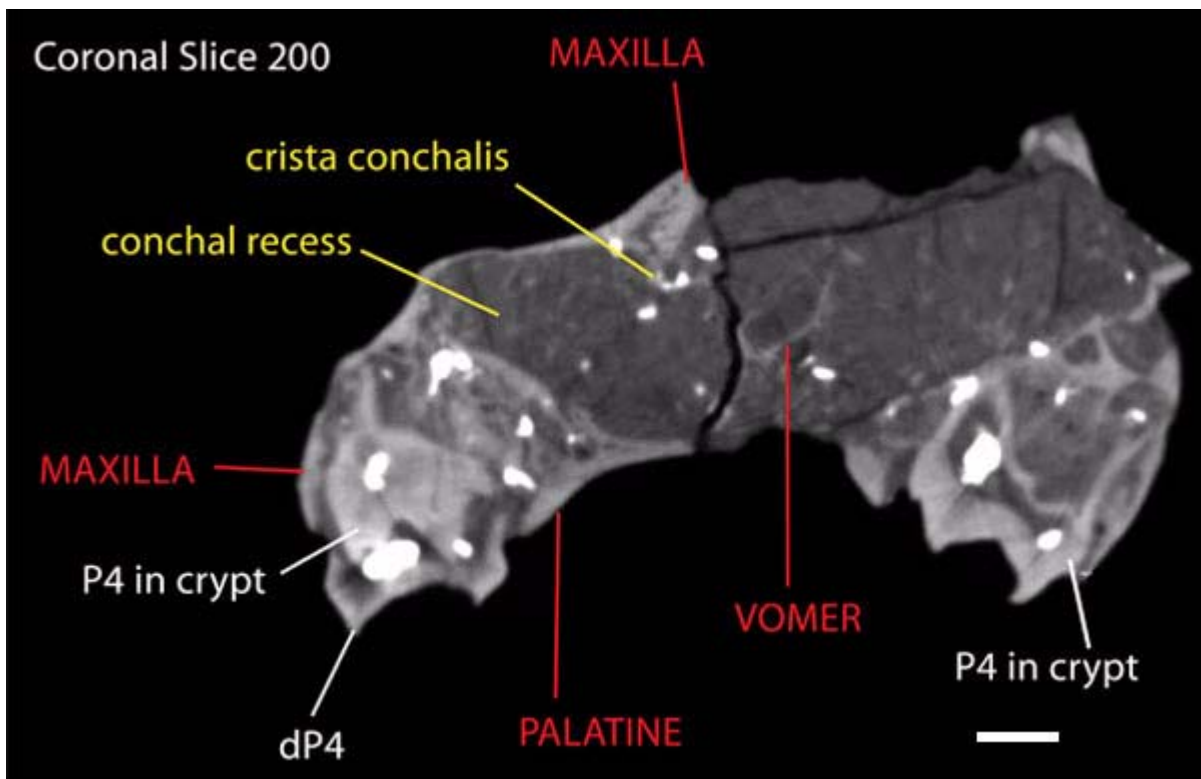


Figure 8. Coronal slice 200 from scanned data set for AMNH 42891. Grayscale levels have been adjusted to increase contrast. Scale bar equals 10 mm.

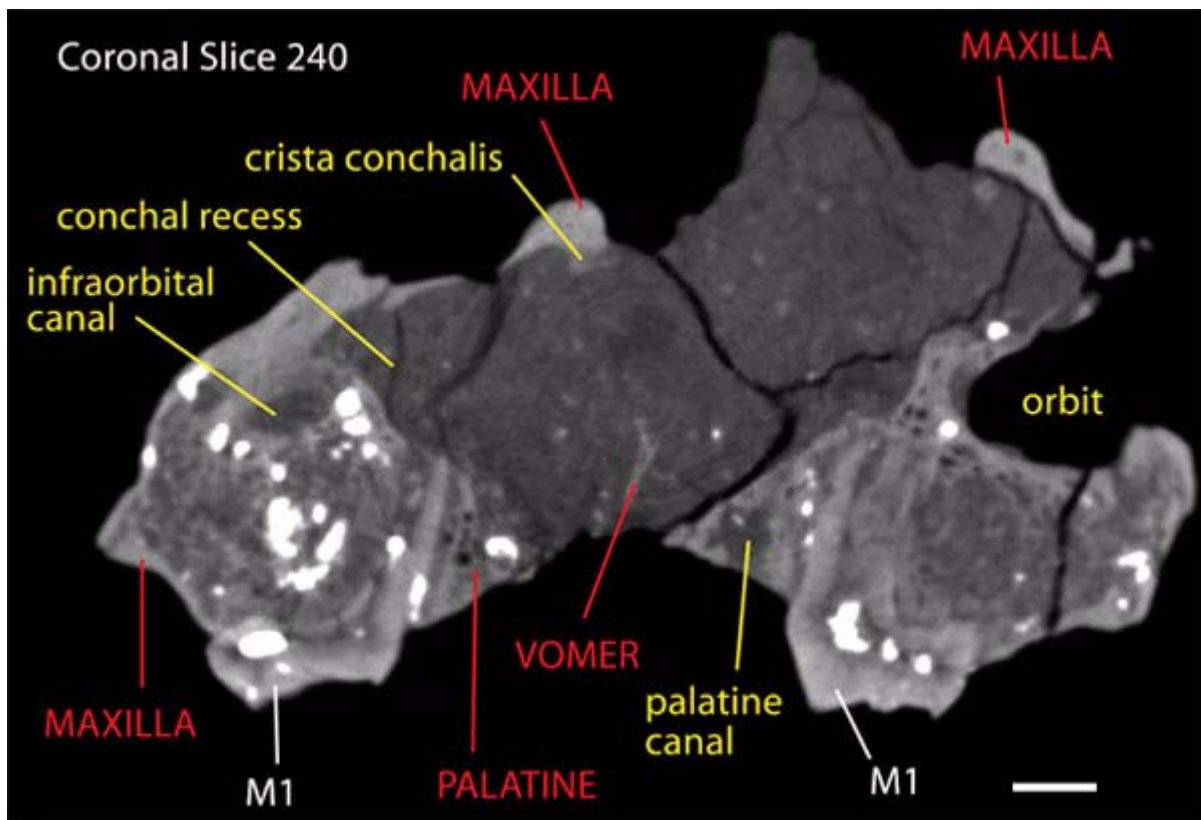


Figure 9. Coronal slice 240 from scanned data set for AMNH 42891. Grayscale levels have been adjusted to increase contrast. Scale bar equals 10 mm.

