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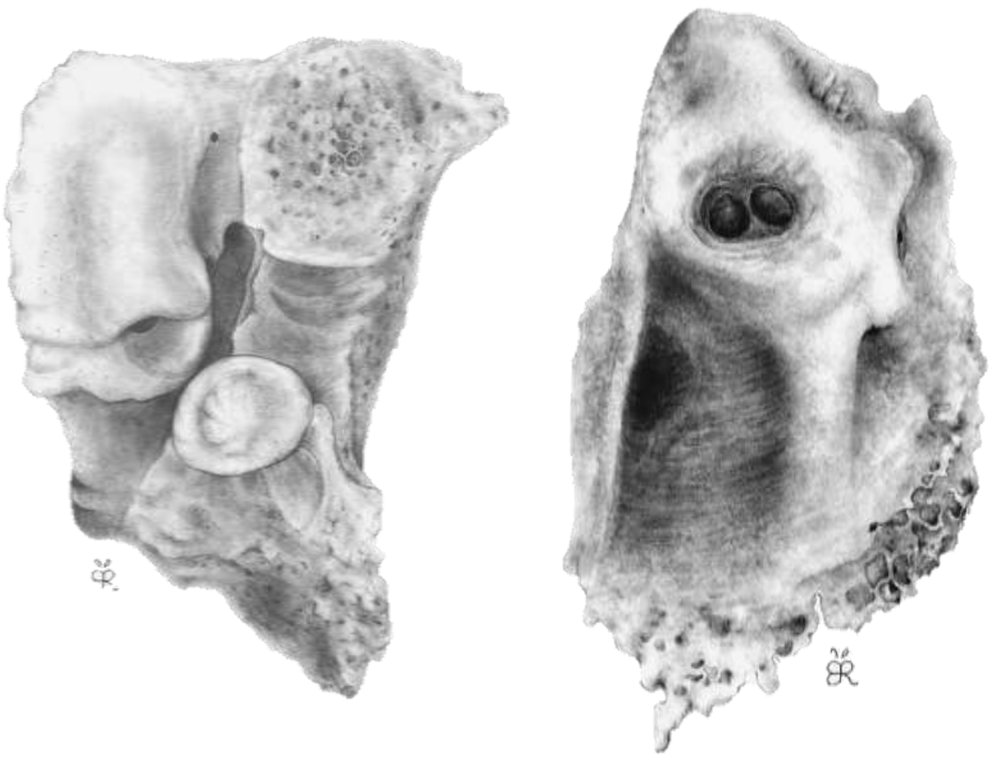

Ana Luísa Damaceno Mateus

Março, 2018

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Dissertação apresentada ao Programa de Pós-graduação em Zoologia do Instituto de Ciências Biológicas da Universidade Federal de Minas Gerais, como requisito parcial para obtenção do título de Mestre.

Orientador: Dr. Mario Alberto Cozzuol
Co-orientador: Dr. Rodrigo Parisi Dutra

ANA LUÍSA DAMACENO MATEUS
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"... if one advances confidently in the direction of his dreams, and endeavors to live the life which he has imagined, he will meet with a success unexpected in common hours. He will put some things behind, will pass an invisible boundary; new, universal, and more liberal laws will begin to establish themselves around and within him; or the old laws be expanded, and interpreted in his favor in a more liberal sense, and he will live with the license of a higher order of beings."

Henry David Thoreau, Walden

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(The petrosal representation in the front page of this dissertation and in some subsequente pages was illustrated by Barbara Rossi).

SUMMARY

ABSTRACT

The petrosal is an important and complex bone of the basicranium that houses the organs of balance and orientation in space (vestibule) and hearing (cochlea) together with the associated tissues related with these functions. Among ungulates, it is extensively applied in Artiodactyla phylogenetic studies, however it is still poorly known and used to study Perissodactyla internal relationships, mainly among the extant representatives. Also, the evolution of the petrosal of perissodactyls, although barely mentioned in literature, was never described and/or accurately analyzed. This study will be the first morphological description of the petrosal of the living species *Tapirus kabomani* Cozzuol, et al., 2013, *Tapirus indicus* Desmarest, 1819 and the extinct *Tapirus cristatellus* Winge, 1906; as well as extend the knowledge of the ear region of genus *Tapirus* Brisson, 1762. It will be also a major contribution to the analysis of the petrosal of Perissodactyla available in literature. Besides to contribute to the descriptive collection of petrosal of the order Perissodactyla we will trace the evolution of some petrosal characters among Perissodactyla, with emphasis in Tapiridae, investigating the evolutionary similarities and differences between the petrosal of some extinct and extant perissodactyls representatives and tracing how some petrosal characters behave when added to a existing phylogeny.

Key words: Petrosal, Description, *Tapirus*, Tapiridae, Perissodactyla, Characters.

INSTITUTIONAL ABBREVIATIONS

AMNH: American Museum of Natural History;

IVPP: Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences;

MACN: Museo Argentino de Ciencias Naturales Bernardino Rivadavia;

MN: Museu Nacional do Rio de Janeiro;

MCL: Acronym of the Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais;

SDSNH: San Diego Society of Natural History;

UFMG: Universidade Federal Minas Gerais.

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C) Caudal tympanic process – position (character 3) mapped in the phylogeny.

D) Hiatus Falopii (character 4) mapped in the phylogeny.

E) Sulcus for stapedial artery (character 5) mapped in the phylogeny.

F) Promontorial surfasse (character 6) mapped in the phylogeny.

G) Subarcuate fossa – depth (character 7) mapped in the phylogeny.

H) Subarcuate fossa – size (character 8) mapped in the phylogeny.

I) Epitympanic recess (character 9) mapped in the phylogeny.

J) Secondary facial foramen (character 10) mapped in the phylogeny.

K) Cochlear aqueduct – position (character 11) mapped in the phylogeny.

L) Cochlear aqueduct – slit (character 12) mapped in the phylogeny.

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1- GENERAL INTRODUCTION

1.1 <u>Systematic review</u>

The Order Perissodactyla Owen, 1848

The order Perissodactyla is composed by mesaxonic ungulates, with the axis of the limb passing on digit III that is normally the most developed digit (Paula-Couto, 1979). According to morphological studies, the specialization of limbs for running and the pattern of molar cusp and jaw musculature are evidence that the order Perissodactyla originated in the late Paleocene (from approximately 65.5 Ma to 56 Ma). This group originated from a group of "Condylarthra", an archaic, non-monophyletic taxon of the family Phenacodontidae, with the genus *Tetraclaenodon* being morphologically closest to the ideal Perissodactyla ancestor (Cifelli, 1982, Radinsky, 1966). Still, molecular studies using mitochondrial genome suggest that Perissodactyla is part of an eutherian group including also Artiodactyla, Pholidota and Carnivora. It diverged from its sister group (Artiodactyla or Carnivora) by the late Cretaceous: 83.4 +/- 0.7 (Bininda-Emonds et al. 2007) or 97.5 – 88.8 million years ago (Eizirik et al. 2001) from Artiodactyla, or even approximately 80 million years ago from Carnivora (Springer et al. 2003). Yet, no intermediates between the small phenacodontid (which was supposed to have originated three groups, including a proto-perissodactyl) and the first true perissodactyl, *Hyracotherium sp.,* were found.

Currently the order Perissodactyla comprises 17 extant species, a low diversity if compared with the past (Price and Bininda-Emonds, 2009). However, despite the decrease in diversity of the group, perissodactyls have an important participation and impact in modern ecosystems (Price and Bininda-Emonds, 2009).

Perissodactyls are diverse in body size, color patterns, food habits and presents a wide distribution. The smallest living representative of this order is *Tapirus kabomani*, the black little tapir, with less than 110 kg, while the largest representative is *Ceratotherium simum*, the white rhino, with 3.500 kg. With exception of the tapirs, males tend to be larger than females.

Perissodactyls occur from deserts to tropical rainforests and are found in Africa, part of Asia and Americas. Among the 16 extant species, only 3 are not classified as threatened or endangered. The rest of them have been increasingly exposed to danger, reflecting threats related with human activities, as habitat destruction and hunting. However, despite the increasing emergence of conservation programs and groups focused on perissodactyl preservation, it is still not sufficient to stop the problem, even if considering the important position occupied by this group in human communities. Tapirs, for example, still are one of the main food resources of some communities and the domestication of some equids also impacted perissodactyl populations (Olmos 1997).

Another populational challenge to the conservation of Perissodactyla is its very slow process of reproduction. It takes two years to reach sexual mature in equids to five years in rhinos, but each species presents its own singularity that complicates the repruduction. For example, rhino females can bear its first cubs only between the age of six to eight years old, and male equids, can breed only after leaving its family group by the age of five to six years old, when it find other females. Also, the gestation period last about a year (Seamons, 2003).

All perissodactyls are terrestrial and herbivorous. Tapirs usually feed on C3 plants, which is less aggressive to the tooth enamel, fruits, some leaves and some seeds. They also have an important ecological role as seed dispersers, since some eaten seeds are not damaged by the digestive tract. However, other seeds, as most seeds of fleshy fruit are commonly crushed, making them seed predators as well. Rhinos are foragers of woody and grassy vegetation, rarely feeding of fruits. Equids are grazers generally eating fiber-rich foods. However, they also can eat fruits, leaves, roots, bark, and buds (Seamons, 2003).

The order Perissodactyla was first described by Owen (1848), including four extant families: Rhinocerotidae (rhinos), Tapiridae (tapirs), Equidae (horses, asses and zebras) and Hyracoidea (hyraxes). In 1869, Huxley excluded the Hyracoidea and elevated it to an order of its own. Later, molecular analysis made by Madsen et al. (2001) and Murphy et al. (2001) showed strong evidence of Hyracoidea as part of Afrotheria, closely related to proboscideans (elephants) and sirenians (dugongs and manatees), and Perissodactyla as part of Laurasiatheria and sister-taxon of Artiodactyla.

Based on the morphology of lower molars, Wood (1934, 1937) separated the order in two major groups diverging in the beginning of the early Eocene (from approximately 41 Ma to 34 Ma): Hippomorpha, which includes the horses, among others representatives, and Ceratomorpha which includes rhinoceroses and tapirs. Using a superfamily criterion, five superfamilies are recognized in the order: the extinct Brontotherioidea Marsh, 1873, Chalicotherioidea Gill, and the living Equoidea Gray, 1821, 1872, Tapiroidea Burnet, 1830 and Rhinocerotoidea Gray, 1825 (Holbrook, 1999). It is worth mentioning that the species-level relationships still remain unclear so that there is little or no consensus about it. This situation indicates the need of more phylogenetic studies about the Perissodactyla not only for taxonomic application, but also to contribute to conservation policies (Purvis et al. 2005).

The oldest perissodactyls date from the early Eocene. The *Hyracotherium* Owen, 1841 was found in the London Clay formation and is considered to have equid afinities (Hooker, 1994). The second genus is *Homogalax* Hay, 1899, a tapir-like herbivore, considered the earliest ancestral of ceratomorphs, including rhinoceroses and tapirs. The differentiation of the ancestral and origin of Perissodactyla dates from the late Paleocene and the perissodactyl first adaptive radiation happen right after the differentiation event, still in the late Paleocene (Radinsky, 1966b). Also according to Radinsky (1966b), at least three of the five known Perissodactyla superfamilies already existed in the early Eocene, the Equoid *Hyracotherium*, the tapiroid *Homologax*, and the chalicotherioid *Paleomoropus* (Kitts, 1956; Radinsky, 1963,1964). Following adaptive radiations originated fourteen perissodactyla families, distributed between the five superfamilies: Rhinocerontoidea, with the oldest representatives dated from the beginning of late Eocene of North America and Asia (around 48 Ma); Tapiroidea, originated during Eocene (approximately 55 Ma to 34Ma) and was present in North America, Europe and Asia by this time; Equoidea, from the early Eocene of North America and Europe (from approximately 41 Ma to 34 Ma); Brontotherioidea, from the early Eocene of North America; and Chalicotherioidea, from the Eocene of North America and Asia. Soon after the beginning of the perissodactyl history, the ceratomorphs were separated into the tapiroid families Isectolophidae and Helaletidae, the first including the genus *Homologax* (Radinsky, 1969). Studies about the tapiroid evolution are extremely important, since tapiroids are one of the key groups to understand the evolutionary radiation dynamics of perissodactyls (Holbrook et al., 2004).

During the Eocene, perissodactyls were more diverse than Artiodactyla. However, by late Oligocene (approximately 34 Ma to 30 Ma), many families were extinct and the only surviving groups were tapirids, chalicotheriids, rhinocerotids and equids. By the early Miocene (23 Ma to 10 Ma), many ecological niches formerly occupied by perissodactyls were occupied by artiodactyls (Colbert, 2007).

The superfamily Tapiroidea

The suborder Ceratomorpha was divided by McKenna & Bell (1997) into two infraorders: the extinct Selenida, which include Chalicotherioidea and Brontotherioidea, and the Tapiromorpha, which includes all living ceratomorphs, Rhinocerotoidea and Tapiroidea. However, Holbrook (1999) and Colbert (2005), considering only living organisms, named Tapiromorpha as a suborder of Perissodactyla and as the Hippomorpha sister-group, while Ceratomorpha became an infraorder of Tapiromorpha. Previously, Cope (1889) considered Ancylopoda as a separate order. Later, Scott (1941) and Radinsky (1964) recognize as a third suborder in Ceratomorpha, Ancylopoda, containing only the superfamily Chalicotherioidea.

Holbrook (1999) stated that Tapiromorpha was defined by the five following synapomorphies; reduction of metastilid; oblique orientation of the postglenoid process; fussion of paraconule, protocone and paracone in the protoloph of the molars, and the loss of the diastema posterior to first upper premolar.

Considering Ceratomorpha as a suborder (and inside the infraorder Tapiromorpha), the superfamily Tapiroidea as treated by Radinsky (1963) was paraphyletic (Holbrook, 1999). Radinsky (1963) and Schoch (1989) also adopted a parayletic Tapiroidea based on dental characters, but Hooker (1989), considered it as a monophyletic clade, restricting Tapiroidea to Tapiridae + Helaletidae.

Representatives of Tapiroidea are commonly found in Eocene paleontological sites from northern continents (Hooker, 1989; 2005), and they have reached the higher diversity of the group during this time. However despite the great number of studies about the tapiroids, the phylogenetic relationships among the different families is not yet fully understood. McKenna and Bell (1997) divided this superfamily in six groups: Lophiodontidae, found only in Europe (Holbrook, 2009), Deperetellidae and Lophialetidae, found only in Asia (Radinsky, 1965a), and Isectolophidae, Tapiridae, and Helaletidae, found in both Asian and North-American continents and considered a key group to understand the intercontinental divergence, dispersion and resulting distribution dynamics among North America and Europe.

Tapirids are medium-size perissodactyls with four digits in their anterior limbs and three fingers in posterior limbs (Wortman and Earle, 1963; Kleiman et al., 1972; Paula-Couto, 1979). They have 42 teeth with the dental formula 3I / 3i, 1C / 1c, 4P / 3p, 3M / 3m, absence of p1 and a diastema separating the canines from P1 and p2. Their dentition is brachiodont and bilophodont wearing out only the lophos. This dentition points to a herbivory diet specialized in the consumption of soft components as leaves and fruits with low fibers, that is, food that don't need to peeled and/or grounded (Janis, 1984; Holanda, 2011). Thus, as indicated by tapirid dentition, its diet is generalist composed preferably of leaves, shoots and small branches, all of them containing few cellulose, and also aquatic plants and fruits (Nowak, 1991; Holanda, 2011). They have an important role of predation and dispersal of seeds in ecosystems as rain forests, high mountains and the Brazilian Cerrado and Pantanal (Olmos 1997; Cozzuol et al., 2013). One of the most remarkable features of tapirids is the extensible proboscis, an appendix derivative from the elongation of the nose and upper lip, related to cranial bones shifts. It helps in the manipulation and searching of food, to pull fruits and leaves and, probably, in sniffing predators and other tapirs (MacDonald, 1985; Brooks et al., 1997).

Most authors consider that the family Tapiridae includes a single extant genus, *Tapirus* Brünnich, 1772, with five living species. They are distributed throughout

Southeast Asia (*Tapirus indicus*), Central America (*Tapirus bairdii*) and South America (*Tapirus terrestris, Tapirus pinchaque* and *Tapirus kabomani*) (Nowak and Walker, 1999, Cozzuol et al., 2013, 2014). However, the diversity and geographic distribution of the genus was larger in the Neogene and Pleistocene (Simpson 1945; Nowak and Walker, 1999; Hulbert 1999; Holanda et al. 2011). The first fossil record of the genus *Tapirus* of South America is from the Pliocene-Pleistocene of Venezuela (Holanda e Rincon, 2012), probably arriving during the Great American Biotic Interchange (Cione et al., 2015). They survived the late Pleistocene extinction that extirpated it from North America and became the largest terrestrial mammal of South America (Woodburne 2010).

Modern tapirids, all placed in the genus *Tapirus* (but see Groves & Grubb, 2011 for different view), are found in low and mountain woodland areas, but also in grassy open areas close to waterbodies (Brooks et al., 1997; Holanda, 2011), in all continents, except in Africa and Australia, within the tropics. Their meat is consumed by some human populations of Amazonia, as part of the Amerindian tradition, but also by local non-indigenous people. Modern tapirs weighs up to 300 kg and are morphologically and behavioraly conservative among ungulates (Seamons, 2003).

The classification of some fossil species from Eurasia in the genus *Tapirus* generated some doubts (Simpson, 1945; Hershkovitz, 1954; Guanfu and Yulu, 1987; Hulbert, 1999; Spassov and Ginsburg, 1999; Holanda and Cozzuol, 2006; Ferrero and Noriega 2007; Holanda et al. 2011; Cozzuol et al., 2013). These doubts occur due of many reasons, as the descriptions and classifications made using diagnostically poor materials and inaccurate analysis.

The oldest record of true Tapiridae dates from the early Eocene of North America, possibly having Helaletidae as sister group (Seamons, 2003; Holanda and Ferrero, 2013). After that, tapirids dispersed from North America to other regions, reaching Asia and Europe, through the Bering Strait. Dispersal to South America was part of the Great American Biotic Interchange (GABI) event in which the Isthmus of Panama established a link connecting the continents (O'Dea et al., 2016). Despite some authors suggesting the arrival of tapirs in South America by late Miocene (Campbell et al. 2010), those records seems to be misinterpretation of the geological context and all the known reliable data indicates that this group entered the continent as part of the GABI. According to Janis (1984) and Holanda (2011), the first record of the genus *Tapirus* is *Tapirus helveticus* Meyer, 1867, dated from the mid-late Oligocene of Europe, where it could be found until the Pliocene (Radinsky, 1965; Mckenna and Bell, 1997), but later studies contested these Oligocene European species as *T. helveticus* seemed to be described and erroneously classified as a tapir species. These studies defended that the current genus *Tapirus*, as we know, dates from the Miocene (Simpson, 1980; Prothero and Schoch, 1989, 2002; Absolon, 2013) of North America (Seamons, 2003), considering *Tapirus johnstoni* Schultz et al. 1975 as the most basal branch of the genus and *Tapirus polkensis* Olsen, 1860 as the oldest. North American both species are found in the Miocene of North America (Holanda and Ferrero, 2013; Absolon, 2013).

The presence of the before mentioned proboscis is a diagnosis feature to differentiate the Tapiridae from other tapiroid. The development of this appendix implies in a series of anatomical derivations like the nasal cavity retraction (Fig. 1). The first tapirid to present those features is the genus *Protapirus*, an upper Oligocene species found in North America and Europe (Seamons, 2003). Almost contemporary to it *Tapirus helveticus* have a relative primitive tapirid skull with more advanced cranial modifications. They shared characteristics with some recent tapirs, as the groove for the nasal diverticulum curling onto the posterior border of the nasals, and the anterior part of the skull similar to *Tapirus pinchaque*, making *Tapirus helveticus* morphological intermediate between the genus *Protapirus* and modern tapirs (Radinsky, 1965).

Currently, the discontinuous distribution of tapirs is considered consequence of extinction of the genus in several localities by the end of the Pleistocene. Also, it's worth to emphasize that the consequent physical isolation was the possible responsible for the allopathric process of speciation of the extant representatives of this clade (Thoisy et al., 2010).

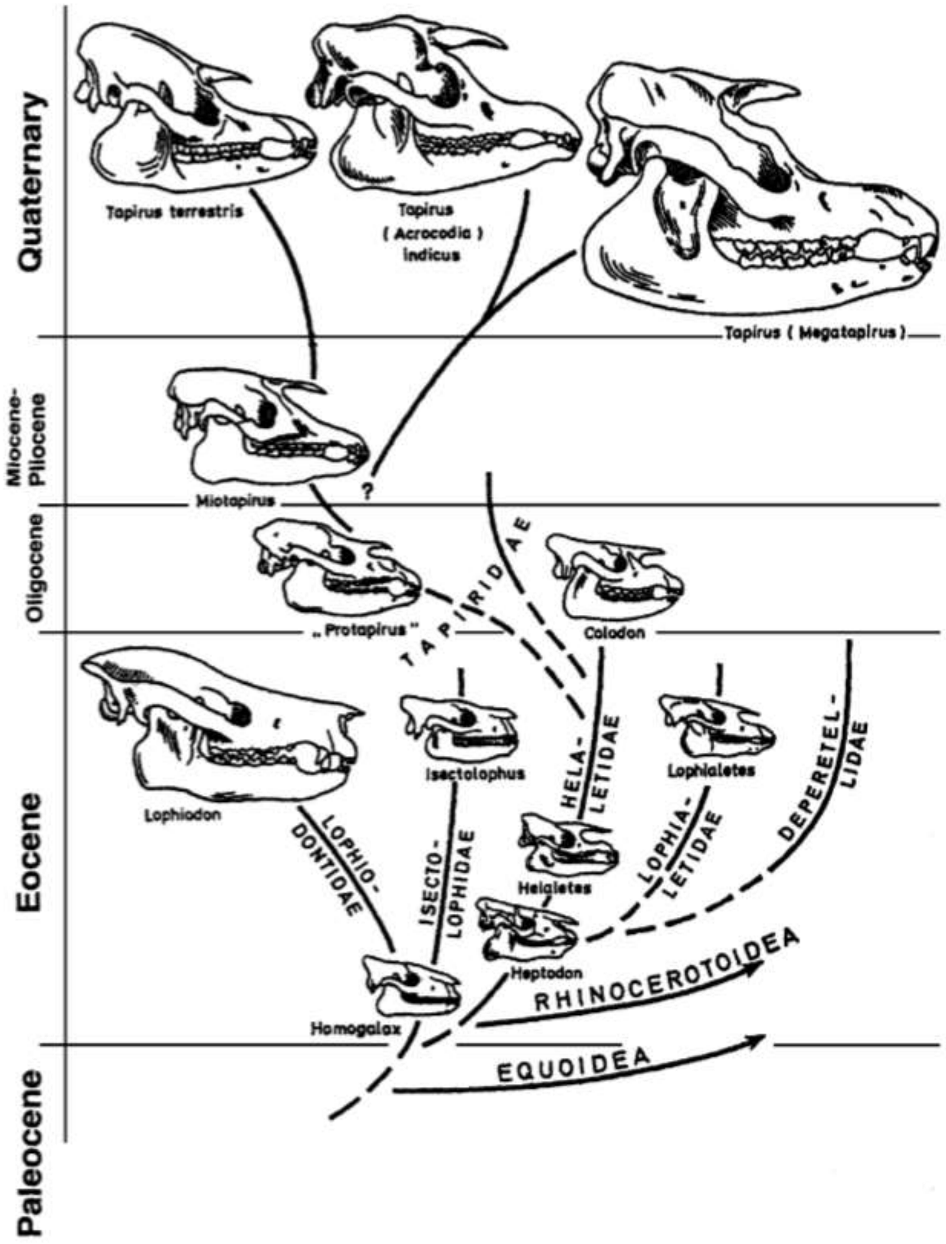

Figure 1 – The cranial evolution of tapirs showing the enlargement of the proboscis by the retraction of the nasal notch. Obtained from Prothero (2009) and modified from Prothero & Schoch (2002).

During the Miocene, there are records of the genus *Tapirus* in Europe, Asia and North America. In Europe, there are five species registered in the literature: *Tapirus priscus* Kalp, 1833; *Tapirus antiquus* Kaupp, 1833; *Tapirus hungaricus* Meyer, 1867; *Tapirus telleri* Hofmann, 1893; *Tapirus balkanicus* Spassov & Ginsburg, 1999. In Asia, three species are found: *Tapirus telleri* Hofmann, 1893; *Tapirus teilhardi* Zdansky, 1935; *Tapirus hezhengensis*, Deng et al., 2008. In North America, there are four cataloged species: *Tapirus polkensis* Olsen, 1960; *Tapirus* *simpsoni* Schultz et al., 1975; *Tapirus johnsoni* Schultz et al., 1975; *Tapirus webbi* Hulbert, 2005.

In the Pliocene of Europe, there are two species described: *Tapirus arvenensis* Croizet & Jobert, 1928; *Tapirus jeanpiveteaui* Boeuf, 1991; in Asia, two species, *Tapirus teilhardi* Zdansky, 1935 and *Tapirus yunnanensis* Shi et al., 1981; and in North America, two species were described: *Tapirus haysii* Leidy, 1860 and *Tapirus merriami* Frick, 1921.

During the Pleistocene the genus *Tapirus* reached its higher diversity in South America while it was extirpated from Europe. In Asia, three species were described: *Tapirus sinensis* Owen, 1870; *Tapirus peii* Li, 1979; *Tapirus sanyuanensis* Huang, 1991. In North America there were six species: *Tapirus haysii* Leidy, 1860; *Tapirus bairdii* Gill, 1865; *Tapirus californicus* Merriam, 1912; *Tapirus veroensis* Sellards, 1918; *Tapirus merriami* Frick, 1921; *Tapirus lundeliusi* Hulbert, 2010. In South America, ten species were described: *Tapirus terrestris* Linnaeus, 1758; *Tapirus tarijensis* Ameghino, 1902; *Tapirus cristatellus* Winge, 1906; *Tapirus greslebini* Rusconi, 1934; *Tapirus rioplatensis* Cattoi, 1957; *Tapirus oliverasi* Ubilla, 1983; *Tapirus mesopotamicus* Ferrero & Noriega, 2007; *Tapirus rondoniensis* Holanda, Ribeiro & Ferigolo, 2011. Two aditional species are *Tapirus dupui* Cattoi, 1951 and *Tapirus australis* Rusconi, 1928, however there are controversies about the validity of these species.

Some species, as *Tapirus excelsus* Simpson 1945 and *Tapirus tennesseae* Hay 1920, described for the Pleistocene of North America, were later considered synonyms of *Tapirus veroensis*. Also, *Tapirus californicus* Merriam, 1912, *Tapirus copei* Simpson 1945 and *Tapirus merriami* Frick 1921 from North America were considered by Ray and Sanders (1984) synonyms of *Tapirus haysii* (Hulbert, 1995, 2005, 2010; Sanders, 2002; Graham, 2003; Lucas et al., 2007; Holanda, 2011). Finaly, *Tapirus webbi* Hulbert, 2005 and *Tapirus simpsoni* Schultz et al., (1975) are also considered synonyms (Holanda & Ferrero, 2012).

The name tapir is derived from the Brazilian Tupi "tapi'ira" (Cabrera and Yepes 1960). The Brazilian portuguese name of tapir is "anta" and is originated from the Arabic "lamTa", a word derived from the Spanish moose, "danta" (Hershkovitz 1954). Chinese, Korean and Japanese names of tapir are based on a mythological beast with an elephant like proboscis.

Cozzuol et al. (2013, 2014) proposed a *Tapirus* phylogeny using morphological data and including all living and some fossil species from North and South America (including *Tapirus kabomani*). Their morphological cladistic analysis resulted in a single most-parsimonious tree, in which the genus *Tapirus* was recovered as a monophyletic group. Also, the North American taxa, *Tapirus johnstoni* (from middle-late Miocene) and *Tapirus webbi* (from late Miocene) had a successive divergence, with *T. johnsoni* in the base of *Tapirus* phylogeny followed by *T. webbi*. The later taxon is the sister group of all the other *Tapirus* species that diverges in the two major clades: the South American representatives, supported by five synapomorphies, and the Asian, North American and Central American representatives, supported by two. In the South American clade, *T. mesopotamicus* appears as the sister group of all the others. *T. rondoniensis* and *T. kabomani* are sister groups, and the clade containing both taxa is the sister group of the *T. terrestris* + *T. pinchaque* + *T. cristatellus* group. In the later clade, *T. pinchaque* appears as sister group of *T. terrestris* + *T. cristatellus*. In the Asian + North American + Central American clade, *T. indicus* is the first to diverge and the sister group of the remaining taxa, followed by *T. polkensis* and *T. bairdii* successively. The later is sister group of the clade composed by *T. haisii* + *T. veroensis*. They also made a molecular analysis of the living *Tapirus* taxa and recovered the same general results as in the morphological analysis, partially agreeing with other molecular phylogenies as Norman & Ashley (2000), de Thoisy et al., (2010) and Steiner & Ryder (2011). Cozzuol et al. (2013, 2014) studies mentioned that the *T. bairdii* grouping with *T. indicus* and many North American fossil species is the major non-agreement point between morphological and DNA analysis, since many other genetic markers (Steiner & Ryder, 2011) and their mtDNA analyses pointed to *T. bairdii* as sister group of the South American tapirs, but the reason for this is unknown. More analyzes are required to better understand these relations.

No phylogenetic study was done including European tapirs and there are very few including the Asian species. In addition, most of these species were described by fragmentary material (Dumbá, 2018). However, since the European and most of the Asian material is fossil, the available material is often poor and fragmentary, usually composed only by teeth. Among mammals, the degree of bilophodonty can be used to differentiate its representatives. In Tapiridae, the degree of molarization of premolars can be used to access their affinities. However, many Euroasiatic tapirs present a very low degree of bilophodont, and a variable degree of molarization (Holanda et al., 2011). In situations as this one, it is difficult to determine which character is more reliable to be used in the analyses, so that the use of these characters in these cases needs to be carefully applied (Holanda et al., 2011). Therefore, it is necessary to define reliable characters that 1) brings phylogenetic information; 2) that can be used both to fossil and to recent species, and 3) to define what species belongs to genus *Tapirus* and what species belongs to the Tapiridae family, but not to *Tapirus*.

The relationships between the Southern Asian extant specie *Tapirus indicus* Desmarest, 1819 and the four extant species from South America, *Tapirus kabomani* Cozzuol et al., 2013, *Tapirus pinchaque* Roulin, 1829, *Tapirus terrestris* Linnaeus, 1758 and the Central American *Tapirus bairdii* Gill, 1865 is still a matter of discussion. In the Neotropics, tapir speciation can be explained by two hypothesis, both developed before the description of *T. kabomani*. According to Hershkovitz (1966, 1969), the three Neotropical species of tapirs have entered in South America through Central America in three independent moments. Although the ancestors of *Tapirus pinchaque* and *Tapirus terrestris* entrance in South America occured in different moments, with different climate and topography, it happened through the same oversea route. However the order in which each species arrived is not completely clear. It is only suspected that *T. bairdii* arrived after the others. On the other hand, according to Haffer (1970), the three species originated in Pleistocene from the same ancestor, probably a Pliocene species. From this ancestor, *T. pinchaque* originated in the Andes, *T. terrestris* in the east of the Andes, and *T. bairdii* in the west of the Andes. Adding to the Haffer's hypothesis, Downer (2001) proposed an allopatric speciation, with a treeless habitat resulted by the rise of the Andes above the tree line at two thousand meters, and it became the barrier between two populations of this Pliocene species. From this event, the two population differentiated in two independent species, *T. terrestris* and *T. pinchaque*. Following this same hypothetical line, Tonni (1992), defended that the South American species are more close related to *T. bairdii*. More recent morphological studies as Hulbert & Wallace (2005) and Hulbert (2010), found that the South American clade composed by *T. terrestris* + *T. pinchaque* is sister group of the clade composed by the extinct North American Pliocene and Pleistocene species as *T. veroensis, T. polkensis*, *T. haysii* e *T. lundeliusi*. Also, *T. bairdii* would be closer to the North American tapir species than to the South American species. The study of Ferrero e Noriega (2007) found this same result when included the South America extinct specie *T. mesopotamicus*. The analysis also consider *T. mesopotamicus* closer to *T. pinchaque* than to *T. terrestris*.

On the other hand, *Tapirus indicus* affinities were explained by two hypotheses. According to Janis (1984) and Eisenberg (1997), the relictual distribution of this species is derived from a North American species that migrated to Asia, probably during Plio-Pleistocene warmer episodes. Under this view *Tapirus indicus* would descend from North American tapirs and not from the Euro-Asiatic ones. Paula-Couto (1979) and Tonni (1992), on the other hand, defended the origin of *T. indicus* from Euro-Asiatic lineages. Molecular data points to a closer relationship between *T. terrestris* and *T. pinchaque*. It also indicates that *T. bairdii* would be closer to *T. kabomani* + *T. terrestris* + *T. pinchaque* clade than to *T. indicus*, despite some molecular data pointing to a different view (Norman & Ashley, 2000), and contradict all morphological studies made including *T. bairdii* and *T. indicus* in which both taxa are always recovered as sister-taxa. Thus, the South American representatives would come from the same unic lineage, after the GABI (Ashley et al, 1996; Norman & Ashley, 2000; Price and Bininda-Emonds, 2009), as suggested by Haffer (1970). To better understand the biogeography of the genus *Tapirus* there is a real necessity of new studies about its origin (Padilla et al. 2010).

Tapirus indicus Desmarest 1819 (Fig. 2), also called Malayan tapir or Asian tapir**,** is the first species to diverge among the current species according to the Cozzuol, 2013, 2014 phylogeny. It can reach the length of 2.5 m and weight from 250 to 540 kg, which makes it the largest extant specie (Holanda, 2011). One significant feature of *Tapirus indicus* is the proboscis, which is bigger than in other tapirs, and its color pattern composed by two contrasting and sharply separated colors in the anterior and posterior sections of the body, being white from shoulders to just before its hind legs, and black in all the rear end and front. It is found in Toba islands and part of the Malay Peninsula, Thailand, Burma, Sumatra, Vietnam and Cambodia (Brooks et al., 1997).

Figure 2 – *Tapirus indicus*. Photograph by Michal Sloviak.
Obtained from www.biolib.cz

Tapirus bairdii Gill, 1865 (Fig. 3), the Central American tapir, can reach 2.0m length and weight from 150 a 300 kg (Holanda, 2011). It is found from the southeast

Mexico to the west of the Andes, in Colombia and Ecuador (Brooks et al., 1997). This specie is the largest tapir from the Americas and the largest endemic land mammal of Central and South America. It also present two colors, but they show a smoother transition, not so abrupt as in *Tapirus indicus*. Its face and throat are cream-colored

Figure 3 – *Tapirus bairdii*. Photograph by San Diego Zoo.
Obtained from www.library.sandiegozoo.org

that smoothly becomes darker in the rest of its body.

Tapirus pinchaque Roulin, 1829 (Fig. 4), also called mountain tapir or woolly tapir**,** can reach the weight of 150 kg and 1,8m length (Holanda, 2011). It lives at high altitudes in the páramos of the Andes in Peru, Ecuador and Colombia (Brooks et al., 1997). The name "pinchaque" derived from a large animal of the Colombian mythology that was supposed to live in the same area (Allen 1942; Cabrera and Yepes 1960; Geroudet 1970). According to Hershkovitz 1954, this animal was an extinct proboscidean that inhabit the region up to the end of Pleistocene. To support the low temperatures of its habitat, it presents thick and characteristic black or very dark brown hair, with a white band around its lips.

Figure 4 – *Tapirus pinchaque*. Photograph by San Diego Zoo.
Obtained from www.library.sandiegozoo.org

Tapirus terrestris Linnaeus, 1758 (Fig. 5), also called Brazilian tapir, lowland tapir, common tapir, gameleira-tapir, shoemaker-tapir, antaxuré, batuvira, pororoca, tapiira, tapira and tapiretê, can reach 2 m of lenght and weight between 150 e 250 kg. The name "tapiretê" comes from the Brazilian tupi word "*tapire'tê*", the "true tapir" (Holanda, 2011). It is the largest terrestrial Brazilian mammal and the second largest in South America. It is found from the southeast Andes to the north of Argentina (Brooks et al., 1997). Two important features to differentiate this specie from the other tapirs are the prominent sagittal crest and a consequent high mane, running from the neck to the forehead of the head, on the top of the sagittal crest.

Figure 5 – *Tapirus terrestris*. Photograph by San Diego Zoo.
Obtained from www.library.sandiegozoo.org

Tapirus kabomani Cozzuol et al., 2013 (Fig. 6), also called small black tapir, is the smallest living tapir. It was the 5th and most recently described living species of *Tapirus* . Its name comes from the term "Arabo kabomani", the tapir name in the Paumarí native language from southern Amazonas. It reach 130cm length and approximately 110kg weigth. This species, endemic from the Amazon region, is found in southern Amazonas, Rondônia, and Mato Grosso states in Brazil, and the Amazon region of Colombia, Peru and Bolivia. The validity of the species is still questioned by some authors (Voss et al, 2014, Ruiz-Garcia et al., 2016), however there are many strong morphological and molecular evidence the existence of this species. *Tapirus kabomani* is diagnosed from the other extant *Tapirus* and from the extinct species *T. webbi*, *T. veroensis*, *T. johnsoni*, and *T. cristatellus* by its relatively short limbs, characterized by a shorter femur length when compared to the dentary length. It was considered as part of *Tapirus terrestris*, but its broad and inflated frontals (behind the nasals) that extends up to the suture between frontal and parietal, smaller size, darker hair, broader forehead, lower sagittal crest and lower mane helps to externally differ one to another (Cozzuol et al., 2014).

Figure 6 – *Tapirus kabomani*. Photograph by Luciano Malanski.

Few morphological studies about the genus *Tapirus* were made comparing postcranial characters of this group with the extinct perissodactyls. Those studies, as Janis (1984) concluded that there were very few differences between the postcranium of them, making the impression that not only the genus *Tapirus*, but all perissodactyls morphology is highly conservative.

1.2 The inner ear

The auditory region of mammals enclose the organs of balance and orientation in space (vestibule) and hearing (cochlea), together with the associated tissues related with these functions (MacPhee, 1981). These organs are specifically contained into the petrosal (Fig. 7.A, B), a paired and very complex basicranium bone covered ventrally by a bony shell, the tympanic bulla (when it is present), and fused to the posterior part of the skull with other bones, as mastoid, squamosal, exoccipital and tympanic (the latter does not ossify in many species), through its ventrolateral face (Fig. 8.A, B, C, D). The petrosal, found only in mammals as such, is in contact with the tympanic bulla through the anterior process of tegmen tympani, on the medial and posterior petrosal faces. Also, it is in contact with the ectotympanic, through the external acoustic meatus (MacIntyre, 1972).

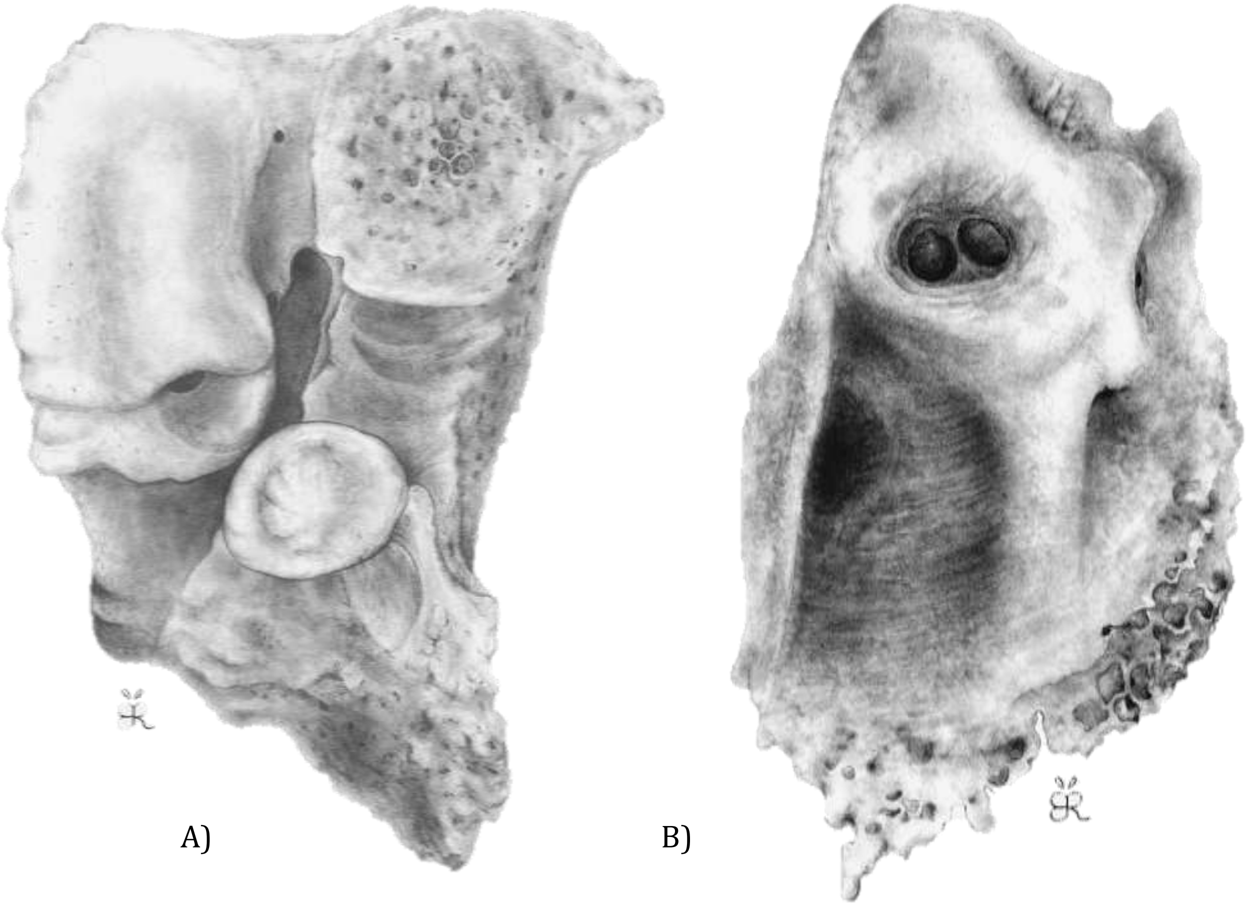

Figure 7 – Schematic illustration of a general petrosal bone of the genus *Tapirus* made by the compilation of petrosal of the species *Tapirus terrestris*, *Tapirus kabomani* and *Tapirus indicus*. The petrosal is seen above from two different views: A) Ventrolateral (or tympanic) in the left, and B) Dorsomedial (or cerebellar) in the right. Illustration by Bárbara Rossi.