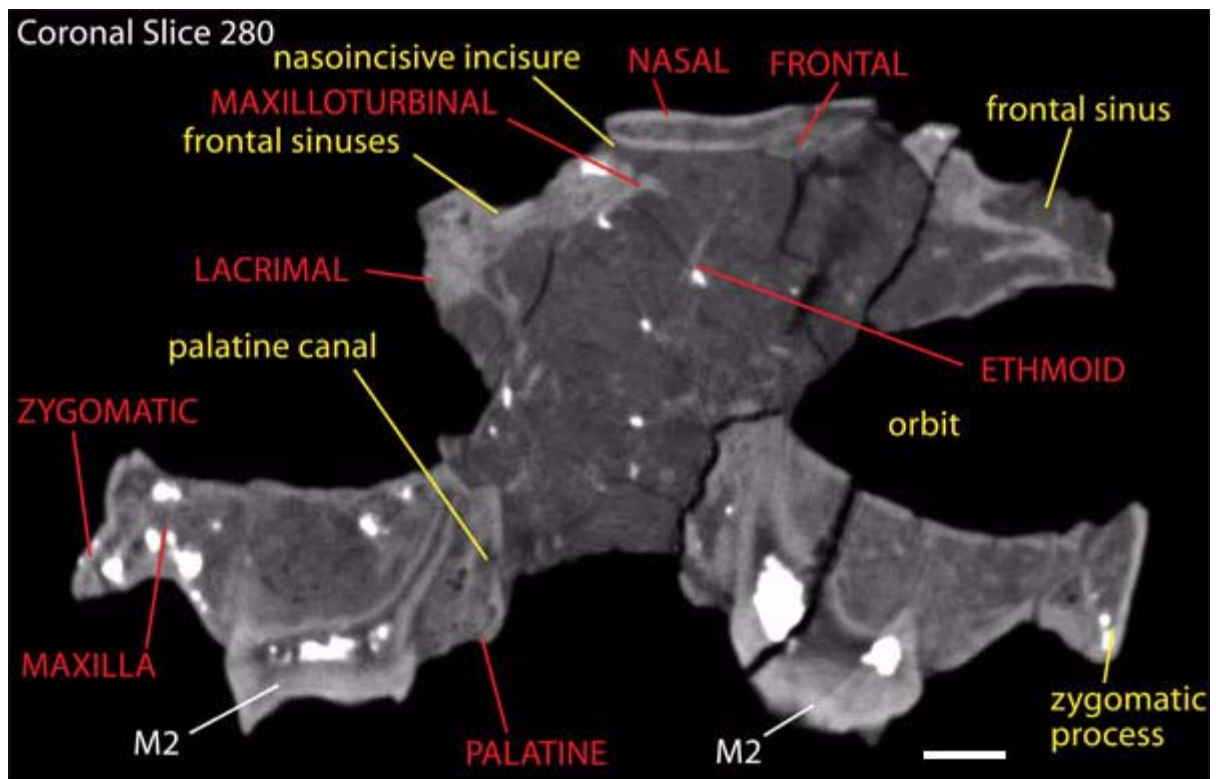


Figure 10. Coronal slice 280 from scanned data set for AMNH 42891. Grayscale levels have been adjusted to increase contrast. Scale bar equals 10 mm.

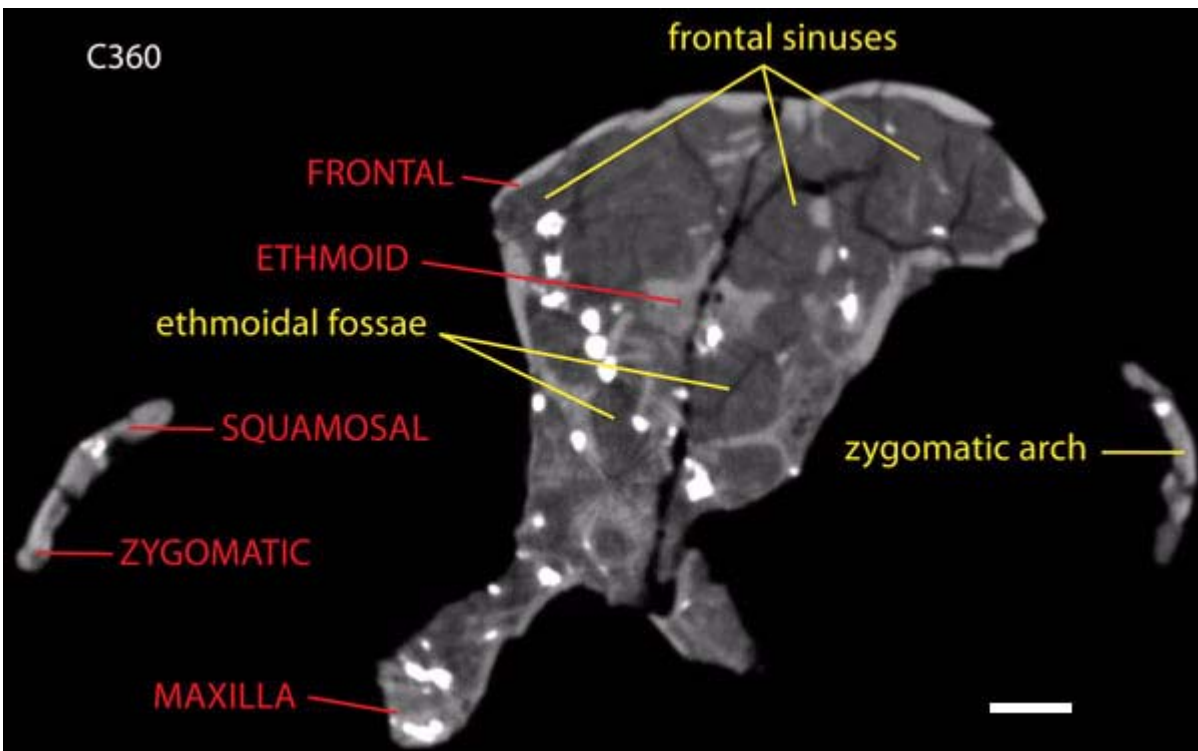


Figure 11. Coronal slice 360 from scanned data set for AMNH 42891. Grayscale levels have been adjusted to increase contrast. Scale bar equals 10 mm.

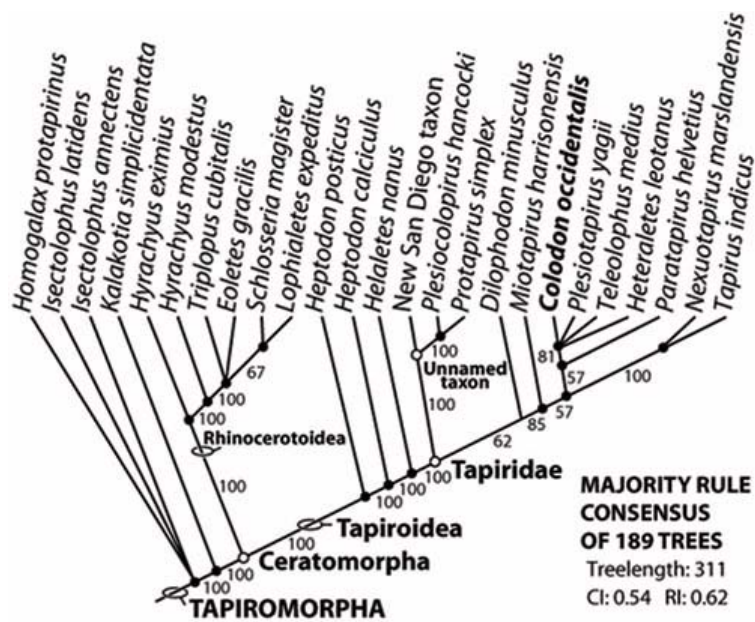


Figure 12. Majority-rule consensus tree based on the characters and scored matrix presented in Appendices 4 and 5.

Figures 12 and 13 for majority-rule consensus tree and adam's consensus tree, respectively.