Figure 8.A) – Cranium of *Tapirus indicus* MACN 30351 in lateral view, on the left, and in ventral view, on the right (showing the position of the petrosal in the cranium). The color of the cranium was modified in Photoshop to resemble with the original color, since photos effects turned it bluish. The petrosal of *T. indicus* described in this study is not from this specimen. It was used only for didactic purposes. The cranium of the described petrosal can be seen in Appendix 1. Photograph by Mario Cozzuol.

Figure 8.B) – Cranium of *Tapirus terrestris* UFMG 4556 in lateral view, on the left, and in ventral view, on the right (showing the position of the petrosal in the cranium). Photograph by Larissa Dumbá.

Figure 8.C) – Cranium of the holotype of the species *Tapirus kabomani* UFMG 3177 in lateral view, on the left, and in ventral view, on the right (showing the position of the petrosal in the cranium). Photograph by Larissa Dumbá.

Figure 8.D) – Cranium of *Tapirus cristatellus* MCL 5643/01 in left lateral view, on the top, in ventral view, on the right (showing the position of the petrosal in the cranium), and in right lateral view, in the bottom. Photo by the author.

The inner ear pattern of ossification is an apomorphic character of mammaliforms. The first step in the evolution of the ear of mammals started from the separated prootic and opisthotic bones in Cynodonts to their fusion into a single bone in mammaliaforms. The single petrosal bone developed encapsulating all the organs of the inner ear inside of it, and this new bone now presented a bigger promontorium capable to shelter an elongated cochlear canal. The inner ear of Cynodonts, besides having separate prootic and opisthotic bones, also had the basisphenoid wing as part of fenestra vestibuli. But the petrosal development partially shift off the basisphenoid wing from the fenestra vestibuli (Luo et al. 2016) (Fig. 9).

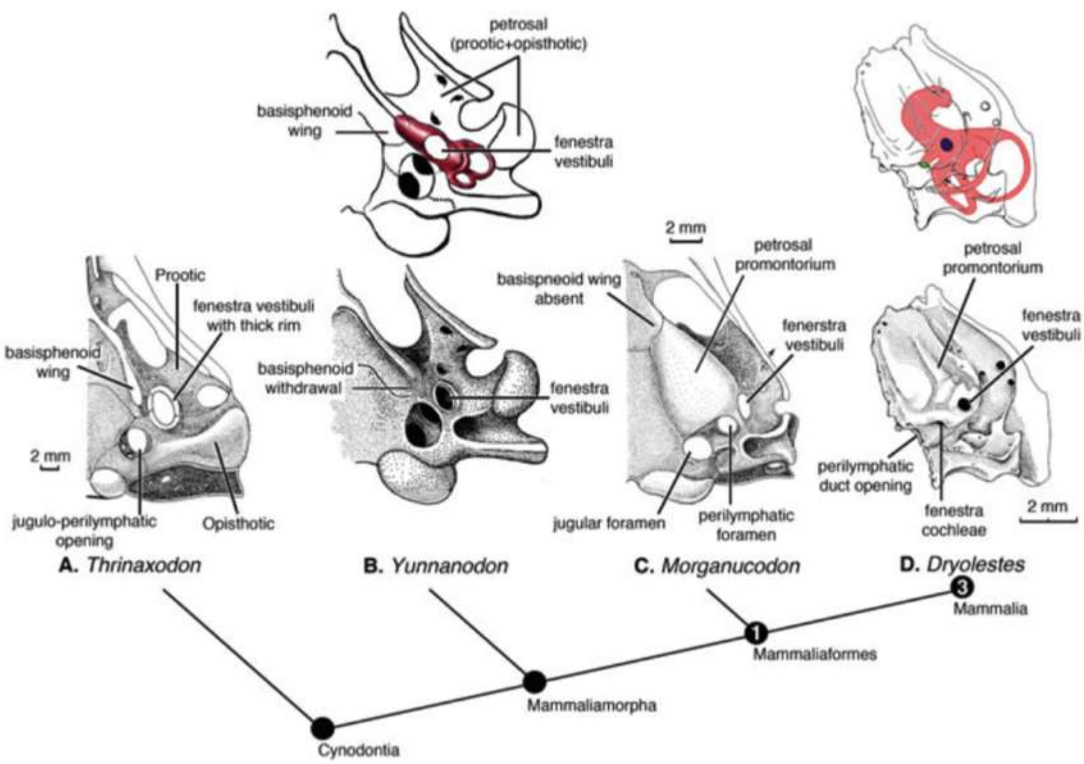

Fig. 9 - Evolution of the inner ear of mammals from the separated prootic and opisthotic bones with the participation of the basisphenoid wing in the fenestra vestibuli in Cynodonts to a single petrosal bone encapsulating the organs of the inner ear with the basisphenoid wing partially disconnected from the fenestra vestibuli. (A) cynodont outgroup, *Thrinaxodon*, (B) mammaliamorph outgroup, tritylodontid *Yunnanodon*, (C) *Morganucodon*, (D) crown mammal *Dryolestes*. From Luo et al. (2016).

Besides sheltering the balance, hearing and orientation organs (Fig. 10), the petrosal also supports structures attached to the skull, to the neck and to the face like arteries, veins, muscles and nerves of central and peripheral nervous system (O'Leary

2010). The soft structures are usually poorly preserved, since it is consisted of delicate elements (Martinez et al., 2016). However, it leave marks where they are inserted in the bone, enabling its reconstruction even in fossil specimens in some cases (Orliac, 2012).

Sound vibrations are transmitted from the three middle ear ossicles (malleus, incus, and stapes - all of them branchial arch derived bones) to the tympanic membrane and then to the inner ear through a petrosal opening within the promontorium. This vibrational osseous chain transmits the sound to the inner ear by fenestra vestibuli that settle the footplate of the stapes down.

Until recently, phylogenetic studies using the mammalian auditory region were scarce, probably due to its low functional understanding (Novacek, 1977) and the difficulty to access this region by traditional techniques. The only way to study it was in-situ and/or after it has been removed from the skull, with a high chance of damage. The emergence of less intrusive techniques, as high-resolution X-ray computed tomography (Macrini et al. 2010), is improving its use, since it can digitally reconstruct not only the external structure of the bone, but also the internal structure, preserving the skull intact (Fig. 10). In addition, the information collected from now on can open a new range of important predictions that were impossible to be previously foreseen. An example of that is the correlation found between the radius of curvature of the semicircular canals, the body mass and the agility of many extant mammals (Spoor et al. 2007; Cox & Jeffery, 2010). With this anatomic information, the agility capabilities can be approximately calculated (Silcox et al. 2009) even in extinct animals (Macrini et al. 2010).

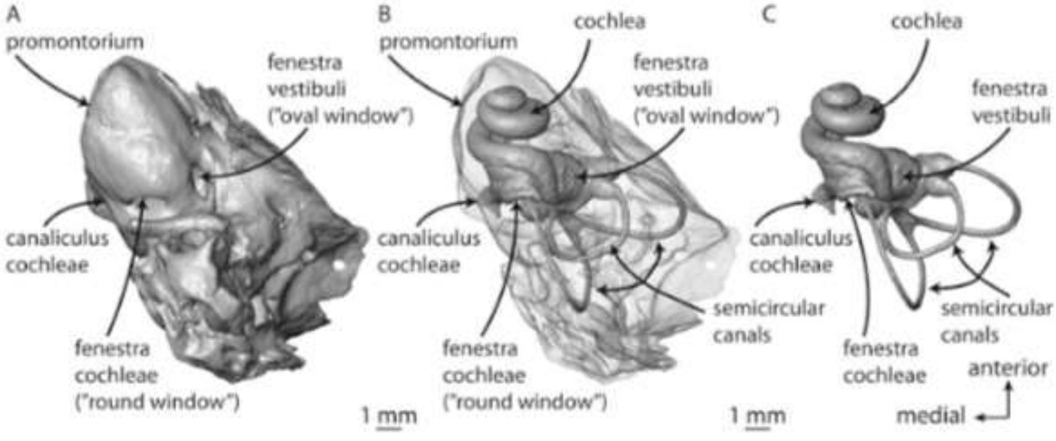

Figure 10 - CT scan data showing the left petrosal bone and bony labyrinth on ventral view. The petrosal belongs to *Dasypus novemcintus* (Although it is not one of the groups studied here, the arrangement of the structures within the petrosal is shown in a very didactic way). Obtained from Ekdale (2016).

Another reason for the increasing use of petrosal bone in mammalian phylogenetic studies is because its structures can reflect deep evolutionary divergences among mammalian group. The petrosal complexity and anatomical preservation over evolution makes it an important potential source of phylogenetic information (Kielan-Jaworowska et al., 2004; Rougier & Wible, 2006). It is also compact and resistant, contributing to a usually well-preserved fossil record (Ruf et al., 2009). Orliac (2012), for example, testing if petrosal characters would support the monophyly of Suoidea and major suoid families and subfamilies, analyzed 30 petrosal characters alone and inside a global cranium-dental matrix composed of 155 characters in total. Indeed, the analysis showed not only that both the partial analysis using only petrosal characters and the global cranium-dental matrix support Suoidea monophyly, but also that many petrosal characters are potential synapomorphies of the groups retrieved.

Other examples of studies using only the inner ear and the petrosal as phylogenetic source of information in therian systematic as Orliac (2010), include the Van der Klaauw (1931) study with the auditory region with emphasis on the structure of the tympanic bullae, Hough (1953) and Hunt (1974,2001) use of the petrosal in Carnivora studies, Butler (1956), McDowell (1958) and Asher *et al*. (2002) in insectivorans, Russel (1960,1964) brief discussion of the petrosal in his studies of cranial morphology in arctocyonids and meniscotheriids, Gazin (1965, 1968) in the 'condylarths' *Meniscotherium* and *Hyopsodus*, MacIntyre (1972) use of the *Protungulatum* petrosal as a mammalian reference of ancestrality, Cifelli (1982) in 'condylarths', Wahlert (1974) in rodents, Szalay (1975) and MacPhee (1981) in primates, Ladeveze & De Muizon (2007) in Metatheria, Wible *et al*. (1995, 2001) in mammals.

Among the studies cited above, those about the inner ear of Perissodactyla are minority and there is only one study directly related to the Tapiridae family. Radinsky (1965) described the petrosal of *Heptodon*, a Tapiroid from the Eocene, but as the petrosal was not the focus of the study, it was commented very briefly and superficially. Cifelli (1982) described the petrosal of *Hyopsodus*, a member of "Condylarthra" related to Perissodactyla origin, and compared it to other Ungulates to verify its phylogenetic application. At last, in studies of Hulbert Jr. et al. (2009) and Moyano & Giannini (2017), the petrosal is only mentioned, but it is not used in the analysis.

1.3 The use of the inner ear characters in Perissodactyla studies

There are very few studies about the inner ear of Perissodactyla, if compared with the extensively studied inner ear of Artiodactyla and other mammals. Even the existing studies about it are superficial and do not cover all the features of the region nor a significant taxonomic sample of this group. Studies of perissodactyl or closely related taxa petrosals as that of Cifelli (1982), on *Orohippus*, *Hyopsodus*, Kitts (1956), on *Hyracotherium*, Radinsky (1965b), on *Heptodon*, Savage et al. (1965), on *Pachynolophus*, Li and Wang (2010), on *Schlosseria*, Colbert (2006), on *Hesperaletes*, Bai et al. (2010), on *Litolophus*, Mader (2009), on *Protitanotherium*, O'Leary (2010), on *Tapirus* and *Equus*, (the last as part of a work mostly dedicated to Artiodactyla) are examples of some representatives already studied.

Below there are some brief descriptions of the petrosal of Perissodactyla representatives. They will help to set a mainframe to understand the polarity of some characters. The structures mentioned in the petrosal descriptions are represented in Fig. 12. A, B (the schematic illustration of the petrosal) on pages 52 and 53, in section "4.1 - Guide for the description".

Mader (2009) described the cranial anatomy, including the petrosal features, of a primitive Brontotheriidae, cf. *Protitanotherium*, from the Wiggins Formation of Wyoming. The petrosal of this specimen have a quadrangular aspect when seen from the dorsomedial view (called cerebellar side in the study). The ventrolateral view (called by him tympanic side) is almost all broken. Structures as the fenestra vestibuli (called by him fenestra ovale), the fenestra cochlea (called by him fenestra rotunda) were damaged. The study differentiate the term "facial canal" and "facial sulcus" so that the facial sulcus is the anterior and only portion of the facial canal that has been preserved. It probably means that the non preserved portion of the facial canal was closed by the crista parotica, since it was called a "canal". The promontorium is poorly defined and there is no sulcus on it. The mastoid region (called by him mastoid portion) is big, rounded and massive. In the dorsomedial view, the vestibular aqueduct (called by him aqueductus vestibulae) is elongated and curved, while the cochlear aqueduct (called by him aqueductus cochlea) is smaller. The cochlear aqueduct is located posterior to the promontorium and the vestibular aqueduct is located dorsally to it. The internal acoustic meatus is large, presents an elliptical opening and two foramen, the foramen acusticum superius and inferius (referred as foramen for the facial nerve - cranial nerve VII - and foramen for the auditory nerve - cranial nerve VIII - respectively). The subarcuate fossa is shallow and, since there is no mention of a petromastoid canal, this structure being, probably, absent.

Ciffeli (1982) described the petrosal of *Hyopsodus*, comparing it with some other ungulates and discussed its phylogenetic implications. The dorsomedial surface of the petrosal of *Hyopsodus* is flat, and the internal acoustic meatus is shallow. The foramen acusticum inferius (called medial/cochlear foramen) is rounded and faces dorsally, while the foramen acusticum superius (called lateral foramen) is oval and faces medially, both are of the same size. The subarcuate fossa is "large, moderately deep and spheroidal", and the vestibular aqueduct (called aquaeductus vestibuli), located anterolateral to the fossa, is a small slit that faces posteriorly. There are three visible grooves in this view. One of them crosses the posterodorsal border of the petrosal, starting from the dorsal edge to the paroccipital edge. The second groove starts from the paroccipital edge and extends until near the jugular sulcus. The third one is the sulcus medialis, located in the anterodorsal portion of this view and running posteriorly following the medial bulge of the promontorium from near the lacerate foramen. In the ventrolateral view (called tympanic side), the promontorium is distinct and presents a drop format with a sharply pointed edge. There is a groove (promontory sulcus that extends through the promontorium from the fenestra cochleae - called fenestra rotunda) to near the lacerate foramen. The fenestra cocleae is larger than fenestra vestibuli (called fenestra ovalis) and faces posteromedially, but both present an oval shape in spite of being oriented in opposite directions. The fenestra vestibuli presents an evident mark equivalent to the footplate of stapes. The cochlear aqueduct (called aqueductus cochleae) is located laterally to the fenestra cochleae in a "broad, shallow, irregular depression". There is a groove continuous with the facial sulcus (called sulcus facialis) from where the stapedial muscle originate (This groove is referred as stapedial muscle fossa in later studies). The mastoid portion of the petrosal is seen only by the occiput and presents the format of an acute isosceles triangle. There is no separated sulcus for stapedial artery, but Cifelli (1982) suggests that if the stapedial artery was present it was housed with the tensor tympani muscle and the eustachian tube in a broad groove covered by the hiatus Fallopii (called aquaeductus fallopii). The hiatus Fallopii extends anteriorly from the tympanic opening of the facial canal to its anterior margin. And the facial canal is located anterolateral to the fenestra vestibuli. The tegmen tympani is described as bulbous and expanded, located anterior and lateral to the epitympanic recess.

Kitts (1956) described the skeleton of *Hyracotherium*, a steam Equoidae , from the Lower Eocene, and compared it with *Phenacodus* and *Mesohippus*. He stated that the *Hyracotherium* characters seems to be closer to *Mesohippus* instead of *Phenacodus*. The differences between the skull of those taxa may be associated with the anterior elongation of the *Hyracotherium* skull compared to the others. Also the cranial characters of *Hyracotherium* are considered by Kitts (1956) "a definitive departure from the condylarth cranial morphology in direction of the later horses". In *Hyracotherium*, the foramen lacerum medium and foramen ovale don't seem to be separated. If the foramen ovale was separated from the foramen lacerum it will not be so anteriorly located as seen in the *Hyracotherium* petrosal. In *Phenacodus*, there is a big and bean-shaped foramen that seems to join the foramen lacerum anterius, the foramen rotundum and the anterior opening of the alar canal in the confluent optic foramen posteroventral. In *Mesohippus*, the foramina of the cranial nerves, as the foramen acusticum superius and inferius, are similar to *Equus*. The foramen lacerum anterius, the foramen rotundum, the anterior opening of the alar canal in one confluent foramen and optic are separated but close located. The conserved tympanic bulla seems to be oval and slightly inflated.

Bai et al. (2010) described craniodental material of *Litolophus gobiensis*, a perissodactyl of the family “Eomoropidae” from Mongolia. In this specimen the right petrosal was used, since it was well preserved. In the ventrolateral view, the promontorium is smooth and flat. The fenestra vestibuli (called fenestra ovalis) and the fenestra cochleae (called fenestra rotunda) seems to have almost the same size according to the photograph used in this study, but they open to different directions. The fenestra vestibuli opens ventrally, is weakly separated from the promontorium by a narrow bone ridge, and presents a very small foramen located lateral to it. The study mentioned that this small foramen is possibly a nutrient foramen as seen in *Heptodon posticus* petrosal, described by Radinsky (1965). The facial sulcus is described as a relatively long groove located anterior to fenestra ovalis and extending along the lateral border of the petrosal. They also use the term "facial canal" when mentioned that this groove "is probably the tympanic aperture of the facial canal". The fenestra cochleae presents its opening arranged posteriorly and is larger than fenestra vestibuli. The stapedial muscle fossa (called fossa for stapedius muscle) is described as a "deep fossa located posterolateral to the fenestra ovalis".

Radinsky (1965b) analysed the evolution of tapiroid skeleton, comparing the cranial and post-cranial morphology of the extinct tapiroid genus *Heptodon* with *Tapirus pinchaque*, considered by the author the most derived extant *Tapirus* representative. As mentioned by Cifelli (1982), the petrosal of *Heptodon* is in contact by its medial part with the basisphenoid, by its lateral portion with the squamosal, and by its posterior portion with the basioccipital. The ventral surface of the promontorium, as seen in other tapiroids, is smooth with no arteries grooves, including the sulcus for stapedial artery and the sulcus for internal carotid arteries. Also, the petrosal presents openings, as the cochlear aqueduct, associated with it. In

Radinsky (1965b) analysis, the dorsomedial (cerebral) view of the petrosal of *Heptodon* was not described, since the petrosal seems to be still articulated with the skull. The ventrolateral surface of the petrosal is anteroventrally flat, with a relatively long and convex ventral border and a relatively short and concave anterior border. The promontorium of the *Heptodon* petrosal is flat, does not present any artery grooves or visible fossa for the tensor tympani or stapedial muscles. The tegmen tympani is ventrally extended and constitute the lateral part of the roof of the facial sulcus (called by him groove for the facial nerve). The facial nerve, in turn, is ventrally open in *Heptodon* as in the recent *Tapirus*. On the lateral view of the tegmen tympani there are two small foramina: the facial hiatus, located more medially, and the foramen that transmits the small superficial petrosal nerve, more laterally. Close to the fenestra vestibuli (called by him fenestra ovalis) in both petrosal there is a small foramen that Radinsky identified as a nutrient foramen. The fenestra cochlea (called by him fenestra rotunda) presents a deep V-shaped groove that starts from its anterior extremity and extends posteroventrally. Radinsky hypothesizes that the groove houses the auricular branch of the facial nerve, since it is located in the same position. However, the groove is too large to this nerve only. The fossa for stapedial muscle is absent, as seen in recent tapirs. Also there is no separated fossa for tensor tympani, unlike recent tapirs. The muscle associated with these fossae attach at the facial sulcus. The stapedial muscle attaches at the posterior portion of the sulcus and the tensor tympani at the anterior portion. In the dorsomedial view of the petrosal, the internal acoustic meatus is described as large and vertically elongated. The vestibular and cochlear aqueducts are located near the posterior petrosal edge. The vestibular aqueduct is posterodorsal located and the cochlear aqueduct is posteroventrally located.

Holbrook (2001) described briefly and discussed the osteology of early Tertiary tapiromorphs. According to him, the periotic of tapiromorphs presents the petrosal region and the mastoid region, a triangular and narrow region located laterally between the squamosal and exoccipital bones in a number of tapiromorphs, as *Cardiolophus, Heptodon, Helaletes, Colodon, Hyrachyus, Triplopus, Hyracodon*, amynodontids, and *Teletaceras*. However, in some perissodactyls, as some rhinocerotids, presents the mastoid covered by the squamosal and exoccipital bones. Tapirids present a third condition intermediate to it in which the mastoid exposure is reduced but not absent. The petrosal region, in turn, is generally conservative in perissodactyls. Although Hoolbrook indicated that the petrosal morphology doesn't “vary in any systematic way among tapiromorphs”, he also mention that some characteristics seen in tapiromorphs and other perissodactyls “are important for higher-level phylogenetic studies”.

Although the lateral exposure of the mastoid is not common in mammals, it is characteristic of all mastoid perissodactyls and, consequently, primitive for tapiromorphs. Because of the lateral exposure of the mastoid in *Radinskya*, McKenna et al. (1989) included this genus in Perissodactyla. The slit cochlear aqueduct located ventrally was considered a derived character shared by perissodactyls and *Phenacodus* by Cifelli (1982). However, although the slit cochlear aqueduct is present in *Hyracotherium* and *Omhippus*, Court (1990) observed a primitive condition more dorsal and rounded in *Pachynolophus*, *Plagiolophus* and *Tapirus*. The course of the internal carotid artery in mammals and the course of the stapedial arteries are still controversial. A promontorium without grooves is probably related with a medial, or extrabullar, course and, as is seen in perissodactyls, marsupials, monotremes, xenarthrans, and hyracoids, it is probably a primitive condition for mammals. In turn, Wible (1986) defended a transpromontorial course condition as the primitive condition for mammals, since a medial course of the internal carotid besides is derived and not homologous among monotremes, marsupials and eutherians. Besides all these controversies, Fischer (1986, 1989) still treated it as a synapomorphic feature of hyracoids and perissodactyls. Hoolbrook also reinforces that since each one of the hyracoids, perissodactyls, and tethytheres presents one of two derived conditions, the relationship between them and the polarity of characters stays unclear.

Bai et al. (2017) described the petrosal of *Paracolodon*, an Eocene Helaletidae from the Irdin Manha Formation of the Erlian Basin, Inner Mongolia. The promontorium presents an almond shape and its anterior portion is pointed. In the posterolateral side of the petrosal there is a depression that seems to be the fossa for the tensor tympani, and, more laterally, there is a groove that may house the anterior branch of the greater facial nerve (this groove is possibly the anterior portion of the facial sulcus). A distinct bone ridge separates the fossa and the groove. The hiatus Falopii is not evident, being absent or not preserved. Therefore, it is not possible to know where the greater petrosal nerve of the facial branched from the facial nerve, within the middle ear or the petrosal bone. Bai et al. (2017) tried to associate a groove medial to the promontorium with the transpromontorial sulcus, starting from the fenestra cochleae and running through the promontorium, and another groove medial to the transpromontorial sulcus, with the basicapsular groove for the inferior petrosal sinus. The rounded fenestra cochleae face posteriorly and the smaller and oval fenestra vestibuli faces ventrally. The portion of the crista interfenestralis located right between the fenestrae is bulged, but mediolaterally flattened anteriorlly and posteriorly the fenestrae. Also it ends right anteriorly to the stapedial muscle fossa. This fossa is triangular and large and it is located posterior to the fenestra vestibuli. Near the stapedial muscle fossa, a large secondary facial foramen is located posteriorly to the facial sulcus. The epitympanic recess was not preserved, and although the tegmen tympani is incomplete it seems to be convex.

Colbert (2006) described the tapiroid *Hesperaletes* from the middle Eocene of South California. In the dorsomedial view of the petrosal (called cerebellar surface) the internal acoustic meatus (called internal auditory meatus) is described as "centrally located, deep, and somewhat irregularly-shaped". In the meatus, it describes an oval foramen, referred as the medial foramen, which faces dorsally. It is probably the foramen acusticum inferius. Laterally, there is a more pronounced oval-shaped foramen that faces more medially, probably the foramen acusticum superius. The subarcuate fossa (called subfloccular) seems to be absent. The vestibular aqueduct (called aquaeductus vestibuli) is small, slit-like shaped and is located in a cleft facing posteriorly. It suggests that a broad and shallow groove located dorsolaterally to the crista petrosa might be the sulcus for the superior petrosal sinus. In turn, the crista petrosa contribute to the internal acoustic meatus as it forms its dorsal lip. The well-developed basicapsular groove (called sulcus medialis) is located immediately ventromedial to the promontorium. In anterior view the petrosal is very concave and its medial edge extends "further anteriorly than the crista petrosa’s anterior process". Also, close to this concavity there is a soft depression similar in the *Heptodon* petrosal described by Radinsky (1965b: 74). In the ventrolateral view (called tympanic view), the promontorium is conspicuous, tear-shaped, and presents a well-defined groove that starts from the fenestra cochleae an runs anteriorly to the promontorium, the promontory sulcus. It suggests that this sulcus probably accommodate the internal carotid artery’s promontory branch as in the genus *Hyopsodus* studied by Cifelli (1982) rather than the auricular branch of the vagus nerve as seen in the *Heptodon* described by Radinsky (1965b). The fenestra cochleae is described as large and subtriangular, opening posterolateral to the fenestra vestibuli, on the promontorium posterior edge. The facial sulcus (called tympanic aperture of the facial canal) is similar to the recent *Tapirus* and "opens into a ventrally open groove".

Li & Wang (2010) described the skull of *Schlosseria magister, a* Lophialetidae, from central Nei Mongol, China, including its right petrosal. In the ventrolateral view (called tympanic side) the promontorium presents an almond shape and three evident grooves for arteries. The medial ramus starts from the medial side of the fenestra cochleae running through the promontorium and curving rostrally. The sulcus for stapedial artery (called stapedial artery sulcus) is short but wide, running anteroventrally across the fenestra vestibule (called vestibular fenestra). The promontory artery sulcus runs from the front of the fenestra vestibular to the rostral end of the promontorium, extending laterally. The stapedial muscle fossa, located immediately lateral to fenestra vestibuli (called vestibular fenestra) and caudal to fenestra cochlea (called cochlear fenestra) is distorted. In the dorsomedial view (called cerebellar side) the internal acoustic meatus presents two foramen separated by a strong crest, the crista transversa (called transverse crista). The dorsal foramen is the foramen acusticum inferius and it is smaller and flat, while the ventral and larger foramen acusticum superius is rounded. The subarcuate fossa is very shallow, almost flat, and as there is no mention of the petromastoid canal, and it is probably absent.

2- OBJECTIVES

The aim of this study is:

1) To describe in detail the morphology of the petrosal of four species of *Tapirus* Brisson, 1762 (Perissodactila, Tapiridae): *Tapirus kabomani* Cozzuol, et al., 2013, *Tapirus indicus* Desmarest, 1819, 🖓 *Tapirus cristatellus* Winge, 1906 and *Tapirus terrestris* Linnaeus, 1758, in order to contribute to the descriptive collection of petrosals of the family Tapiridae and the order Perissodactyla, as well as some associated groups little discussed in the literature;

2) Trace the evolution of some petrosal characters in a supra-especific and higher levels among Perissodactyla. To verify this, the study will investigate the evolutionary similarities and differences between the petrosal of some extinct and extant perissodactyls representatives and trace how some petrosal characters behave when added in a phylogeny already made using other characters (considering that the petrosal was considered useful to understand evolutionary relationships and phylogenetic questions among and between other mammal groups, as seen in Artiodactyla studies as Orliac, 2010 and O'Leary, 2012).

3- MATERIALS AND METHODS

The four petrosal of *Tapirus kabomani* from the specimens UFMG 3177 (holotype), UFMG 3183, UFMG 3176, UFMG 6030, the seven petrosal of *Tapirus terrestris* from UFMG 4556, UFMG 4557, UFMG 4558, UFMG 4559, UFMG 4560, UFMG 4586, UFMG 4583, UFMG 4195 and the petrosal of *Equus caballus* (a yet non-identified petrosal in UFMG collection) used in this study are from the Coleção de Mastozoologia Universidade Federal de Minas Gerais. The *T. kabomani* petrosal MN 1700, MN 57069 and the petrosal of *Tapirus indicus* MN 57063 are from the Coleção de Mastozoologia do Museu Nacional, and the petrosal of *Tapirus cristatellus* MCL 5643/01 is from the Coleção de Paleontologia da Pontifícia Universidade Católica de Minas Gerais. General information about the specimens, as locality where they were collected, age, molarity degree, etc. can be found on the Supplementary Material at the end of the dissertation.

The information about the other petrosal used in this study come from the available literature. They are IVPP V 16391 of *Schlosseria magister* of Li & Wang (2010), IVPP V 22640 of *Paracolodon fissus* of Bai et al. (2017) and IVPP V16139 of *Litolophus gobiensis* of Bai et al. (2010) are from the Institute of Vertebrate Paleontology and Paleoanthropology; the petrosal AMNH 95495, AMNH 95496 and AMNH 95497 of *Hyopsodus* of Cifelli (1982) and AMNH 117163 of *Protitanotherium* of Mader (2009) are from the American Museum of Natural History; the petrosal SDSNH 38602 of *Hesperaletes borineyi* of Colbet (2006) is from the San Diego Society of Natural History; the petrosal USNM 22672 of *Meniscotherium chamense* Williamson & Lucas (1992) is from Natural Museum of Natural History, Smithsonian Institution; and the petrosal MSZ 17670 of *Heptodon posticus* of Radinsky (1965) is from Museum of Comparative Zoology. It is worth to mention that the matrix information of *Hyracotherium* and *Phenacodus*, taxa also included in this study but not mentioned in this paragraph, were based in Ciffeli (1982) matrix and not from the original studies.

Although the petrosal is not covered ventrally by the tympanic bulla in *Tapirus* (despite statement on contrary of O'Leary, 2010), as can be seen in other groups such as most Artiodactyla, it is fused to the skull and is found articulated with the mastoid, squamosal, exoccipital and tympanic bone (which does not ossify). It makes the study of petrosal very difficult if the bone is not disattached from the skull or if the study doesn`t use a virtual segmentation from CT-scan data in the analyses. To describe the *Tapirus* petrosal that was not already loose from the skull naturally or by previous extraction, the individuals underwent a mechanical preparation procedure to remove it from the skull, attending to the orientation of the petrosal in the specimen before the process.

Once the petrosal is separated from the skull, the quantitative and qualitative characters of the petrosal of *Tapirus cristatellus*, *Tapirus kabomani*, *Tapirus terrestris* and *Tapirus indicus* were described and compared one to another after meticulous observation. Some characters of *Tapirus* petrosal were included in a matrix modified by Cifelli (1982) (made in Mesquite version 3.31 (build 859)) together with other Perissodactyla petrosal from this same study or from other studies available in the literature and portrayed in illustrations and/or photographs. These studies about the inner ear and/or cranium features of Perissodactyla used here were: Kitts (1956), about *Hyracotherium;* Radinsky (1965b), about *Heptodon;* MacIntyre, about the ancestral petrosal pattern of Mammals; Cifelli (1982), about description and comparison of *Hyopsodus* petrosal and other ungulates; Thewissen (1990) about Phenacodontidae; Williamson & Lucas (1992), about *Meniscotherium*; Colbert (2006), about *Hesperaletes*; Mader (2009), about the cranium anatomy of *Protitanotherium;* Li and Wang (2010), about the lophialetid *Schlosseria magister,* Bai et al. (2010), about *Litolophus*; Bai et al. (2017) about description of a fossil material of the tapiroid *Paracolodon*; and O'Leary (2010), for terminology and morphology comparison of the petrosal of *Tapirus* and *Equus*. The nomenclature used in the description is based on O'Leary (2010), a detailed and complete study about the petrosal morphology of Artiodactyla and its use as a taxonomic tool in phylogenetic studies.

The available petrosal of perissodactyls of the literature were also added to the matrix modified from Cifelli (1982) in which the characters of the petrosal of

Hyopsodus was described and compared with other extinct mammals, most ungulates representatives historically associated with *Hyopsodus*. In Cifelli (1982), the ancestral characters states were polarized according to MacIntyre (1972). In MacIntyres study an ancestral petrosal pattern of Mammals is described and discussed since according to him, the mammals of the early Cenozoic and late Cretaceous presents a petrosal pattern composed by common features that can be compared. To this primitive petrosal pattern MacIntyre (1972) named *The trissulcate petrosal pattern*. The other taxa included in Cifelli`s matrix were referenced in Matthew (1909), Russell (1960, 1964), Radinsky (1965), Gazin (1965, 1968), Clemens (1966), MacIntyre (1972), Wahlert (1974).

From 21 mammal taxa of Cifelli (1982) matrix, the five closest related with/among Perissodactyla were included in this study: *Hyopsodus*, *Meniscotherium*, *Phenacodus*, *Hyracotherium* and *Heptodon*. It was added to these 8 undoubtedly perissodactyl taxons: *Protitanotherium*, *Hesperaletes*, *Litolophus*, *Paracolodon* and *Schlosseria*, analysed from pictures and descriptions from the literature, *Equus caballus*, and the 4 species of *Tapirus* described in this study: *Tapirus cristatellus*, *Tapirus terrestris*, *Tapirus indicus* and *Tapirus kabomani*, were analyzed in hands from the piece itself. Cifelli's (1982) characters were modified in order to reduce ambiguity according to later discussions about it. Also, some Cifelli's (1982) characters were merged with characters from O'Leary (2010) matrix.

Since there are not an unique comprehensive phylogeny including all taxa included in this study, the characters were plotted in a topology composed by six different but concordant phylogenies that include all the analyzed taxa. The phylogenies used were Holbrook and Lapergula (2011) for perissodactyls, Colbert (2005) for tapiromorphs non *Tapirus*, Bai et al. (2017) for *Paracolodon*, Cozzuol et al. (2013, 2014) for *Tapirus*, and Perini (2010) and Halliday et al. (2017) for condylarths (Fig. 11). Then, each character were traced, discussed and inferred to groups containing no petrosal information, by parcimony reconstruction in Mesquite.

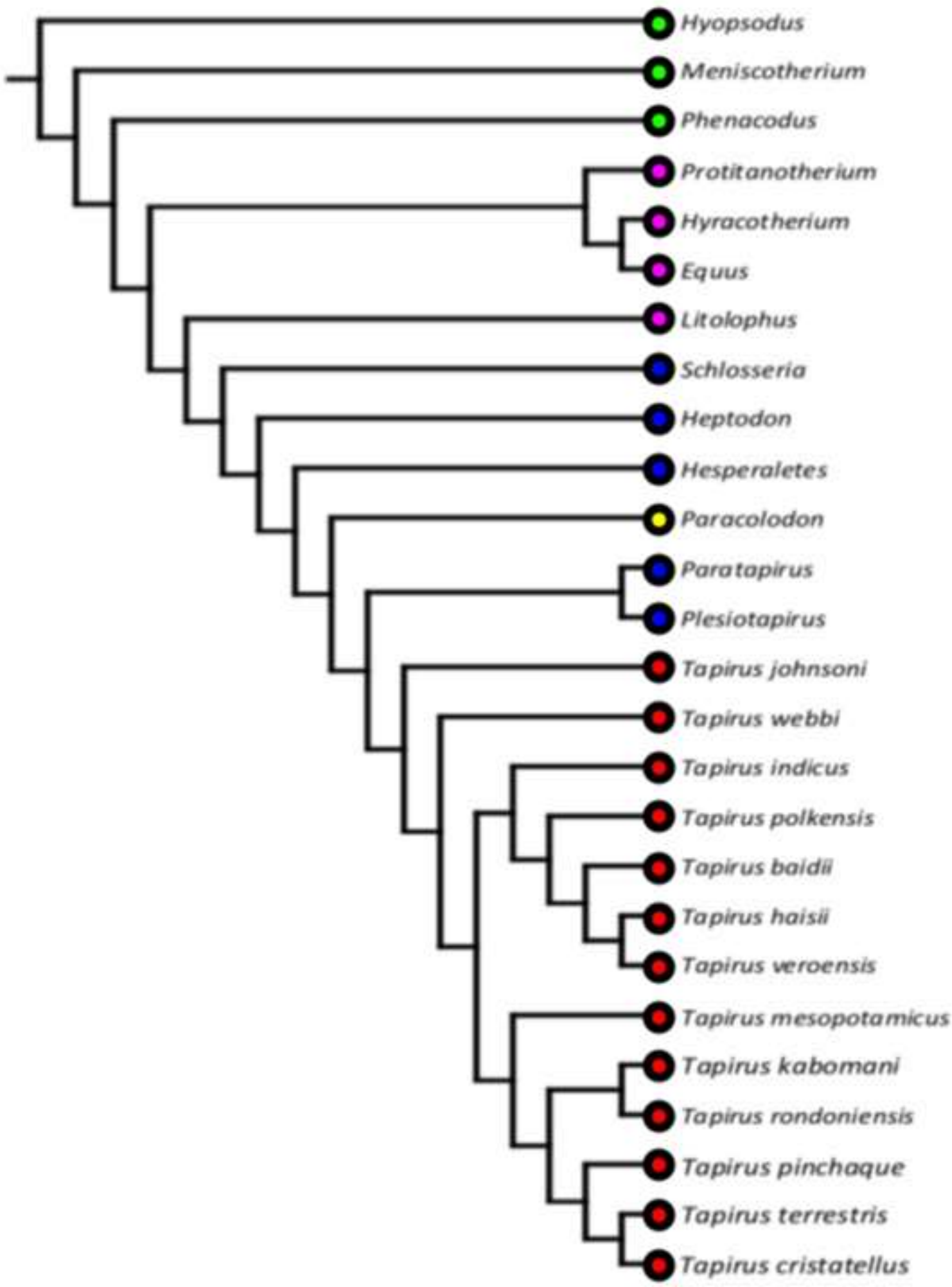

Figure 11 – The phylogeny used in this study, composed by the junction of Holbrook and Lapergula (2011) to perissodactyls in pink, Colbert (2005) to tapiromorphs non *Tapirus* in blue, Bai et al. (2017) to *Paracolodon* in yellow, Cozzuol et al. (2013) to *Tapirus* in red and Perini (2010) and Halliday et al. (2017) to condylarths in green.

The structures described are represented in the following schematic illustration.

Guide for the description (Fig. 12. A, B).

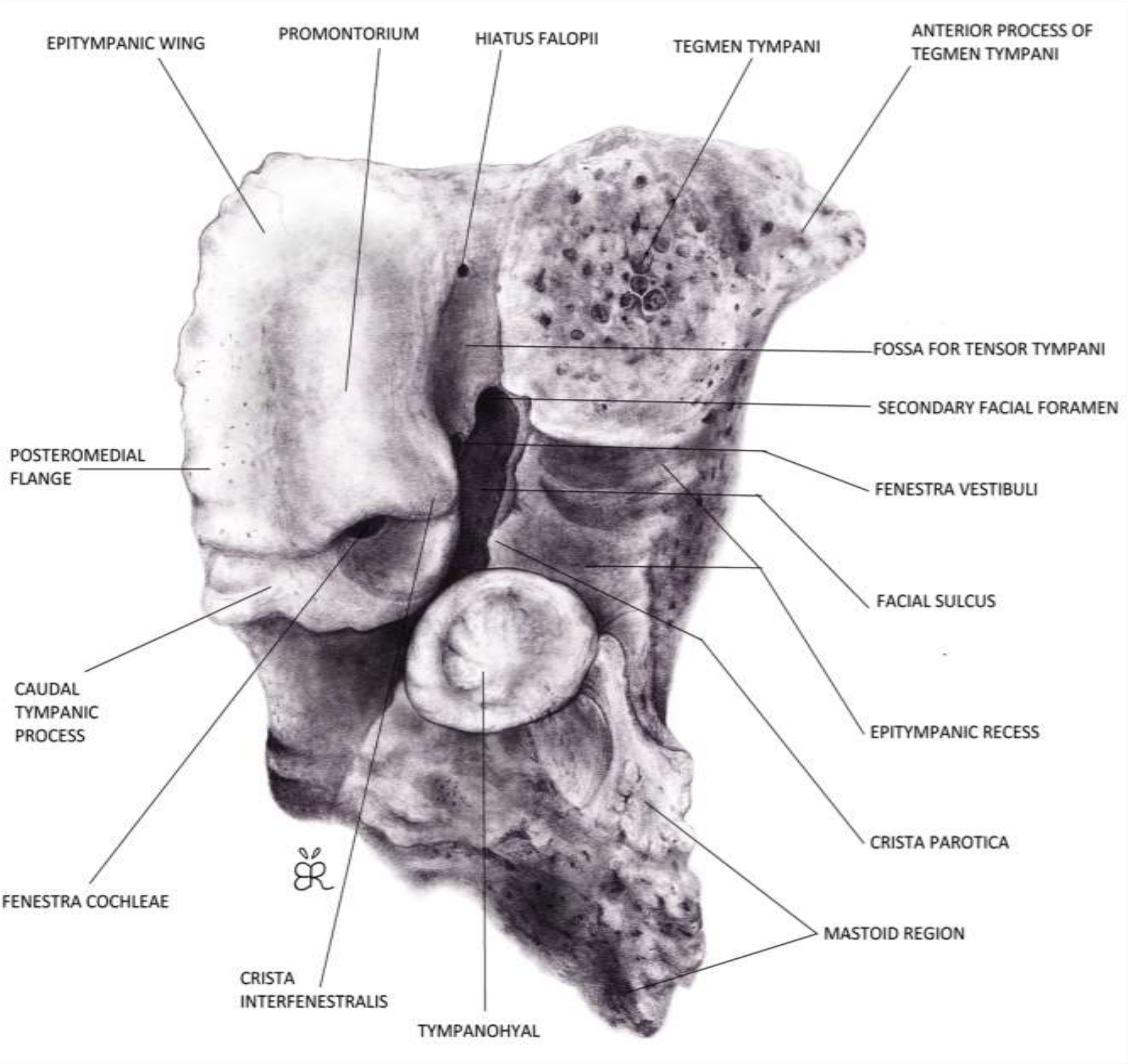

Figure 12.A) – Petrosal in ventrolateral view. Schematic illustration of a general petrosal bone of the genus *Tapirus* made by the compilation of petrosal of the species *Tapirus terrestris*, *Tapirus kabomani* and *Tapirus indicus*. The structures described in the following text are represented above. Obs.: Illustration by Bárbara Rossi.