This analysis supports the unorthodox placement of *Colodon occidentalis* closer to *Tapirus* than is *Protapirus*. Most previous analyses considered *Colodon* to be a divergent lineage tracing its ancestry to the Bridgerian *Helaletes* (e.g., Radinsky 1963), because it was considered 'too specialized' to be an ancestor of tapirids (e.g., Radinsky 1963). This was based partly on the supposition that "the molariform premolars of *Colodon* exclude all known species of that genus from the ancestry of *Protapirus*" (Radinsky 1963, p. 96). *Protapirus* was deemed closer to *Tapirus* than *Colodon* on merit of its presumed greater degree of narial incision retraction, and shortening of its nasals, which cannot be confidently coded in *Protapirus* (Colbert 1999). As noted above, the only figured *Colodon* skull in the literature (Radinsky 1963, figure 21) does not accurately depict the actual morphology of the narial region (see description) and has misled earlier interpretations of *Colodon's* evolutionary affinities (e.g., Colbert and Schoch 1998).

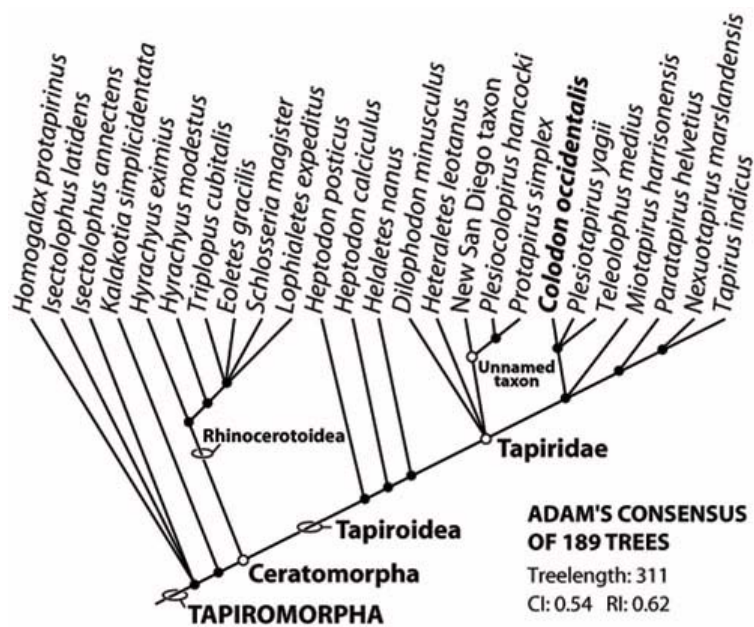
Several cranial characters support *Colodon* being closer to *Tapirus* than is *Protapirus*, including: the nasoincisive incisure extending to the level of M2 (character 56), the supraorbital process being reduced to a small rugosity (character 76), and the moderate inflation of the frontals (character 78). The following dental characters also support this relationship: having a P1 with a hypocone (character 28), having P3 and P4 with a divided protocone and hypocone (characters 34 and 37), and having the postprotocrista join the protocone rather than the hypocone (character 38). Most of

these dental characters relate to the degree of 'molarization' of the premolars. The chronostratigraphic occurrence the two skulls described here documents an earlier origin for these derived cranial morphologies than previously hypothesized.

DISCUSSION

The *Colodon* skulls described above document a tapir that, although only half the size of an extant tapir skull, had a surprisingly modern aspect to the facial skeleton. Many of the observed features are directly comparable with features in *Tapirus*, including several skeletal indicators of a prehensile proboscis similar to that of *Tapirus*. In particular, details of the anatomy surrounding the retracted nasoincisive incisure are similar to those of *Tapirus*, including the occurrence of apomorphic fossae for cartilaginous meatal diverticula on the dorsal frontals and nasal, and ascending maxillae. Other similarities with *Tapirus* include details of the telescoping of the skull, which is correlated with: the anteroposterior shortening of the frontals, and the development of frontal sinuses; the conformation of the rostral processes of the frontals, the descending processes of the nasals, and the ascending process of the maxillae; and the apparent embracing of the cartilaginous nasal septum by the premaxillae.

By contrast, the skull of *Protapirus*, which is larger, shares less apomorphies with *Tapirus*. Among the more plesiomorphic conditions of *Protapirus* are: a less retracted nasoincisive incisure; a pronounced postorbital constriction; and a lack of frontal sinuses above the cranial cavity, to name a few. In these features, *Protapirus* more closely



Figures 13. Adam's consensus tree based on the characters and scored matrix presented in Appendices 4 and 5.

resembles the late Eocene *Plesiocolopirus* (which some consider to be *Protapirus*, see Hanson 1996), and also a new taxon of diminutive tapir from the Uintan of southern California (see Colbert, 1999; Figure 12). Indeed, it is possible that these three taxa form a monophyletic group, based on their similarities (Colbert 1999).

Because the scanned *Colodon* skulls are subadults, much of their morphology potentially records juvenile conditions. The ontogenetic trajectory of these features in *Colodon* can be interpreted by comparison with *Tapirus*, however, as well as with other mammals. During the ontogeny of *Tapirus*, the facial skeleton shows the following transformations: a posterior retraction of the nasoincisive incisure relative to the anterior margin of the orbit; posterior migration of the palatal edge of the choanae relative to the molars; the formation and expansion of the frontal sinuses, and other sinuses; and the elongation of the face relative to the cranium as a whole. The last two of these transformations are common in many other mammals.

These observations suggest that, if there were any further ontogenetic transformations in the facial skeleton of *Colodon* from the condition described above, they would have led to a more deeply retracted nasoincisive incisure, larger frontal sinuses, and a relatively longer face. All of these hypothetical more mature conditions are also considered to represent more derived evolutionary states for these characters, such that further ontogenetic change would be expected to strengthen the special relationship of *Colodon* to *Tapirus* relative to *Protapirus*. In a broader evolutionary con-

text, it might be hypothesized that the evolution of the facial skeleton in the Tapiroidea involves peramorphosis (e.g., see Alberch et al. 1979), with the ontogeny of *Tapirus* 'recapitulating' various evolutionary character transformations in the facial skeleton of ancestral forms.

The hypothesis that *Colodon* is more closely related to *Tapirus* than is *Protapirus* potentially extends the chronostratigraphic range of the Tapiridae to the middle Eocene. This is based on the reported occurrence of *Colodon* from the late Uintan Sage Creek Formation of North America (Radinsky 1963). Unfortunately, as discussed above, *Colodon* is a very poorly known taxon based primarily on dental remains and may not be a natural group.

CONCLUSIONS

The facial skeleton of the early Oligocene *Colodon* shares several derived characters with both *Tapirus* and with other fossil tapirs from the late Oligocene to the Holocene (Colbert 1999). These characters involve morphological novelties, many of which are osteological correlates for a prehensile proboscis. These features are not known from other early Oligocene tapirs, or from geologically older tapirs. *Protapirus simplex*, which is roughly contemporaneous with *Colodon*, preserves less derived states for many of these same features. Thus, the evidence from the facial skeleton supports a phylogeny in which *Colodon* is more closely related to the crown-group *Tapirus* than is *Protapirus*. Because *Protapirus* has historically been considered the earliest tapirid, this also suggests that *Colodon* is a tapirid, and corroborates the assertion

that the “Helaletidae,” to which *Colodon* had traditionally been referred, is not monophyletic (e.g., Colbert and Schoch 1998).

Regardless of the systematic significance of these specimens, they also serve as a foundation for interpreting the evolutionary modifications of the tapiroid facial skeleton. The two skulls illustrate a less derived state for tapiroids, that nonetheless have a number of osteological correlates for a prehensile proboscis, and that also show a telescoped condition. In many ways, the skull of *Colodon* represents an intermediate condition that bridges the morphological gap between the derived morphology of *Tapirus* and that of other Eocene and early Oligocene tapiroids which lack well-developed osteological indicators for a prehensile proboscis.

ACKNOWLEDGMENTS

I first met Will Downs in the 1970s during my childhood summers visiting my grandparents in Flagstaff, Arizona. My grandfather had ‘retired’ to an emeritus position at the Museum of Northern Arizona, and my brother Denis and I would hang out there pestering the scientists and staff. The MNA was a vibrant place in the 1970s, employing a host of exciting young paleontologists, including such luminaries as R. Cifelli, L. Jacobs, and T. Rowe, to mention a few. But the highlight of any research center visit was the geology prep lab, where Will could be found sorting matrix or air scribing some fossil. He was extremely generous to us boys, always taking time to share some off-color tale, to offer his seasoned opinion on the delicate art of interacting with the ladies, or to help with one of our volunteer projects (a particular turtle that I was charged to prepare remains a staple feature of my nightmares to this day). Will was a major influence in my formative years, and I will always remember him with the greatest affection.

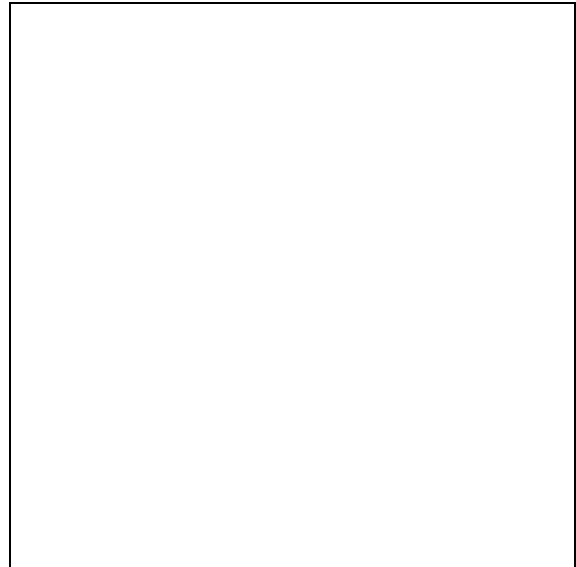
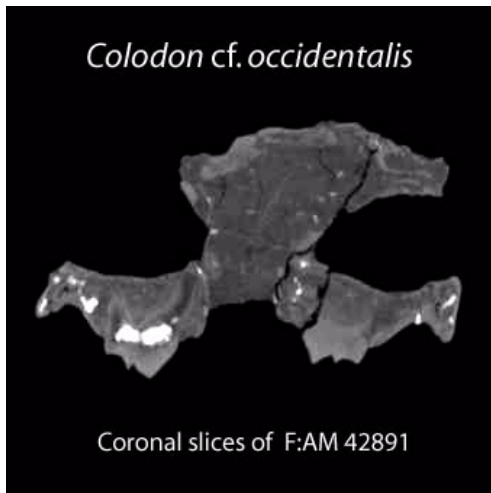
Regarding this contribution, many thanks to M. Greenwald and C. Herbel (SDSM), and to D. Tedford (AMNH) for their specimen loans. At UT, thanks always to T. Rowe (guidance, suggestions, and support), R. Ketcham and R. Racicot (help with the scanning and image processing), and to the rest of the CT lab personnel for general support. Thanks to L. Jacobs for the invitation to contribute to this volume, and to two anonymous reviewers who improved the quality of this report. As we all know, Will was a remarkable individual — it was an honor to have known him.

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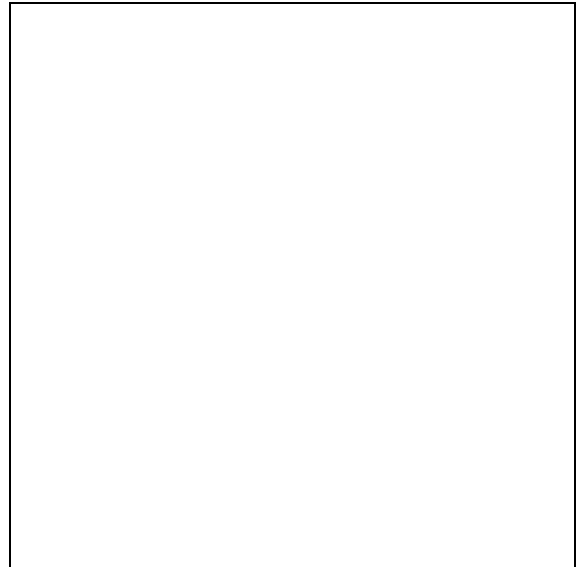
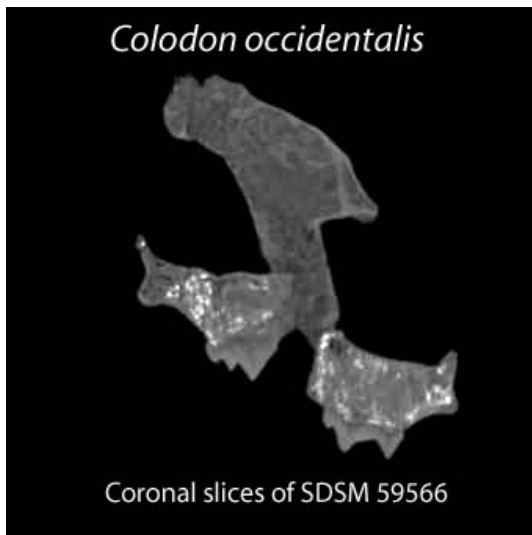
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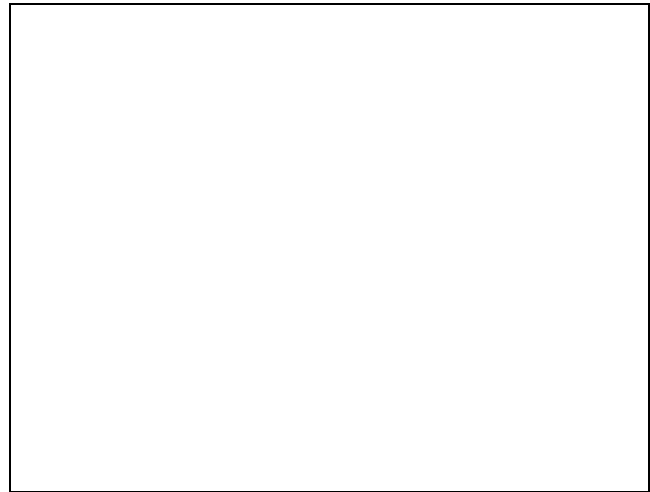
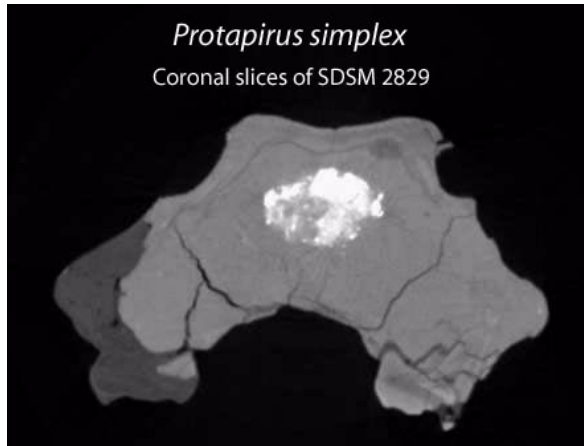
Appendix 1. Animation of the original coronal slice data set for *Colodon cf. occidentalis* (F.AM 42891). Images are reduced from their original image size for web viewing. [Click to run movie.](#)



Appendix 2. Animation of the original coronal slice data set for *Colodon occidentalis* (SDSM 59566). Images are reduced from their original image size for web viewing. Click to run.