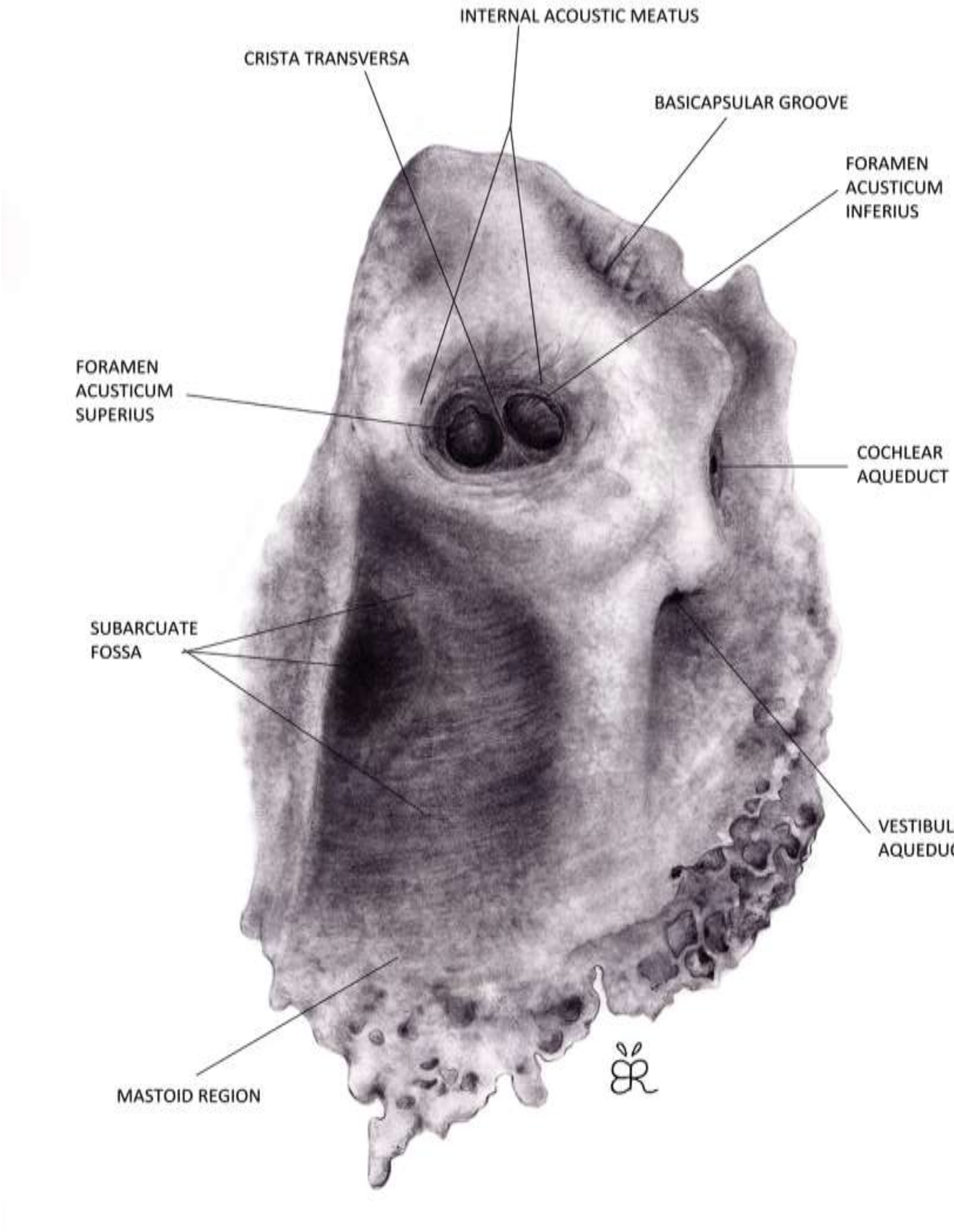

Figure 12.B) – Petrosal in dorsomedial view. Schematic illustration of a general petrosal bone of the genus *Tapirus* made by the compilation of petrosal of the species *Tapirus terrestris*, *Tapirus kabomani* and *Tapirus indicus*. The structures described in the following text are represented above. Obs.: Illustration by Bárbara Rossi.

Two additional analysis were made using the present matrix. First, the petrosal matrix of the present study was made using Mesquite version 3.31 (build 859) (Maddison & Maddison, 2011), and analyzed with TNT (Windows no taxa limit version) (Goloboff et. al, 2008), with and without grouping constrains for well-supported clades in literature. This analysis resulted in many different tree topologies, so that the consensus tree was an unresolved and inconclusive polytomy, even when constrains were used (see Appendix 5). Second, the petrosal matrix was included to a more comprehensive cranium-dental and postcranial matrix of Cozzuol et al. (2013, 2014) including only the five common taxa between both matrix: *Heptodon*, *Tapirus cristatellus*, *Tapirus indicus*, *Tapirus terrestris* and *Tapirus kabomani*, in order to test if the petrosal characters used in this study supports the topology of the phylogeny of Tapiridae obtained by Cozzuol et al. (2013, 2014). The matrix were build with Mesquite version 3.31 (build 859), and the resulting matrix was analyzed with TNT.

4- RESULTS

4.1- Anatomic description of the petrosal of the genus *Tapirus*

The petrosal of *Tapirus* is described in more than 2 views, while the following figures portray only the ventrolateral and dorsomedial views. However, all the described structures can be seen in those views.

Petrosal of *Tapirus terrestris* (Fig. 13)

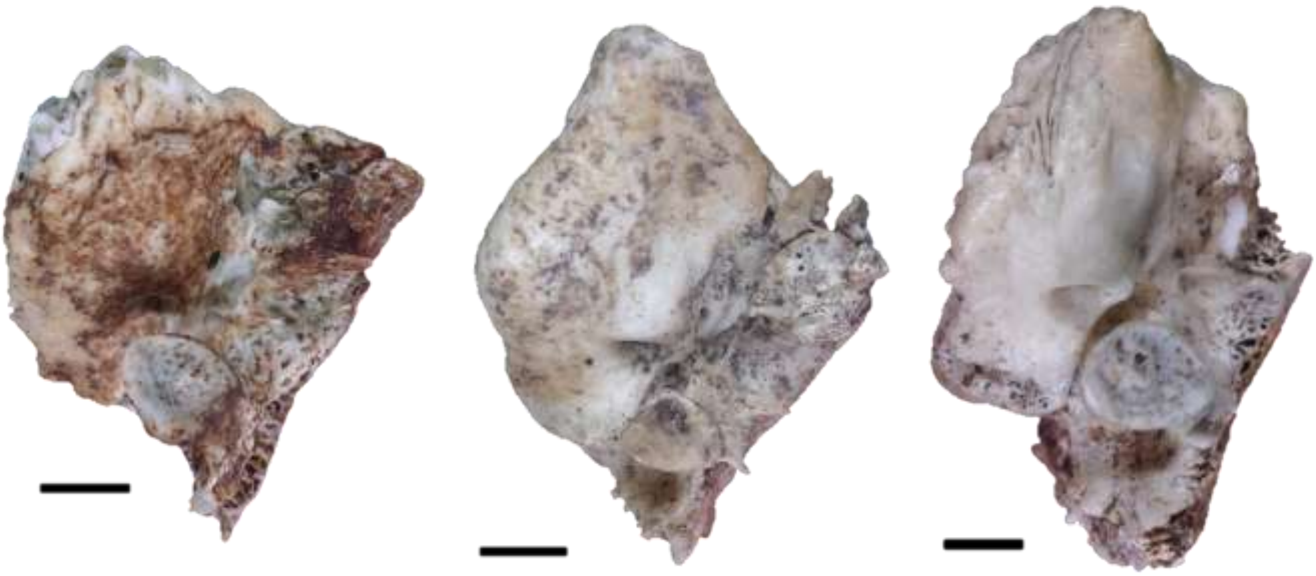

Fig. 13.A) Ventrolateral view of the petrosal of *Tapirus terrestris* UFMG 4583, UFMG 4558, UFMG 4559 from left to right. The petrosal of UFMG 4583 and UFMG 4558 are the left petrosal, and UFMG 4559 is the right (its picture has been mirrored to standardize all petrosal).

In ventrolateral view (Fig. 13.A), the promontorium of all *T. terrestris* specimens are very slightly inflated, with a mediollaterally flat surface and a hemi-ellipsoid shape. Only UFMG 4195 presents its promontorium totally flattened with no inflation. Both cochlear and vestibular fenestrae are oval, with the fenestra cochlea approximately two times larger than the fenestra vestibuli. The later is arranged anteroventral-posterodorsally, while the fenestra cochlea is arranged in the opposite direction, posteroventral-anterodorsally in all petrosals. Separating the fenestrae, there is a crest called crista interfenestralis, slightly flattened antero-posteriorly and inclined diagonally from posterodorsal face to the anteroventral face of the petrosal. The flattening degree of crista interfenestralis is variable among *T. terrestris* petrosal but increases from its posterior edge to anterior edge in all specimens. The crista interfenestralis also presents a process that extends laterally towards the posterior process of the crista parotica. The extension of the processes varies among specimens, from very discreet in UFMG 4560 to continuous with posterior process of crista parotica in UFMG 4558. The transpromontorial groove and the sulcus for the stapedial artery are absent in all *Tapirus* studied. The more medial structure of the petrosal is the epitympanic wing. Its edge forms a V with an slightly sharp apex. The apex acuity of the epitympanic wing is variable, as the surface of its edge. The petrosal UFMG 4557 and 4558 presents a more irregularly sharp apex, while UFMG 4583, despite presenting a more regular V-shape apex, has the surface of the epitympanic wing more porous. The posteromedial flange is flat and continuous with the epitympanic wing in all specimens, but it is porous in UFMG 4557, and UFMG 4586 presents a bulge in the epitympanic wing/posteromedial flange contact. Its border is also variable, being extremelly regular in UFMG 4195, but undulated in UFMG 4558. The fossa for tensor tympani is small, shallow, and excavates part of the tegmen tympani. In the fossa, the secondary facial foramen is anterior to the fenestra vestibuli in all petrosals but in UFMG 4559, where it is located far anterior to the fenestra. The roof of the secondary facial foramen consists of a very thin bone lamina, easily broken during the mechanical preparation and rarely preserved in fossils. The facial sulcus depth varies along its extension, reaching its deeper depth just dorsally to the fenestra vestibuli. The shallower facial sulcus belongs to UFMG 4560, and the deeper is UFMG 4559. The deeper portion of facial sulcus, right posterior to fenestra vestibuli, is the stapedial muscle fossa, relatively similar in all petrosals. The facial sulcus is partially ventrally wrapped by the crista parotica, a flat crest that extends medially in the ventrolateral view of the petrosal. Its extension is also variable among the specimens, so as the development degree of the triangular posterior process of the crista parotica. In UFMG 4560, the process is a very slight protuberance; in UFMG 4586, 4583, 4559, 4557, 4195 it is a small triangular process and in UFMG 4558 it extends until it merges with the process of the crista interfenestralis. The tegmen tympani is broken in UFMG 4195 and 4559, but it is possible to notice its ventrally directed position and its anterior flattening. Although they are all inflated, they present a variable degree of inflation, bone pneumatism and porportion of the extension of the anterior process of the tegmen tympani in relation to petrosal in general. The epitympanic recess is wider in UFMG 4559 and less broad in 4557, but none of the specimens present a distinct fossa for the head of the malleus. The caudal tympanic process is long in all petrosals, but its position (ventral or dorsal to the fenestra cocleae) is variable. The UFMG 4560, 4559, 4558 and 4195 present an evident sulcus extending from the facial sulcus to the posterior edge of the petrosal. The shape of the tympanohial is similar, but their sizes can vary from delicate, as in UFMG 4586 and 4557, to a robust structure in UFMG 4558.

Fig 13.B) Dorsolateral view of the petrosal of *Tapirus terrestris* UFMG 4583, UFMG 4558, UFMG 4559 from left to right. The petrosal of UFMG 4583 and UFMG 4558 are the left petrosal, and UFMG 4559 is the right (its picture has been mirrored to standardize all petrosal).

In dorsomedial view (Fig. 13.B), the internal acoustic meatus presents a broad opening, but with diferent formats. In UFMG 4559, 4557 and 4560, it is circular while in UFMG 4195 and 4558 its is oval. In UFMG 4583 and 4586 it is irregular and presents a bridged bulge in the dorsal portion of its border that partially covers this cavity. In the internal acoustic meatus, the crista transversa separates the foramen acusticum superius and foramen acusticum inferius. It is variably flattened, concave and directionally arranged among specimens. In UFMG 4559 and 4558 they are less concave; UFMG 4583, 4557, 4558 and 4559 are almost horizontally arranged and UFMG 4560 it is mediolaterally flat instead of anterodorsally flat. The foramens acusticum inferius and acusticum superius also presents diferent flattening degree, but the size proportion from one to another is similar. UFMG 4558, 4559, 4583, 4560 and 4557 are flat, while the others are more rounded. However, the foramen acusticum superius is the largest and flatter of them. On the other hand, the foramen acusticum inferius is always more rounded than the foramen acusticum superius, although both are arranged in the same direction in all petrosals. The subarcuate fossa varies from very shallow in UFMG 4560, 4586 and 4559, to shallow in UFMG 4557 and 4558, to less shallow in UFMG 4195, and neither of the cited subarcuate fossae present a petromastoid canal. The vestibular aqueduct is slit-like, lateromedially flattened, except for the rounded aqueduct of UFMG 4583, but its size and openning degree is variable. The mastoid region is triangular in all specimen and presents a rounded border, but in UFMG 4558, 4557, 4560 and 4583 it is more porous than seen in the others. In the petrosal of *Tapirus*, the cochlear aqueduct is ventrally located and can be seem from this view. It lies inside a broad slit-like depression, but its openning is small and rounded. The basicapsular groove is very evidente in UFMG 4559, 4557 AND 4558, but in the others specimens is almost continuous with the rest of the dorsomedial surface.

In lateral view, the caudal tympanic process is short, not exceeding mediolaterally the posterior process of crista parotica, and in some individuals it is located ventral to fenestra cocleae, and in others it is dorsal to fenestra cochleae (seen also from the ventrolateral view, Fig. 13.A).

In ventral view, the hiatus Falopii differs among specimens. It is bigger and ventrally located in UFMG 4559 and 4583. In the others petrosal, it is smaller and located in the terminal medial edge of the petrosal (seen also from the ventrolateral view, Fig. 13.A).

Common features of *Tapirus terrestris*

In ventrolateral view (Fig. 13.A), the fenestra cochlea and vestibuli are similar in all analysed petrosal. Both fenestrae are oval, however the fenestra vestibuli is arranged anteroventral-posterodorsally, while the fenestra cochlea is anterodorsal-posteroventrally. In the dorsal edge of the fenestra vestibuli there is a sulcus that extends posterodorsally reaching the facial sulcus. The promontorium is flat and doesn't present any groove or sulcus throughout its extension. The epitympanic wing is continuous with the posteromedial flange and its ventral edge is V-shaped. The tegmen tympani is flat in its anterior and lateral side and the anterior process of the tegmen tympani is small but very evident. The fossa for the tensor tympani is oval, shallow and excavates slightly the tegmen tympani. The secondary facial foramen is broad and is located anteroventrally to the fenestra vestibuli. The facial sulcus extends posteriorly increasing the sulcus diameter through the same direction. The epitympanic recess is small and presents some attachment fossas in its floor.

The dorsomedial view is laterally flat (Fig. 14.B). The internal acoustic meatus and all its internal associated structures presents variable size and shape. The vestibular aqueduct is flat and the cochlear aqueduct is circular, but located inside a slit-like depression.

Petrosal of *Tapirus kabomani* (Fig. 14)

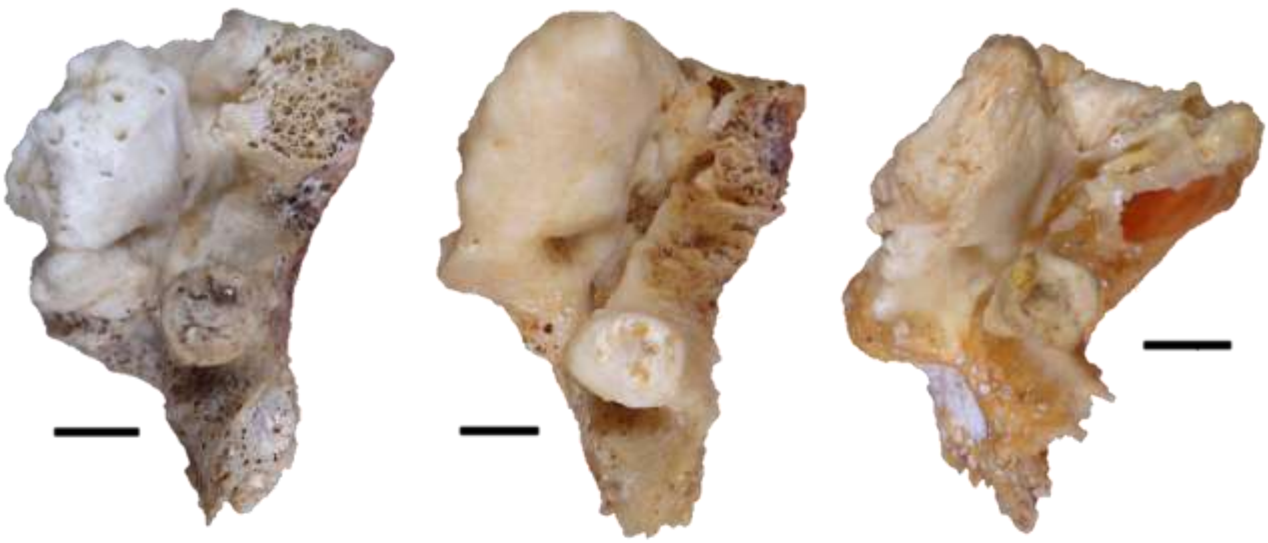

Figure 14.A) Ventrolateral view of the petrosal of *Tapirus kabomani* UFMG 3177, UFMG 3183, MN 57069 from left to right. The petrosal of UFMG 3177 and UFMG 3183 are the left petrosal, and MN 57069 is the right (its picture has been mirrored to standardize all petrosal).

In ventrolateral view (Fig. 14.A), the promontorium surface of all specimens are mediolaterally flattened and hemi-ellipsoid, but in UFMG 6030 and especially in 3177, the promontorium present a slight laterally flat bulge. The fenestra cochleae is oval-shaped and is approximately twice as large as the fenestra vestibuli. In addition, in UFMG 3177, the fenestra cochleae has a small groove extending ventrally from its posterior extremity. The fenestra vestibuli also presents an oval shape and it is approximately half the size of the fenestra cochleae. The fenestra vestibuli has a sulcus of the same width that extends posteriorly from this fenestra to the facial sulcus. The crista interfestralis is variably flat and pronounced. In UFMG 3177 it is very slightly flat and pronounced; in MN 57069 it is very flat, but slightly pronounced; in UFMG 3176 it is pronounced, but slightly flat ; in UFMG 3183 and MN 1700 it is considerably flat and pronounced; and in UFMG 6030 it is very flat and extends laterally until it meets the posterior process of the crista parotica. As seen in all *Tapirus,* there are no transpromontorial groove, as well as sulcus for stapedial artery. The epitympanic wing presents variable format, extension and porosity degree. However, except for UFMG 3177, which presents a porous and rounded border, all the other specimens have, in general, a V-shaped epitympanic wing. Also, this structure in UFMG 3177 is much smaller than in the others. The fossa for tensor tympani is shallow and oval in all specimens, and the secondary facial foramen is positioned anteriorly to the fenestra vestibuli. However, in UFMG 3177 it is located further anteriorly than in the others. The facial sulcus increases its diameter posteriorly in UFMG 6030, 3176 and 3177, while in the others the diameter remains almost the same along all its extension. The crista parotica extends medially over the facial sulcus, but in UFMG 3183, MN 1700 and 57069 it almost enclosures the facial sulcus. In UFMG 6030 it extends considerably and its posterior process merges with the lateral process of the crista interfenestralis. The posterior process of the crista parotica is triangular and small in all the other specimens. In UFMG 3177, however, it is so small that resembles a slight irregularity in the crista parotica border. The tegmen tympani is variably porous and inflated among *T. kabomani*. UFMG 57069 presents a very inflated and very pneumatized (almost hollow) tegmen tympani that extends almost to the same level as the epitympanic wing edge. The other tegmen tympani are porous instead of hollow and they extend almost reaching the same level as the middle of the promontorium. The epitympanic recess of *T. kabomani* is broader than in *T. terrestris* specimens, but it is still considered a small structure. None petrosal present a distinct fossa for the attachment of the head of malleus. The tympanohyal present variable sizes. In MN 1700 it is less robust than in the others and in UFMG 3177 it is closer to the promontorium. The posteromedial flange is flat in all specimens, but in the ventral border of UFMG 3060 there is a concavity not seen in the others. The caudal tympanic process is very flat and short in all specimens, but it can be dorsal to the fenestra cochlea as in UFMG 6030, 3183, 57069 and 3177, or ventral as in all the others. In UFMG 3176 there is a triangular and sharp process posterior to the fenestra cochlea pointing laterally that is not seen in the other *T. kabomani* petrosals. In UFMG 3183, the posterior edge of the caudal tympanic process is very distinct and looks like a triangular bridged process. UFMG 6030 and 3176 presents a sulcus that extends horizontally from the posterior edge of the facial sulcus to the posterior edge of the petrosal through the caudal tympanic process.