Appendix 3. Animation of the original coronal slice data set for *Protapirus simplex* (SDSM 2829). Images are reduced from their original image size for web viewing. Click to run.



Appendix 4. Description of characters used in the phylogenetic analyses. Characters are polarized with respect to *Homogalax protapirinus*, *Isectolophus latidens*, and *I. annectens* as outgroups. All characters are treated as unordered.

- (1) Distinct cuspules on cheekteeth shearing lophs: present (0); absent, lophs continuous (1).
- (2) Upper canine length compared to upper incisors: canines shorter (0); canines longer (1); canines absent (2). Modified from character 18 of Colbert (1993), and character 10 of Hooker, (1989).
- (3) I3 size relative to I2-3: similar size (0); enlarged (1). Modified from character 29 of Colbert (1993).
- (4) I3 posterior cuspule: present (0); absent (1).
- (5) i3 size relative to i1-3: similar size (0); reduced (1); i3 absent (2). Modified from character 30 of Colbert (1993).
- (6) Incisor shape: not spatulate (0); spatulate (1).
- (7) Upper molar metacone enamel surface: wrinkled labially (0); not wrinkled (1).
- (8) M1 metacone buccal surface: broadly rounded (0); ribbed buccally (1); flat to concave (2). Modified from character 4 of Dashzeveg and Hooker (1997), and from character 23 of Colbert (1993). Similar to character 55 of Hooker (1989).
- (9) M2 metacone buccal surface: broadly rounded (0), ribbed buccally (1); flat to concave (2). Modified from character 4 of Dashzeveg and Hooker (1997), and from character 23 of Colbert (1993). Similar to character 55 of Hooker (1989).
- (10) M3 metacone buccal surface: broadly rounded (0), ribbed buccally (1); flat to concave (2). Modified from character 4 of Dashzeveg and Hooker (1997), and from character 23 of Colbert (1993). Similar to character 55 of Hooker (1989).
- (11) M1 parastyle separation from paracone: well separated (0); compressed against paracone, curving around the paracone labial face (1). Modified from character 7 of Dashzeveg and Hooker (1997), similar to character 26 of Colbert (1993).
- (12) M2 parastyle separation from paracone: well separated (0); compressed against paracone, curving around the paracone labial face (1). Modified from character 7 of Dashzeveg and Hooker (1997), similar to character 26 of Colbert (1993).
- (13) M3 parastyle separation from paracone: well separated (0); compressed against paracone, curving around the paracone labial face (1). Modified from character 7 of Dashzeveg and Hooker (1997), similar to character 26 of Colbert (1993).
- (14) M1 ectoloph long axis: essentially straight, joining vertically implanted or slightly distally tilted paracone (0); buccally convex, making U-shaped loph together with protoloph and metaloph, and having a slightly mesially tilted paracone (1). Modified from character 8 of Dashzeveg and Hooker (1997).
- (15) M2 ectoloph long axis: essentially straight, joining vertically implanted or slightly distally tilted paracone (0); buccally convex, making U-shaped loph together with protoloph and metaloph, and having a slightly mesially tilted paracone (1). Modified from character 8 of Dashzeveg and Hooker (1997).
- (16) M3 ectoloph long axis: essentially straight, joining vertically implanted or slightly distally tilted paracone (0); buccally convex, making U-shaped loph together with protoloph and metaloph, and having a slightly mesially tilted paracone (1). Modified from character 8 of Dashzeveg and Hooker (1997).
- (17) M2 ectoloph developed into high shearing blade by lengthening metacone: not developed (0); developed (1).
- (18) Position where M1 metaloph joins ectoloph: near middle (0); slightly in front of metacone (1); at metacone (2). Modified from character 9 of Dashzeveg and Hooker (1997), similar to character 47 of Hooker (1989).
- (19) Position where M2 metaloph joins ectoloph: near middle (0); slightly in front of metacone (1); at metacone (2). Modified from character 9 of Dashzeveg and Hooker (1997), similar to character 47 of Hooker (1989).
- (20) Position where M3 metaloph joins ectoloph: near middle (0); slightly in front of metacone (1); at metacone (2). Modified from character 9 of Dashzeveg and Hooker (1997), similar to character 47 of Hooker (1989).
- (21) M3 metaloph axis relative to ectoloph axis: not directed distinctly posteriorly, forms obtuse angle with ectoloph (0); directed distinctly posteriorly, forms acute angle with ectoloph (1).
- (22) M3 lingual cingulum: incomplete (0); complete (1). Modified from character 11 of Dashzeveg and Hooker (1997).
- (23) M1-2 lingual cingulum: incomplete (0); complete (1). Modified from character 11 of Dashzeveg and Hooker (1997) and from character 25 of Colbert (1993).

- (24) Shape and position of M1-2 ectocingulum adjacent to metacone: forming ridge and marginal (0); bulbous and encroaching on styler shelf (1); ectocingulum absent (2). Modified from character 12 of Dashzeveg and Hooker (1997).
- (25) Upper molar postmetacrista and lower molar paracristid (paralophid): mesiodistally oriented (0); obliquely oriented (1). Character 13 of Dashzeveg and Hooker (1997).
- (26) Molar transverse loph lateral profile: straight (0); curved occlusomesially in uppers and occlusodistally in lowers (1). Character 14 of Dashzeveg and Hooker (1997).
- (27) Upper molar postmetacrista and lower molar trigonid: relatively long (0); slightly shortened (1); greatly shortened (2). Character 15 of Dashzeveg and Hooker (1997).
- (28) P1 hypocone: absent (0); present (1). Character 17 of Dashzeveg and Hooker (1997).
- (29) P2 lingual cingulum: complete (0); broken or absent (1).
- (30) P3 lingual cingulum: complete (0); broken or absent (1).
- (31) P4 lingual cingulum: complete (0); broken or absent (1).
- (32) P3 hypocone presence, metaloph shape: P3 either absent or connects directly to metaloph (postprotocrista) (0); hypocone independent of metaloph (postprotocrista), which joins protocone (1). Character 19 of Dashzeveg and Hooker (1997).
- (33) P3 loph posterior to the protoloph: absent (0); P3 with postprotocrista (1); P3 with metaloph (2). Modified from character 21 of Colbert (1993).
- (34) P3 with protocone and hypocone: not divided (0); divided (1). This character was used Dashzeveg and Hooker (1997) to characterize *Colodon*.
- (35) P4 metaloph (postprotocrista): essentially complete (0); broken buccal of protocone (1). Character 20 of Dashzeveg and Hooker, 1997.
- (36) P4 loph development: P4 with postprotocrista (0); P4 with metaloph (1). Modified from character 20 of Colbert (1993).
- (37) P4 protocone and hypocone: not divided (0); divided (1). This character was used Dashzeveg and Hooker (1997) to characterize *Colodon*.
- (38) P4 postprotocrista (metaloph): joins protocone rather than hypocone (0); joins hypocone (1). This character was used Dashzeveg and Hooker (1997) to characterize *Colodon*.
- (39) P4 ectoloph concave, paracone and metacone displaced lingually relative to preparamacrista/ parastyle, and postmetacrista/metastyle: no (0); yes (1).
- (40) m3 hypoconulid lobe: large (0); small (1); in the form of a cusped cingulum (2); absent (3). Character 16 of Dashzeveg and Hooker (1997). Similar to character 28 of Colbert (1993), and to character 59 of Hooker (1989). This is a continuous multistate character.
- (41) Lower molar posthypocristid: cusped (0); weakly present (1); absent (2). Character 26 of Dashzeveg and Hooker (1997). This is a continuous multistate character.
- (42) Cristid-like structure on the lower molars: absent (0); present (1). Character discussed by Albright (1998). Modified from character 31 of Colbert (1993).
- (43) "Cingulum around the lingual end of the mesial arm of the lower molar paralophid, where the latter recurves slightly distally" Dashzeveg and Hooker (1997: 107): absent (0); present (1). This character was used by Dashzeveg and Hooker (1997) to distinguish *Lophialetes* from *Schlosseria*.
- (44) m1 protolophid and hypolophid parallel: yes (0); no (1).
- (45) m2 protolophid and hypolophid parallel: yes (0); no (1).
- (46) m3 protolophid and hypolophid parallel: yes (0); no (1).
- (47) Relative depth of the horizontal ramus of the dentary: ratio of M2 length to dentary depth of at level of M2 less than 45% (0); greater than 45% (1). Modified from character 15 of Colbert (1993).
- (48) Posterior extent of the fused symphysis of dentary: anterior to anterior edge of p2 (0); posterior to anterior edge of p2 (1). Modified from character 16 of Colbert (1993). Note that in *Breviodon*, the posterior extent of the symphysis is approximately at the level of anterior p3.
- (49) p1: present (0), absent (1).
- (50) p3 paraconid: much lower than protoconid (0); p3 paraconid nearly as tall as protoconid with trenchant paracristid (1). Modified from character 23 of Dashzeveg and Hooker (1997).
- (51) p3 metaconid: weak (0); strong (1). Character 22 of Dashzeveg and Hooker (1997).
- (52) p3-4 talonids: no broader than trigonids (0); broader than trigonids (1). Character 24 of Dashzeveg and Hooker (1997); character 22 of Colbert, (1993).