Figure 14.B) Dorsomedial view of the petrosal of *Tapirus kabomani* UFMG 3177, UFMG 3183, MN 57069 from left to right. The petrosal of UFMG 3177 and UFMG 3183 are the left petrosal, and MN 57069 is the right (its picture has been mirrored to standardize all petrosal).

In dorsomedial view (Fig. 14.B), the internal acoustic meatus is very variable among *Tapirus kabomani* specimens. In UFMG 3183 and MN 1700 the border of the meatus is circular; in UFMG 6030, 3176 and 3177 it is ventrodorsally flattened; and in MN 57069 the meatus is intermediary to both shapes. In UFMG 6030 and 3183 there are diferent processes extending from the anterior portion of the internal acoustic meatus. The first is triangular, sharp, and looks like a piece of bone attached in the petrosal. The later is a pin-like petrosal process pointing medially. The foramina inside the internal acoustic meatus are approximately the same size in all specimens but in UFMG 3177, where it is more circular if compared with the flattened ones of the others. The crista transversa is flattened in all specimens except MN 1700. However, it is arranged in the same direction in all of them. The foramen acusticum superius tends to be larger than the foramen acusticum inferius and anteroposteriorlly flattened in all specimens. It is connected to the secondary facial foramen in ventrolateral view. On the other hand, the foramen acusticum inferius tends to be more circular and smaller. In the mastoid region, the subarcuate fossa is shallow in UFMG 6030, 3177 and 3176; and deep in UFMG 3183 and MN 1700, but in all specimens cited here it is small. In MN 57069 it is very broad and deep, occupying almost all the extension of the mastoid region. All the specimens lack a petromastoid canal. The vestibular aqueduct is distinct in almost all petrosals, but its size and format is very variable. UFMG 3183 and 3177 present a slit-like vestibular aqueduct longer than the others. UFMG 6030 and MN 57069 also present a slit-like vestibular aqueduct, but smaller than the former. UFMG 3186 has the most distinct vestibular aqueduct among *T. kabomani* specimens, wide and circular. The vestibular aqueduct of MN 1700 is very small and doesn't seems to have an external opening. The mastoid region is broken in UFMG 3176, but in UFMG 6030 and 3177 it is clearly rounded, and in the others it is clearly triangular. The cochlear aqueduct can be seen in dorsomedial view in UFMG 3183 and 6030. In the others it is located more ventrally and can be seen only in dorsomedial view (although partially). However, in UFMG 3177 and MN 57069, this structure is entirelly ventral. The cochlear aqueduct itself is rounded and similar in all specimens, and it is located inside a slit-like depression in all specimens, except UFMG 3176. In this specimen there are no depression and the cochlear aqueduct can be described as a hole in the surface, close to the posterior edge in dorsomedial view.

The hiatus Falopii is located anteriorly, at the edge of the petrosal, in UFMG 3183, 3176 and MN 1700. In the others specimens it is ventrolateral, sometimes together with the secondary facial foramen, as in UFMG 3177, and sometimes anterior to it (altough all can be seen in ventrolateral view, Fig. 14.A).

Watching the petrosal of UFMG 3177 in anterior and ventrolateral views (Fig. 14.A), it is possible to notice a cavity excavating the surface of the medial edge of the petrosal that deepens inside the bone until a small orifice in the central and deepest level of this cavity. It is not possible to affirm if it is a small foramen or a pore in the pneumatic bone.

Common features of *Tapirus kabomani*

In ventrolateral view (Fig. 14.A), the fenestra vestibuli of all *T. kabomani* petrosals presents approximately the same size, around 2mm, and the same oval format. In the dorsal edge of the fenestra vestibuli, some of them present a sulcus that runs dorsally and reach the facial sulcus. The fenestra cochlea is also similar among them. The crista interfenestrais presents a variable flattening degree but it is arranged dorsoposterior-ventroanteriorlly in all petrosals. The promontorium is flat and doesn't present any grooves, sulci or attachment marks. The fossa for tensor tympani is oval, shallow and slighly excavates the tegmen tympani. The epitympanic wing format is variable among *T. kabomani*, but in all the individuals it is continuous with the posteromedial flange. The facial sulcus presents approximately the same diameter but, as the crista parotica varies its extension and flatness degree, some of them are more hidden than others. The secondary facial foramen, a small foramen close to the anterior border of the petrosal, are positioned anterior to fenestra vestibuli. The tegmen tympani presents a variation on its degree of ossification that is not associated with the age of the specimens, but in all of the petrosal it is anteriorly flat and laterally inflated, and its anterior process is small. The epitympanic recess is broad and presents a shallow and very discrete fossa on its floor.

In dorsomedial view (Fig. 14.B), the internal acoustic meatus is deep in all the specimens and the crista interfenetralis is arranged dorsoposterior-ventroanteriorlly.

Petrosal of *Tapirus indicus* (Fig. 15)

The petrosal is more robust than both *Tapirus terrestris* and *Tapirus kabomani*, but its posterior insertion in the skull, although smaller, is wider than in the others.

Figure 15.A) Ventrolateral view of the petrosal of *Tapirus indicus* MN 57063. The picture was mirrored to standardize all petrosal sides, since the petrosal of this specimen is the right petrosal.

In ventrolateral view (Fig. 15.A), the promontorium is hemi-ellipsoid, ventrolaterally flattened and presents a very shallow and circular depression on its center. The fenestra cochleae is approximately 2x larger than the fenestra vestibuli, dorsoventrally elongated and anteroposteriorlly flattened. At the posterior edge of the fenestra cochleae there is a sulcus that starts from it and extends ventrally through the petrosal. The sulcus is narrow, very distinct, shallow, and resemble a bone-folding or a unclosed bone suture. It can only be seen in the petrosal of this species, so that in the other petrosals described in this study, there is nothing similar to this. The external opening of the fenestra vestibuli is oval and opens into a wider internal cavity. Between the fenestrae, there is a rounded crest called crista interfenestralis. It is thicker than the flattened crista interfenestralis of the other *Tapirus* studied and it extends slightly inclined dorsoposterior-ventroanteriorlly, following the same direction as the fenestra vestibuli arrangement. In this individual, both the transpromontorial groove and the sulcus for stapedial artery are absent, as in all *Tapirus*. Ventrally to the promontory the epitympanic wing is very reduced. Its border is ventrally flattened and continuous to the posteromedial flange, and the surface of the border is irregular and porous. The posteromedial flange border, just as seen in the epitympanic wing, is also irregular and porous, flat, and extends considerably medially as a bone ridge. The flat crista parotica extends medially and extends along together with the facial sulcus all its length. The crista is mediolaterally flattened and doesn`t extends laterally as seen in other *Tapirus*. Also, the posterior process of the crista parotica is very small and doesn't extends medially to the crista interfenestralis. The secondary facial foramen is located anteriorly to the facial sulcus, inside the fossa for the tensor tympani, and this fossa is deep and excavates the tegmen tympani. The tegmen tympani is posteriorly flat and porous, as in other *Tapirus*, with a (very) thin layer surface. In turn, the anterior process of the tegmen tympani is reduced and blunt. The epitympanic reccess is small and there is no distinct fossa for the head of the malleus. The caudal tympanic process is short and is located ventrally to the fenestra cochleae. The hiatus Falopii is ventraly located and can be seen from this view.

Figure 15.B) Dorsomedial view of the petrosal of *Tapirus indicus* MN 57063. The picture was mirrored to standardize all petrosal sides, since the petrosal of this specimen is the right petrosal.

In dorsomedial view (Fig. 15.B), the internal acoustic meatus is deep and presents a circular external border. The foramen acusticum superius is the larger foramen in the internal acoustic meatus. It is flat, while the foramen acusticum inferius is circular. Separating the foramina, there is a crest called crista transversa, also flat, concave, and extending posterodorsal-anteroventrally. In the mastoid region, the subarcuate fossa is shallow and wide, but there is no petromastoid canal. The mastoid region itself is large and presents a rounded border. The vestibular aqueduct, as the cochlear aqueduct, is flattened, deep, with a wide and very distinct opening. However, the vestibular aqueduct is more dorsal than the cochlear aqueduct and it extends dorsoventrally through a considerable part of the mastoid region. The ventral edge of this view is flat and all its surface is very irregular (rugose).

In ventromedial view, it is possible to see the depth and extension of both aqueducts described above in the dorsomedial view paragraph. The vestibular and cochlear aqueducts are both very deep and flat, like a slit, but the basicapsular groove is not so evident in this petrosal. In the ventral edge of this view, a slit probably is correspondent to the basicapsular groove (Fig. 19.K,L).

Petrosal of *Tapirus cristatelus* (Fig. 16)

This description was based in a piece of the skull containing part of the left petrosal attached (Fig. 8.D). The petrosal was broken mediolaterally, exposing the internal cavity of the fenestra vestibuli. Also, only the dorsomedial view and part of the ventral and lateral view are exposed. Therefore, the description corresponds to the mastoid portion of the dorsomedial view and part of the ventral and lateral structures of *T. cristatellus* (MCL 5643/01).

Fig. 16.A) Ventrolateral view of the right petrosal of *Tapirus cristatellus* MCL 5643/01. As seen in the figure, the petrosal is mediolarerally broken.

In ventrolateral view (Fig. 16.A), the facial sulcus is not as deep as seen in other *Tapirus*. The crista parotica extends considerably medially, and there is just a narrow open cleft almost reaching the medial opposite side. Also, the posterior process of the crista parotica is small and triangular, but evident. The epitympanic recess is small and very similar to other *Tapirus*, with no fossa for the head of malleus. The tympanohyal is also similar in other *Tapirus*.

Fig. 16.B) Dorsomedial view of the right petrosal of *Tapirus cristatellus* MCL 5643/01. As seen in the figure, the petrosal is mediolarerally broken.

In dorsomedial view (Fig. 16.B), the subarcuate fossa is evident, triangular and deep if compared with the other *Tapirus* species but, as seen in other *Tapirus*, there is no petromastoid canal. The vestibular aqueduct is flattened as a slit, but not as flattened as in some *Tapirus terrestris*. In *T. cristatelus*, the opening of the vestibular aqueduct is broader than in *T. terrestris,* and the flattened mastoid region is triangular, proportionally smaller than in *Tapirus terrestris,* and its borders are rounded.

Fig. 16.C) Anterior view of the right petrosal of *Tapirus cristatellus* MCL 5643/01. As seen in the figure, the petrosal is mediolarerally broken.

In lateral view, the caudal tympanic process is long, ventral to the fenestra cochlea, considerably concave, and presents a smooth surface. Also, there is a groove that extends almost anterodorsally from the facial sulcus through the caudal tympanic process (seen also from the ventrolateral view, Fig. 16.A).

An important difference between *Tapirus cristatellus* and other *Tapirus* is the pars mastoidea. In *T. cristatellus* the pars mastoidea is clearly concave, while in the other *Tapirus* species it is flattened (Fig. 16.C).

4.2 - Character mapping

The characters and its respective character states are displayed below (Table 1). They were obtained from Cifelli (1982), most of them were modified to become applicable in this study (each character modification is discussed later in “Discussion” section of this study).

	Characters	State 0	State 1
1	Transpomontorial sulcus	absent	present
2	Caudal tympanic process - extension	short (not exceeds mediolaterally the posterior process of crista parotica)	long (exceeds mediolaterally the posterior process of crista parotica)
3	Caudal tympanic process - position	ventral to fenestra cocleae	dorsal to fenestra cocleae
4	hiatus Falopii	terminally (anterior edge of petrosal)	ventral side (tympanic)
5	Sulcus for stapedial artery	absent	present
6	Promontorial surface	smooth	not smooth
7	Subarcuate fossa - depth	shallow/non existent (same level as vestibular aqueduct in dorsal view)	deep (vertex of concavity deeper than the vestibular aqueduct in dorsal view)
8	Subarcuate fossa - size	small (approximately the same size of internal acoustic meatus)	wide (more than 2x larger than internal acoustic meatus)
9	Epitympanic recess	large (from tympanohyal, reaching secondary facial foramen)	small (from tympanohyal, not reaching secondary facial foramen)
10	Secondary facial foramen	lateral to fenestra vestibuli	anterior to fenestra vestibuli
11	Cochlear aqueduct - position	in ventromedial face	in ventral face
12	Cochlear aqueduct - slit	absent	present
13	Tegmen tympani	thin	inflated

Table 1 - The characters and its respective character states used in this study. They were based on Cifelli (1982) characters ans state of characters, but some of them were modified to be applicable to all the taxa.

Six taxa from Cifelli's (1982) were included in the matrix: *Heptodon*, *Hyopsodus*, *Meniscotherium*, *Phenacodus* and *Hyracotherium*, and 21 more taxa were included in the modified matrix of 13 characters. Ten of these 21 new taxa had information about the petrosal, while the other 11 taxa (all of them *Tapirus* species) were included to verify the evolution and distribition of the petrosal characters inside the focused group of this study, the genus *Tapirus* itself. The resulting matrix is displayed in Table 3.

	Transpomontorial sulcus	Caudal tympanic process - extension	Caudal tympanic process - position	hiatus Falopii	Sulcus for stapedial artery	Promontorial surface	Subarcuate fossa - depth	Subarcuate fossa - size	Epitympanic recess	Secondary facial foramen	Cochlear aqueduct - position	Cochlear aqueduct - slit	Tegmen tympani
Heptodon	absent	?	?	ventral side (tympanic)	absent	smooth	?	?	small (from tympanohyal, not reaching secondary facial foramen)	anterior to fenestra vestibuli	in ventral face	present	inflated
Protitanotherium	absent	long (exceeds mediolaterally the posterior process of crista parotica)	?	terminally (anterior edge of petrosal)	?	smooth	shallow/non existent (same level as vestibular aqueduct in dorsal view)	wide (more than 2x larger than internal acoustic meatus)	?	anterior to fenestra vestibuli	in ventromedial face	absent	inflated
Hyopsodus	present	short (not exceeds mediolaterally the posterior process of crista parotica)	dorsal to fenestra cocleae	terminally (anterior edge of petrosal)	absent	smooth	deep (vertex of concavity deeper than the vestibular aqueduct in dorsal view)	small (approximately the same size of internal acoustic meatus)	small (from tympanohyal, not reaching secondary facial foramen)	anterior to fenestra vestibuli	in ventromedial face	absent	inflated
Paracolodon	present	short (not exceeds mediolaterally the posterior process of crista parotica)	ventral to fenestra cocleae	?	absent	smooth	?	?	?	anterior to fenestra vestibuli	?	?	?
Schlosseria	present	?	?	?	present	not smooth	deep (vertex of concavity deeper than the vestibular aqueduct in dorsal view)	small (approximately the same size of internal acoustic meatus)	?	?	?	?	?
Hyracotherium	absent	long (exceeds mediolaterally the posterior process of crista parotica)	dorsal to fenestra cocleae	?	absent	not smooth	?	?	?	?	in ventral face	present	inflated
Meniscotherium	present	short (not exceeds mediolaterally the posterior process of crista parotica)	dorsal to fenestra cocleae	ventral side (tympanic)	present	not smooth	?	?	?	lateral to fenestra vestibuli	?	?	inflated
Phenacodus	absent	short (not exceeds mediolaterally the posterior process of crista parotica)	dorsal to fenestra cocleae	terminally (anterior edge of petrosal)	present	not smooth	?	?	small (from tympanohyal, not reaching secondary facial foramen)	anterior to fenestra vestibuli	in ventral face	present	inflated
Equus	absent	long (exceeds mediolaterally the posterior process of crista parotica)	dorsal to fenestra cocleae	terminally (anterior edge of petrosal)	absent	smooth	deep (vertex of concavity deeper than the vestibular aqueduct in dorsal view)	wide (more than 2x larger than internal acoustic meatus)	small (from tympanohyal, not reaching secondary facial foramen)	anterior to fenestra vestibuli	in ventral face	present	inflated
Litolophus	absent	?	?	ventral side (tympanic)	absent	smooth	?	?	?	anterior to fenestra vestibuli	?	?	?
Hesperaletes	present	?	?	?	?	?	shallow/non existent (same level as vestibular aqueduct in dorsal view)	_	?	anterior to fenestra vestibuli	?	?	?

Table 2 – Distribution of the states of character among the studied taxa. The taxa studied are in the first colummn, at the left extremity of the matrix, while the characters are in the first line, at the top end of the matrix. The characters were painted as represented in the following figures to facilitate their location in the petrosal. The "?"symbols are missing/unknown data and the "-" symbol is not applicable. The matriz was made in Mesquite version 3.31 (build 859), and colored on Microsoft Excel.

	Transpomontorial sulcus	Caudal tympanic process - extension	Caudal tympanic process - position	hiatus Falopii	Sulcus for stapedial artery	Promontorial surface	Subarcuate fossa - depth	Subarcuate fossa - size	Epitympanic recess	Secondary facial foramen	Cochlear aqueduct - position	Cochlear aqueduct - slit	Tegmen tympani
Tapirus cristatellus	?	long (exceeds mediolaterally the posterior process of crista parotica)	?	?	?	?	deep (vertex of concavity deeper than the vestibular aqueduct in dorsal view)	small (approximately the same size of internal acoustic meatus)	small (from tympanohyal, not reaching secondary facial foramen)	?	?	?	inflated
Tapirus indicus	absent	short (not exceeds mediolaterally the posterior process of crista parotica)	ventral to fenestra cocleae	ventral side (tympanic)	absent	smooth	shallow/non existent (same level as vestibular aqueduct in dorsal view)	small (approximately the same size of internal acoustic meatus)	small (from tympanohyal, not reaching secondary facial foramen)	anterior to fenestra vestibuli	in ventromedial face	present	inflated
Tapirus terrestris	absent	short (not exceeds mediolaterally the posterior process of crista parotica)	ventral to fenestra cocleae & dorsal to fenestra cocleae	terminally (anterior edge of petrosal) & ventral side (tympanic)	absent	smooth	shallow/non existent (same level as vestibular aqueduct in dorsal view) & deep (vertex of concavity deeper than the vestibular aqueduct in dorsal view)	small (approximately the same size of internal acoustic meatus)	small (from tympanohyal, not reaching secondary facial foramen)	anterior to fenestra vestibuli	in ventromedial face	present	inflated
Tapirus kabomani	absent	short (not exceeds mediolaterally the posterior process of crista parotica)	ventral to fenestra cocleae & dorsal to fenestra cocleae	terminally (anterior edge of petrosal) & ventral side (tympanic)	absent	smooth	deep (vertex of concavity deeper than the vestibular aqueduct in dorsal view)	small (approximately the same size of internal acoustic meatus) & wide (more than 2x larger than internal acoustic meatus)	small (from tympanohyal, not reaching secondary facial foramen)	anterior to fenestra vestibuli	in ventromedial face	absent & present	inflated
Tapirus johnsoni	?	?	?	?	?	?	?	?	?	?	?	?	?
Tapirus webbi	?	?	?	?	?	?	?	?	?	?	?	?	?
Tapirus polkensis	?	?	?	?	?	?	?	?	?	?	?	?	?
Tapirus bairdii	?	?	?	?	?	?	?	?	?	?	?	?	?
Tapirus haysii	?	?	?	?	?	?	?	?	?	?	?	?	?
Tapirus veroensis	?	?	?	?	?	?	?	?	?	?	?	?	?
Tapirus mesopotamicus	?	?	?	?	?	?	?	?	?	?	?	?	?
Tapirus rondoniensis	?	?	?	?	?	?	?	?	?	?	?	?	?
Tapirus pinchaque	?	?	?	?	?	?	?	?	?	?	?	?	?
Paratapirus	?	?	?	?	?	?	?	?	?	?	?	?	?
Plesiotapirus	?	?	?	?	?	?	?	?	?	?	?	?	?

Table 2 – Continued.

The characters (structures) were differentiated by colors (Fig. 17.A,B) and illustrated and distributed along the phylogeny following the patterns represented below (Fig. 18.A, B, C, D, E F, G, H, I, J, K, L, M). Each character is individually discussed later in this dissertation.