- (53) Metastylids on dp2: absent (0), present (1). Modified character 22 of Hulbert (1995).
- (54) Metastylids on dp3: absent (0), present (1). Modified character 22 of Hulbert (1995).
- (55) Metastylids on dp4. Absent (0), present (1). Modified character 22 of Hulbert (1995).
- (56) Posterior extent of nasoincisive incisure: P1 (0); P2 (1); P3 (2) P4 (3), M1 (4), M2 (5) M3 (6). Modified from character 1 of Dashzeveg and Hooker (1997); character 4 of Hooker (1989), and character 5 of Colbert (1993). This is a continuous multistate character.
- (57) Anterior extent of orbit: posterior to anterior M1 (0), posterior to anterior M2 (1), posterior to anterior M3 (2), posterior to P4 (3). This is a continuous multistate character.
- (58) Posterior process of premaxilla: long, terminates in acute point (0), short, bluntly terminated (1). Modified character 13 of Hulbert (1995).
- (59) Anteromedial process of maxilla: absent to very slender, little or no lateral exposure (0); moderate lateral exposure (1); broad, well-exposed laterally (2). Modified character 14 of Hulbert (1995).
- (60) Premaxillary–nasal contact: present (0); absent(1). Modified from character 9 of Colbert (1993), and from character 2 of Dashzeveg and Hooker (1997).
- (61) Shape of nasals not contacting premaxillae: have splint-like anterior process (0); lack splint-like anterior extension (1). Modified from character 9 of Colbert (1993), and from character 2 of Dashzeveg and Hooker (1997).
- (62) Oblique lateral ridge on nasals: absent (0); present located posteriorly (1); present located anteriorly (2). Modified from character 10 of Colbert (1993).
- (63) Premaxillary-maxillary suture: descends anterior to canine in lateral view (0), descends to middle of canine (1). Modified character 15 of Hulbert (1995).
- (64) Dorsal maxillary flange: does not embrace mesethmoid (0); embraces mesethmoid to limited extent (1), broadly embraces mesethmoid (2). Modified character 16 of Hulbert (1995). This is a continuous multistate character.
- (65) Maxillary fossa: absent (0); present (1). Modified from character 7 of Colbert, 1993.
- (66) Lateral groove, anterior portion: absent (0); present (1). Modified from character 32 of Colbert (1993)
- (67) Infraorbital foramen position: anterior to anterior edge of P3 (0); posterior to anterior edge of P3, and anterior to anterior edge of P4 (1); posterior to anterior edge of P4 (2). Modified from character 8 of Colbert (1993). This is a continuous multistate character.
- (68) Anterior extent of the masseteric muscle scar: posterior to anterior edge of M2 (0); anterior to anterior edge of M2 (1). Modified from character 12 of Colbert (1993)
- (69) Anterior lacrimal tubercle/ process: weak or absent (0); well developed (1). Modified character 16 of Hulbert (1995).
- (70) Palatine fissures: paired (0); single confluent median fissure (1). Modified from character 6 of Colbert (1993).
- (71) Anteromedial process of frontals: extends between nasals (0); does not extend between nasals (1). Modified character 6 of Hulbert (1995).
- (72) Sagittal crest anterior to frontal crests: absent (0); present (1). Character 1 of Colbert (1993).
- (73) Narrow grooves on posterolateral nasals and frontals at the posterior terminus of the narial incision: absent (0); present, short, largely restricted to posterolateral nasals (1); present, long and straight, extending well onto frontals (2). Modified from character 2 of Colbert (1993).
- (74) Lateral groove, posterior portion: absent (0); present, continues posteriorly to frontal crests (1); present, curled or compressed onto postero-dorsal nasal (2). Modified from character 3 of Colbert (1993).
- (75) Medial grooves on dorsal surface of frontals: absent (0); present (1). Modified from character 4 of Colbert (1993).
- (76) Lateral supraorbital process: broad (0); reduced to small rugosity (1). Modified from character 11 of Colbert (1993).
- (77) Adult width of sagittal crest: relatively narrow (0); broad (1). Modified character 2 of Hulbert (1995).
- (78) Frontal inflation; none or slight (0): moderate to great (1). Modified character 4 of Hulbert (1995).
- (79) Dorsal contour of skull: relatively straight (0); nasals notably stepped down from frontals (1). Modified character 12 of Hulbert (1995).
- (80) Interparietal: present (0); absent (1). Hulbert's (1995) character 5 coded the interparietal either fused early or later in ontogeny. However, based on observation of early postnatal (possibly neona-

tal material) it is clear that the interparietal is lacking in most *T. terrestris*.

(81) Postglenoid foramen on posteromedial portion of postglenoid process: present (0); absent (1). Modified from character 13 of Colbert (1993).

(82) Foramen ovale: distinct (0); confluent with the middle lacerate foramen (1). Modified from character 33 of Colbert (1993). This character is also discussed in MacFadden (1976), and Edinger and Kitts, (1954).

(83) Relative width of paroccipital process: narrow and slender (0); broad and massive (1). Modified character 17 of Hulbert (1995).

(84) Manus digit V: present (0); absent (1). Character 31 of Dashzeveg and Hooker (1997).

(85) Lower canines: present (0); absent (1).

(86) Postglenoid process axis less than 45 degree angle to long axis of skull: no (0); yes (1).

(87) Postglenoid process shape: low and rounded (0); tall and post-like (1); tall and compressed (2)

(88) Astragalus sustentacular and posterior calcaneal facets confluent: no (0); yes (1).

(89) m2 metalophids reduced: no(0); yes (1).

Appendix 5. Taxon-by-character matrix used in phylogenetic analyses. Abbreviations: A, (0,1); B, (1,2); C, (0,2); D, (2,3); N, does not apply.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Homogalax protapirinus</i>	0	0	1	0	0	0	0	0	0	A	0	0	0	0	0	0	0	0	0	0
<i>Isectolophus latidens</i>	0	?	?	?	0	?	1	0	0	0	0	0	0	0	0	?	0	0	0	0
<i>Isectolophus annectens</i>	0	?	?	?	0	?	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hyrachyus eximius</i>	1	0	0	1	1	1	1	0	1	2	0	0	1	0	0	0	1	1	1	1
<i>Hyrachyus modestus</i>	1	0	?	?	1	1	1	1	1	B	0	0	1	0	0	0	1	1	1	1
<i>Heptodon posticus</i>	1	0	1	?	0	1	?	1	1	1	0	1	0	0	0	0	0	1	1	1
<i>Heptodon calciculus</i>	1	?	1	0	0	1	0	A	A	A	0	0	0	0	0	0	0	1	1	2
<i>Helaletes nanus</i>	1	0	0	?	0	1	0	B	B	B	A	1	1	0	0	1	0	1	1	B
<i>Dilophodon minusculus</i>	1	?	?	?	?	?	0	1	1	1	0	0	1	0	1	1	0	1	1	1
<i>Colodon occidentalis</i>	1	2	1	1	1	1	1	2	2	2	1	1	1	1	1	1	0	2	2	2
New San Diego Taxon	1	0	?	?	0	1	1	1	1	A	0	0	1	0	0	1	0	1	1	1
<i>Plesiocolopirus hancocki</i>	1	?	?	?	?	?	1	1	1	2	0	1	1	0	0	1	0	?	1	1
<i>Protapirus simplex</i>	1	?	?	?	?	?	1	0	0	2	?	1	1	?	0	0	0	2	2	2
<i>Teleolophus medius</i>	1	?	?	?	?	?	1	2	2	2	1	1	1	1	1	1	0	1	1	2
<i>Triplopus cubitalis</i>	1	?	?	?	?	?	1	1	2	2	1	1	1	0	0	0	1	1	1	2
<i>Lophialetes expeditus</i>	1	?	?	?	?	1	1	1	1	1	0	0	0	0	0	1	1	1	0	0
<i>Eoletes gracilis</i>	1	?	?	0	?	1	1	2	2	2	0	0	0	A	A	0	1	1	1	2
<i>Schlosseria magister</i>	1	?	?	?	?	?	1	2	2	2	0	0	1	0	0	1	A	1	0	1
<i>Heteraletes leotanus</i>	1	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	0	?	?	?
<i>Miotapirus harrisonensis</i>	1	1	0	1	1	1	?	0	0	0	0	0	0	0	0	1	0	1	1	1
<i>Plesiotapirus yagii</i>	1	1	0	?	1	1	?	?	?	2	?	1	1	?	1	1	0	0	1	2
<i>Paratapirus helvetius</i>	1	1	1	?	?	1	?	0	?	2	0	?	?	0	1	1	0	1	1	1
<i>N. marslandensis</i>	1	1	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0
<i>Kalakotia simplicidentata</i>	?	?	?	?	?	?	?	1	1	1	0	0	0	0	0	0	1	0	0	0
<i>Tapirus indicus</i>	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1

Appendix 5 (continued).

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
<i>Homogalax protapirinus</i>	0	A	A	0	0	0	?	0	0	1	1	0	0	0	1	0	0	0	?	0
<i>Isectolophus latidens</i>	0	0	1	0	0	0	?	?	?	1	1	0	A	A	0	0	0	0	?	0
<i>Isectolophus annectens</i>	0	1	0	0	0	0	?	0	?	?	?	0	1	1	0	0	0	0	?	0
<i>Hyrachyus eximius</i>	1	0	0	0	1	0	0	0	1	1	1	0	1	A	A	0	0	N	?	D
<i>Hyrachyus modestus</i>	1	A	0	C	1	0	0	0	1	1	0	0	1	0	0	0	0	0	?	D
<i>Heptodon posticus</i>	0	0	0	0	1	0	1	0	?	?	?	0	?	0	0	0	0	0	0	1
<i>Heptodon calciculus</i>	?	0	0	0	1	0	?	?	1	1	1	0	1	0	A	0	0	0	?	0
<i>Helaletes nanus</i>	0	0	0	0	A	0	1	0	1	1	1	0	1	A	A	0	A	A	0	1
<i>Dilophodon minusculus</i>	?	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	3
<i>Colodon occidentalis</i>	?	0	0	A	1	0	2	1	1	A	A	0	0	1	0	0	1	1	?	1
New San Diego Taxon	0	0	0	0	1	0	?	0	1	1	1	0	A	0	A	0	0	0	0	3
<i>Plasiocolopirus hancocki</i>	?	0	0	0	1	0	?	0	1	1	1	0	1	0	0	0	0	0	?	1
<i>Protapirus simplex</i>	0	0	0	0	1	0	2	0	1	1	1	0	1	0	0	0	0	0	0	3
<i>Teleolophus medius</i>	0	1	1	1	0	1	2	1	0	0	0	0	1	1	0	0	1	1	0	3
<i>Triplopus cubitalis</i>	1	0	0	2	0	1	0	?	?	?	?	0	1	1	1	0	0	0	0	3
<i>Lophialetes expeditus</i>	1	0	0	0	A	1	0	0	0	0	0	0	1	0	0	0	0	0	A	0
<i>Eoletes gracilis</i>	1	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	1	0
<i>Schlosseria magister</i>	1	0	0	0	A	0	0	0	0	0	0	0	1	0	0	0	0	0	0	A
<i>Heteraletes leotanus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Miotapirus harrisonensis</i>	0	0	0	0	0	?	?	1	1	1	1	0	2	1	0	1	1	1	0	3
<i>Plasiotapirus yagii</i>	0	0	0	0	0	0	?	1	1	1	1	1	2	1	0	1	1	1	0	3
<i>Paratapirus helvetius</i>	0	0	0	0	0	0	?	1	0	?	?	2	2	1	0	1	1	1	0	?
<i>N. marslandensis</i>	1	0	0	0	0	0	0	?	1	1	1	0	1	A	A	1	A	?	0	1
<i>Kalakotia simplicidentata</i>	1	0	1	0	0	0	0	N	0	?	0	N	0	1	0	0	0	0	0	0
<i>Tapirus indicus</i>	0	0	0	A	0	0	?	1	1	1	1	0	2	1	0	1	1	1	0	D

Appendix 5 (continued).