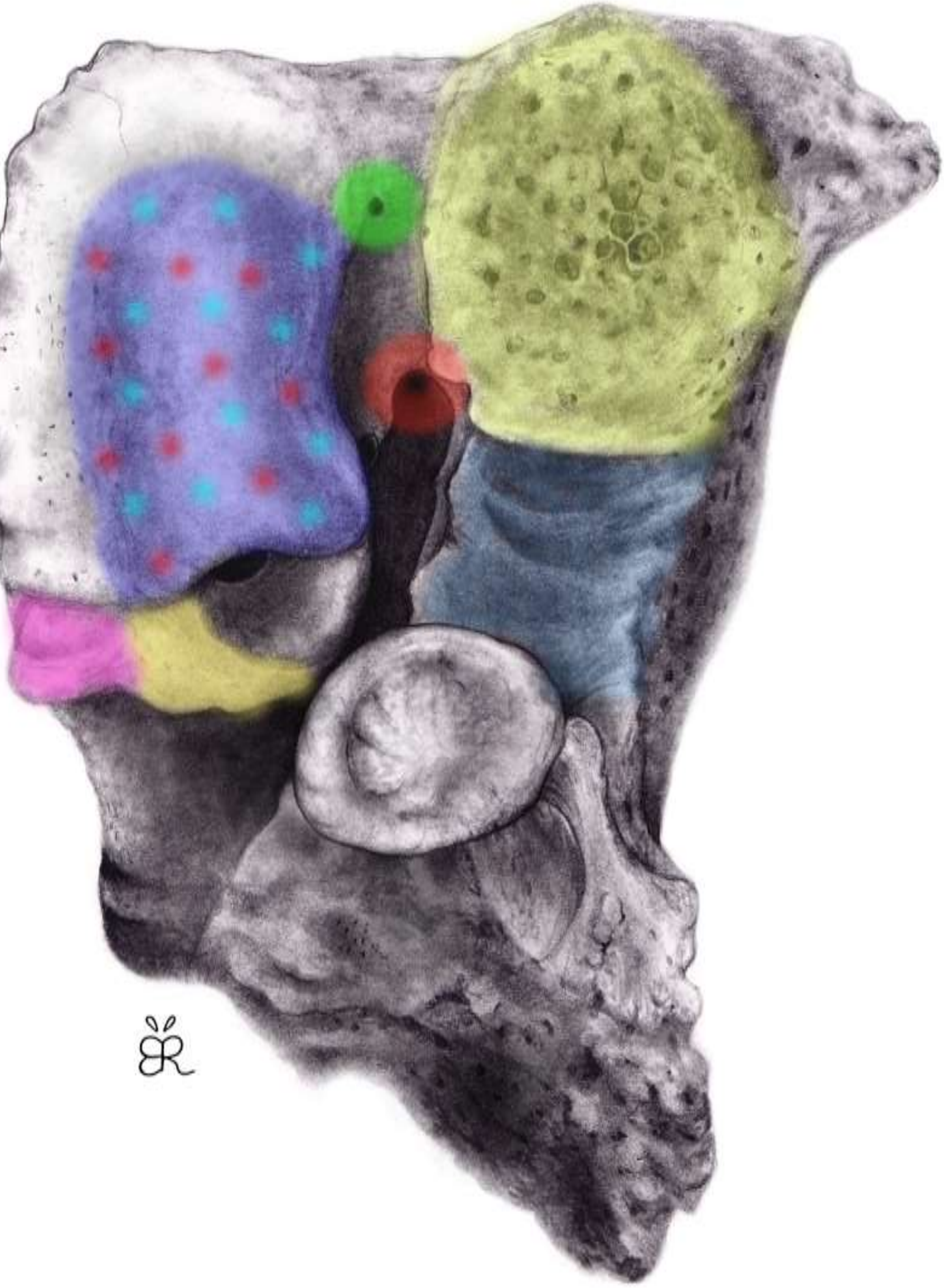

Figure 17.A) – Petrosal in ventrolateral view. Schematic illustration of a general petrosal bone of the genus *Tapirus* made by the compilation of petrosal of the species *Tapirus terrestris*, *Tapirus kabomani* and *Tapirus indicus*. The characters used in the matrix are represented above and its location are indicated by the different colors. The colors were used to facilitate the location identification of each character. Illustration by Bárbara Rossi.

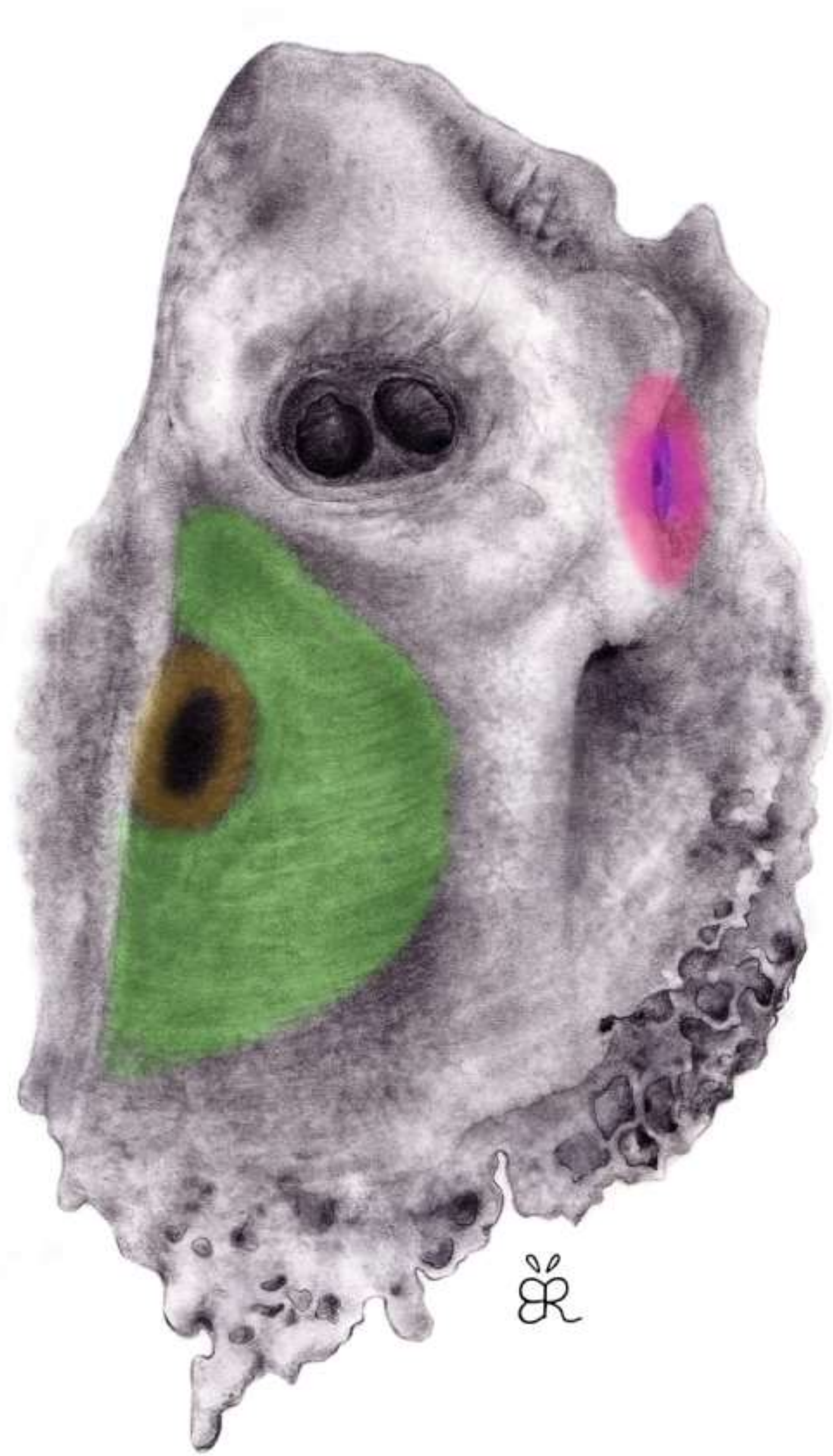

Figure 17.B) – Petrosal in dorsomedial view. Schematic illustration of a general petrosal bone of the genus *Tapirus* made by the compilation of petrosal of the species *Tapirus terrestris*, *Tapirus kabomani* and *Tapirus indicus*. The characters used in the matrix are represented above and its location are indicated by the different colors. The colors were used to facilitate the location identification of each character. Illustration by Bárbara Rossi.

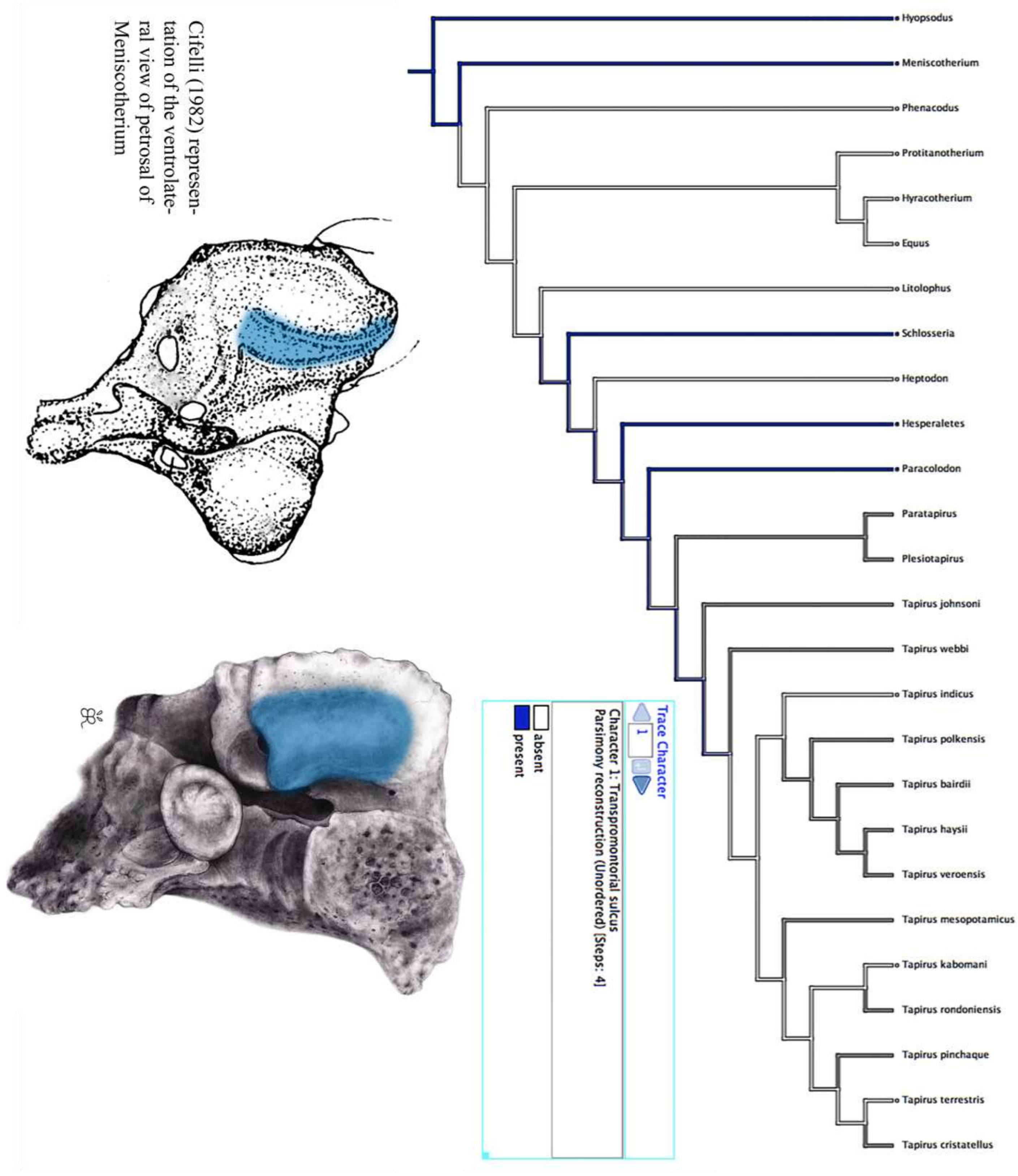

Figure 18.A) Character 1 – Transpromontorial sulcus - represented in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, by the quadrates above the branches. The character "Transpromontorial sulcus" is present in the petrosal of *Meniscotherium*.
The taxa with missing data is in GRAY and present a dot between its name and its tree branch.

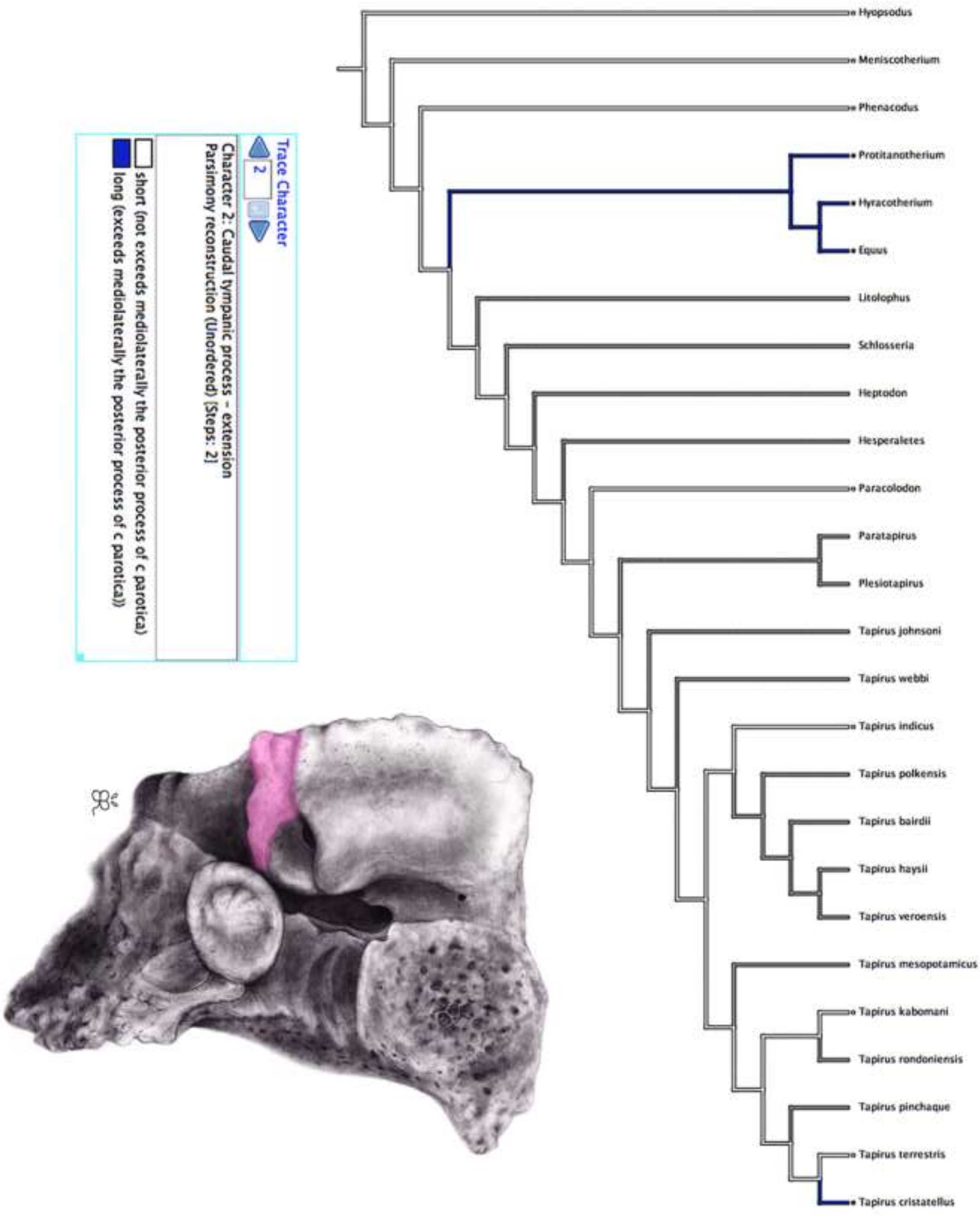

Figure 18.B) Character 2 – Caudal tympanic process (extension) **-** represented in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, by the quadrates above the branches. The character " Caudal tympanic process (extension)" is short in the illustration.
The taxa with missing data is in GRAY and present a dot between its name and its tree branch.

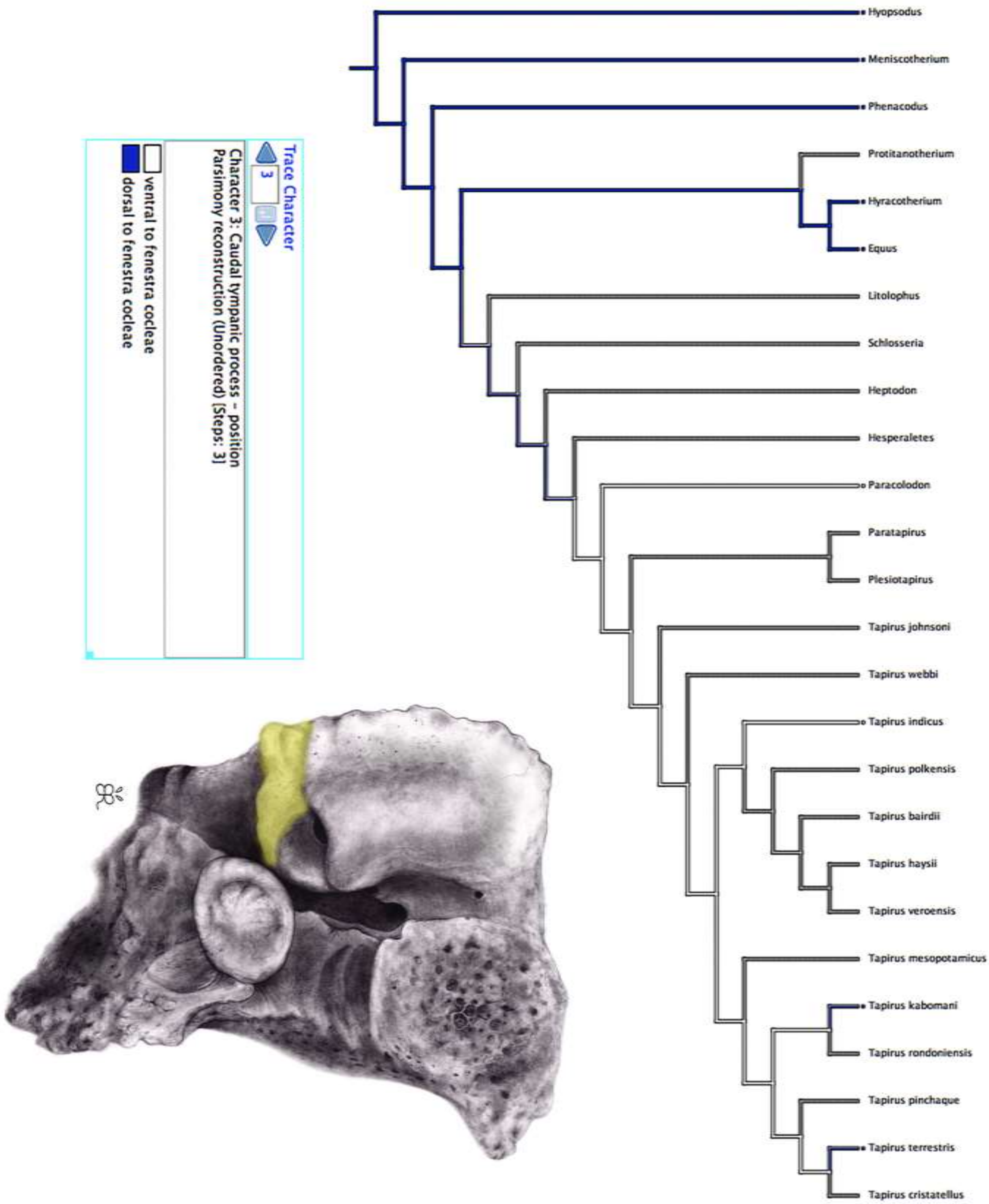

Figure 18.C) Character 3 – Caudal tympanic process (position) - represented in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, by the quadrates above the branches. The character " Caudal tympanic process (position)" is dorsal in the illustration.
The taxa with missing data is in GRAY and present a dot between its name and its tree branch.

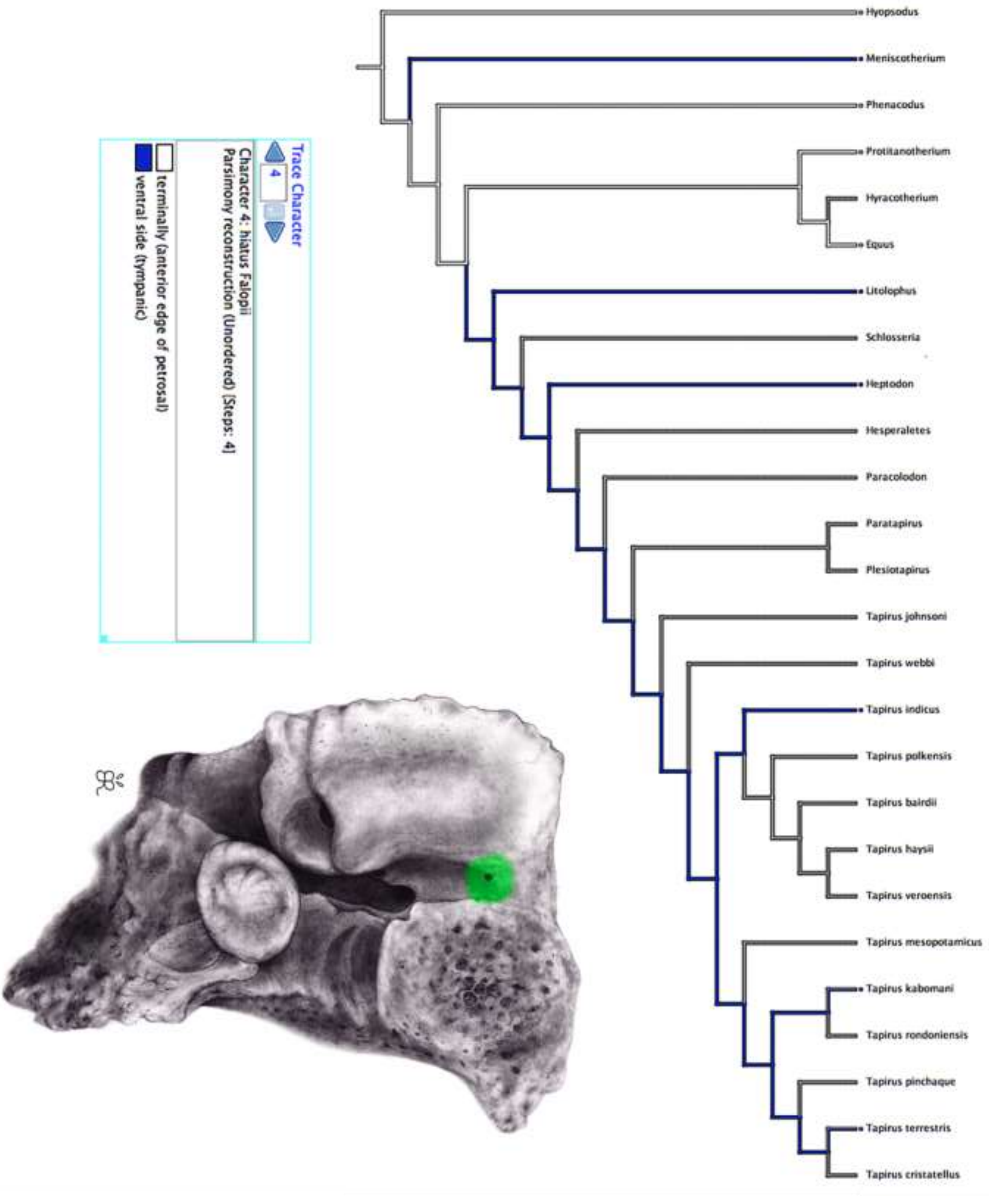

Figure 18.D) Character 4 – Hiatus Falopii - represented in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, by the quadrates above the branches. The character " Hiatus Falopii " is ventral in the illustration.
The taxa with missing data is in GRAY and present a dot between its name and its tree branch.