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
<i>Homogalax protapirinus</i>	0	0	0	0	0	0	A	1	0	0	0	0	0	1	1	0	0	0	0	0
<i>Isectolophus latidens</i>	0	0	A	0	A	A	1	1	0	?	0	1	?	?	?	0	0	?	0	0
<i>Isectolophus annectens</i>	1	0	A	0	0	0	1	1	0	?	?	0	?	?	?	?	?	?	?	?
<i>Hyrachyus eximius</i>	2	0	0	1	1	1	1	1	0	0	1	0	?	?	?	0	1	0	0	0
<i>Hyrachyus modestus</i>	2	0	0	A	A	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0
<i>Heptodon posticus</i>	2	0	0	0	0	0	1	?	0	0	1	0	?	?	?	0	1	0	0	0
<i>Heptodon calciculus</i>	2	0	0	0	0	0	0	1	0	0	1	0	?	0	0	0	?	?	?	1
<i>Helaletes nanus</i>	2	0	A	0	A	1	1	0	1	0	1	0	?	0	0	2	0	1	1	1
<i>Dilophodon minusculus</i>	B	0	0	0	0	A	A	0	1	0	1	1	?	0	?	?	?	?	?	?
<i>Colodon occidentalis</i>	2	0	1	0	1	1	0	0	1	A	1	1	?	0	0	5	0	0	0	1
New San Diego Taxon	2	0	?	0	0	0	0	0	0	0	1	1	?	?	?	3	0	0	0	1
<i>Plasiocolopirus hancocki</i>	2	0	?	0	0	0	0	0	1	0	1	1	?	?	?	3	0	?	?	1
<i>Protapirus simplex</i>	2	0	?	0	0	0	1	?	1	0	1	1	?	?	?	3	0	0	0	1
<i>Teleolophus medius</i>	2	0	0	0	1	1	1	0	0	1	1	1	0	0	0	?	2	?	?	?
<i>Triplopus cubitalis</i>	2	0	0	0	1	1	1	0	?	0	1	0	?	?	?	0	0	?	?	?
<i>Lophialetes expeditus</i>	2	0	A	0	1	1	A	0	0	0	1	1	0	0	0	3	1	0	0	1
<i>Eoletes gracilis</i>	B	0	0	?	?	1	?	?	0	0	1	A	?	?	?	0	?	?	?	0
<i>Schlosseria magister</i>	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0
<i>Heteraletes leotanus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Miotapirus harrisonensis</i>	2	0	?	0	0	0	1	?	1	0	1	A	?	?	?	?	0	0	0	1
<i>Plesiotapirus yagii</i>	2	0	?	0	1	1	0	?	1	?	1	?	?	?	?	6	0	0	?	1
<i>Paratapirus helvetius</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	5	0	0	0	1
<i>N. marslandensis</i>	0	1	?	0	1	1	?	?	1	0	1	1	1	1	1	5	3	0	2	1
<i>Kalakotia simplicidentata</i>	0	0	0	0	0	0	?	?	?	0	0	A	?	?	?	?	?	?	?	?
<i>Tapirus indicus</i>	0	1	?	0	0	1	1	1	1	0	0	0	0	0	0	6	0	0	1	1

Appendix 5 (continued).

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
<i>Homogalax protapirinus</i>	N	0	0	N	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	?
<i>Isectolophus latidens</i>	N	0	?	N	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	1
<i>Isectolophus annectens</i>	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hyrachyus eximius</i>	N	0	0	N	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Hyrachyus modestus</i>	N	0	0	N	0	0	1	0	0	?	0	0	0	0	0	0	0	0	0	1
<i>Heptodon posticus</i>	N	0	0	N	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	?
<i>Heptodon calciculus</i>	?	?	?	?	0	1	B	1	?	?	?	?	?	?	?	?	?	?	?	?
<i>Helaletes nanus</i>	0	2	0	0	0	1	2	0	?	1	1	0	0	0	0	N	0	0	0	1
<i>Dilophodon minusculus</i>	?	?	?	?	?	?	A	?	?	?	?	0	?	?	?	?	0	0	?	?
<i>Colodon occidentalis</i>	?	0	?	0	0	1	2	1	1	1	0	0	0	2	0	1	0	1	0	?
New San Diego taxon	0	1	0	0	1	1	1	1	1	1	0	1	2	1	1	0	0	0	0	?
<i>Plesiocolopirus hancocki</i>	?	?	0	0	?	1	2	?	?	?	?	1	?	1	1	?	?	0	0	?
<i>Protapirus simplex</i>	?	1	0	0	1	1	1	0	1	1	0	1	2	1	1	0	0	0	0	?
<i>Teleolophus medius</i>	?	?	?	?	0	?	2	0	?	?	?	?	?	?	?	?	?	?	?	?
<i>Triplopus cubitalis</i>	?	?	?	?	?	?	?	1	0	?	0	0	0	0	0	0	0	0	0	1
<i>Lophialetes expeditus</i>	?	?	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Eoletes gracilis</i>	N	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?
<i>Schlosseria magister</i>	N	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	?
<i>Heteraletes leotanus</i>	?	?	?	?	0	?	?	?	?	?	?	0	0	0	0	?	?	?	?	?
<i>Miotapirus harrisonensis</i>	0	?	0	0	0	1	2	?	1	1	?	?	?	?	?	?	?	?	?	?
<i>Plesiotapirus yagii</i>	?	?	?	?	?	?	?	?	?	?	?	0	1	0	?	1	0	?	?	?
<i>Paratapirus helvetius</i>	1	?	1	?	0	1	2	?	1	1	0	0	1	2	0	1	0	1	?	?
<i>N. marslandensis</i>	?	?	0	B	0	1	1	0	1	1	0	0	1	2	0	1	?	0	0	?
<i>Kalakotia simplicidentata</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Tapirus indicus</i>	1	0	1	1	0	1	1	1	1	1	0	0	1	2	0	1	1	1	1	0

Appendix 5 (continued).

	81	82	83	84	85	86	87	88	89
<i>Homogalax</i>	?	?	?	?	0	?	?	0	0
<i>protapirinus</i>									
<i>Isectolophus latidens</i>	0	?	0	0	0	0	0	?	0
<i>Isectolophus</i>	?	?	?	?	?	?	?	?	0
<i>annectens</i>									
<i>Hyrachyus eximius</i>	0	0	0	0	0	0	0	?	0
<i>Hyrachyus modestus</i>	0	0	0	0	0	0	1	?	0
<i>Heptodon posticus</i>	0	0	0	0	0	1	0	?	1
<i>Heptodon calciculus</i>	?	?	?	0	0	?	?	1	1
<i>Helaletes nanus</i>	0	0	0	0	0	0	0	?	1
<i>Dilophodon</i>	?	?	0	?	?	?	?	?	1
<i>minusculus</i>									
<i>Colodon occidentalis</i>	1	?	?	1	1	1	2	?	1
New San Diego Taxon	0	1	?	?	0	1	0	0	1
<i>Plesiocolopirus</i>	?	?	?	?	?	?	?	?	1
<i>hancocki</i>									
<i>Protapirus simplex</i>	1	1	0	0	0	1	2	?	1
<i>Teleolophus medius</i>	?	?	?	?	0	?	?	?	1
<i>Triplopus cubitalis</i>	?	?	0	1	0	0	1	?	0
<i>Lophialetes expeditus</i>	1	1	0	1	0	0	1	?	0
<i>Eoletes gracilis</i>	?	?	?	?	?	?	?	?	0
<i>Schlosseria magister</i>	?	?	?	1	0	?	?	?	0
<i>Heteraletes leotanus</i>	?	?	?	?	?	?	?	?	?
<i>Miotapirus</i>	?	?	?	?	0	?	?	?	1
<i>harrisonensis</i>									
<i>Plesiotapirus yagii</i>	?	?	?	?	1	?	?	?	?
<i>Paratapirus helvetius</i>	?	?	?	?	?	?	?	0	?
<i>N. marslandensis</i>	1	?	?	?	0	1	2	?	?
<i>Kalakotia</i>	?	?	?	?	?	?	?	?	0
<i>simplicidentata</i>									
<i>Tapirus indicus</i>	1	1	1	1	0	0	2	0	1