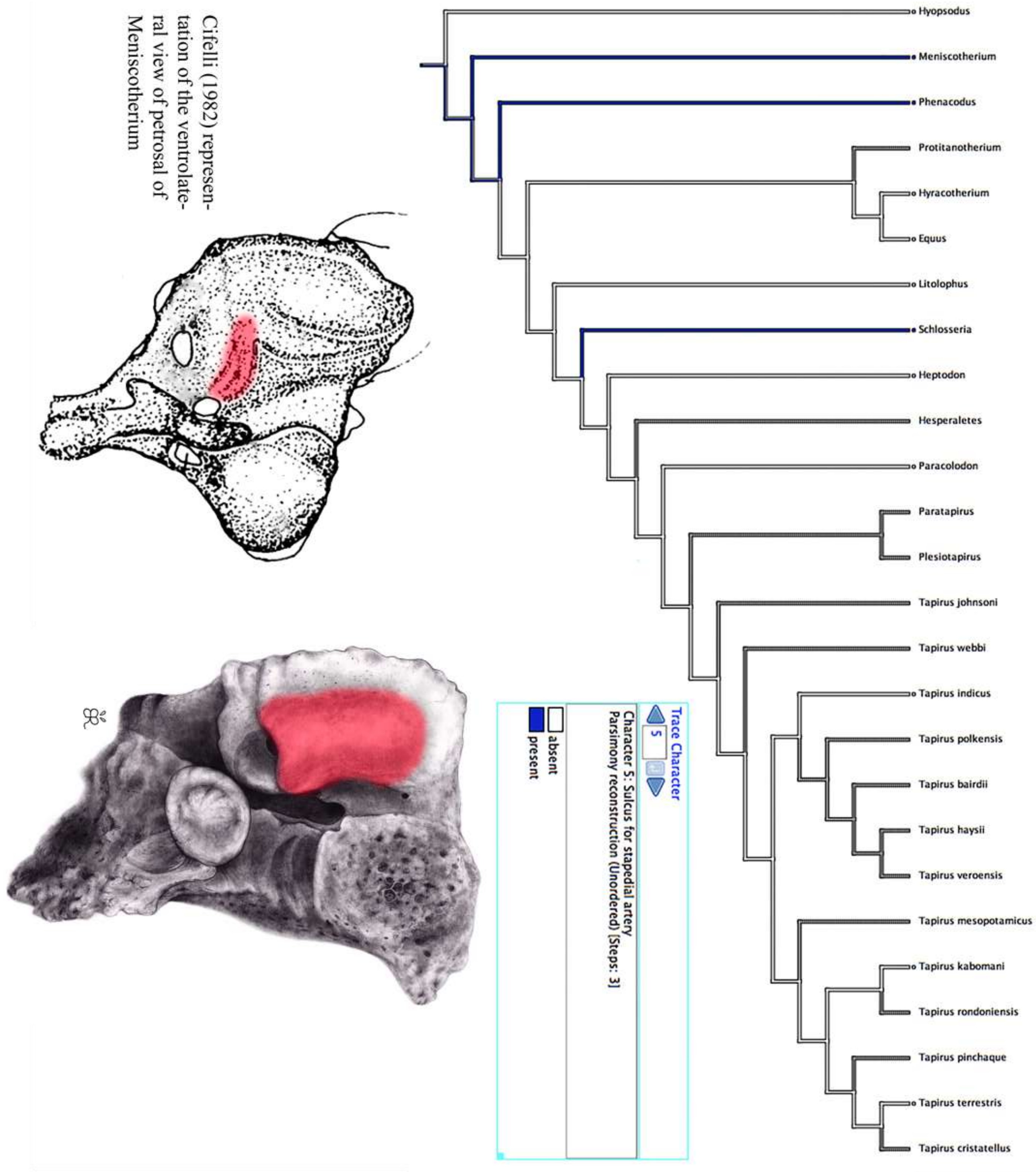

Figure 18.E) Character 5 – Sulcus for stapedial artery - represented in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, by the quadrates above the branches. The character "Sulcus for stapedial artery" is present in the petrosal of *Meniscotherium*.
The taxa with missing data is in GRAY and present a dot between its name and its tree branch.

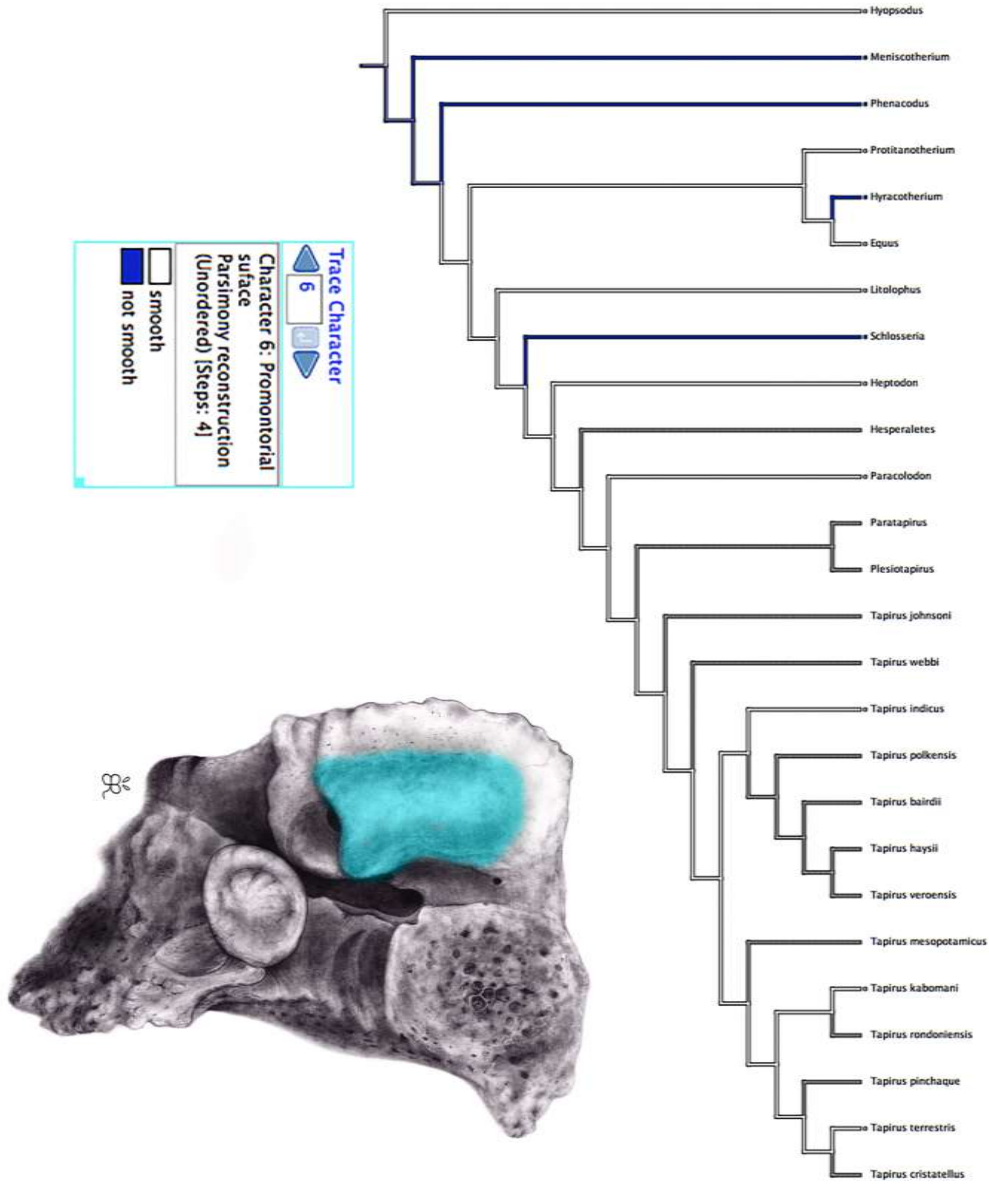

Figure 18.F) Character 6 – Promontorial surface - represented in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, by the quadrates above the branches. The character "Promontorial surface" is smooth in the illustration.
The taxa with missing data is in GRAY and present a dot between its name and its tree branch.

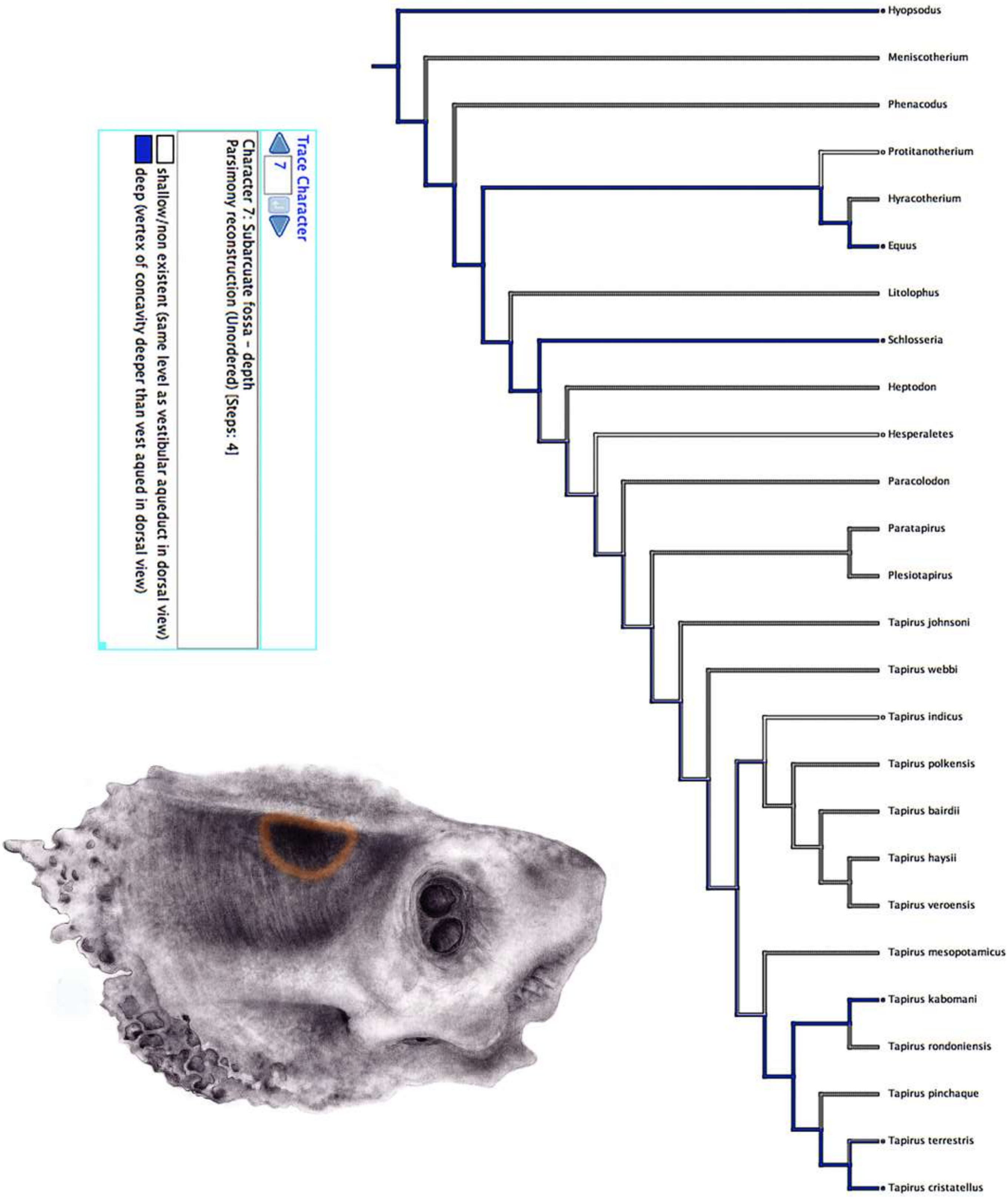

Figure 18.G) Character 7 – Subarcuate fossa (depth) - represented in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, by the quadrates above the branches. The character "Subarcuate fossa (depth)" is deep in the illustration.
The taxa with missing data is in GRAY and present a dot between its name and its tree branch.

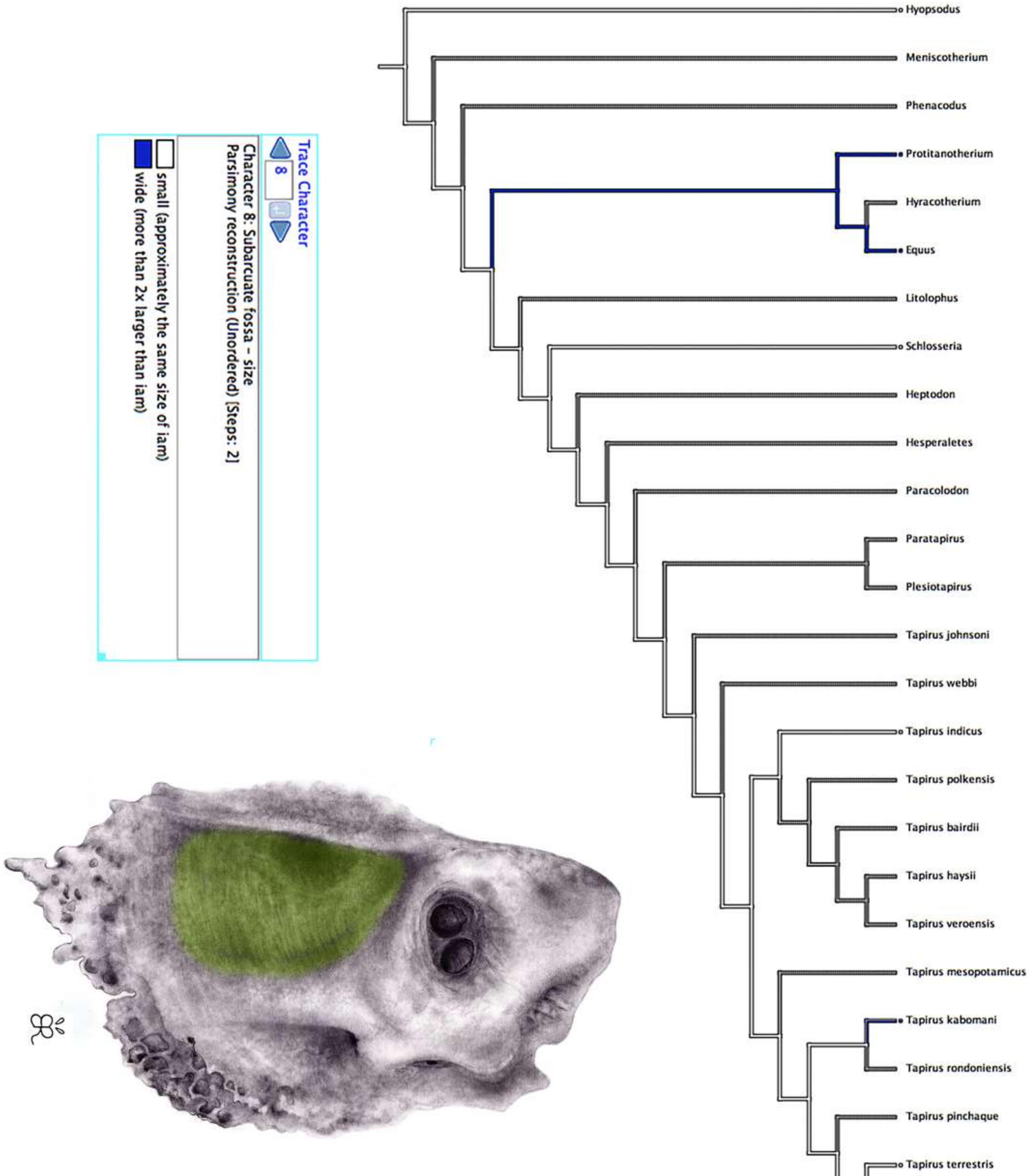

Figure 18.H) Character 8 – Subarcuate fossa (size) - represented in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, by the quadrates above the branches. The character "Subarcuate fossa (size)" is wide in the illustration.
The taxa with missing data is in GRAY and present a dot between its name and its tree branch.

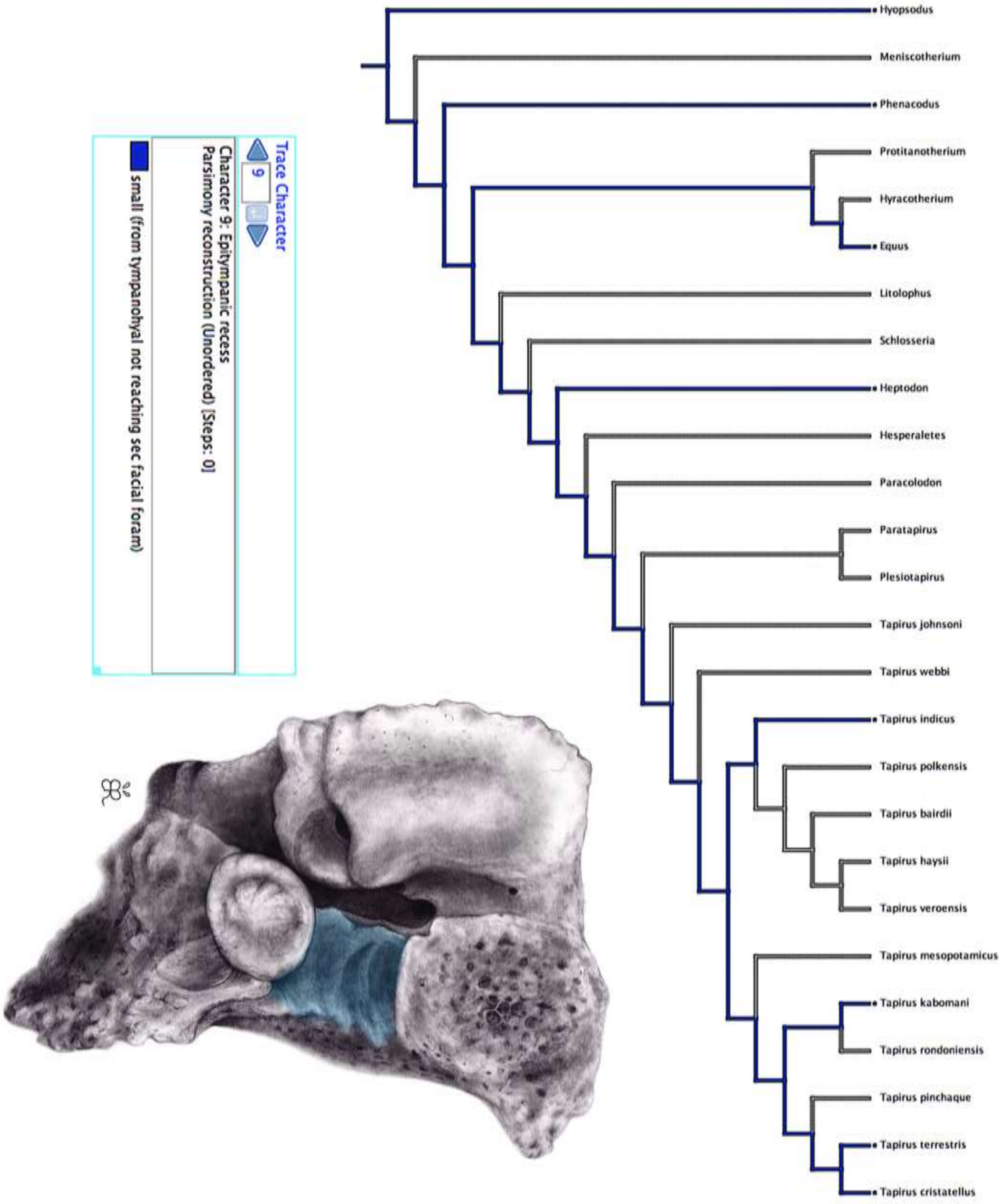

Figure 18.I) Character 9 – Epitympanic recess - represented in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, by the quadrates above the branches. The character "Epitympanic recess" is small in the illustration.
The taxa with missing data is in GRAY and present a dot between its name and its tree branch.

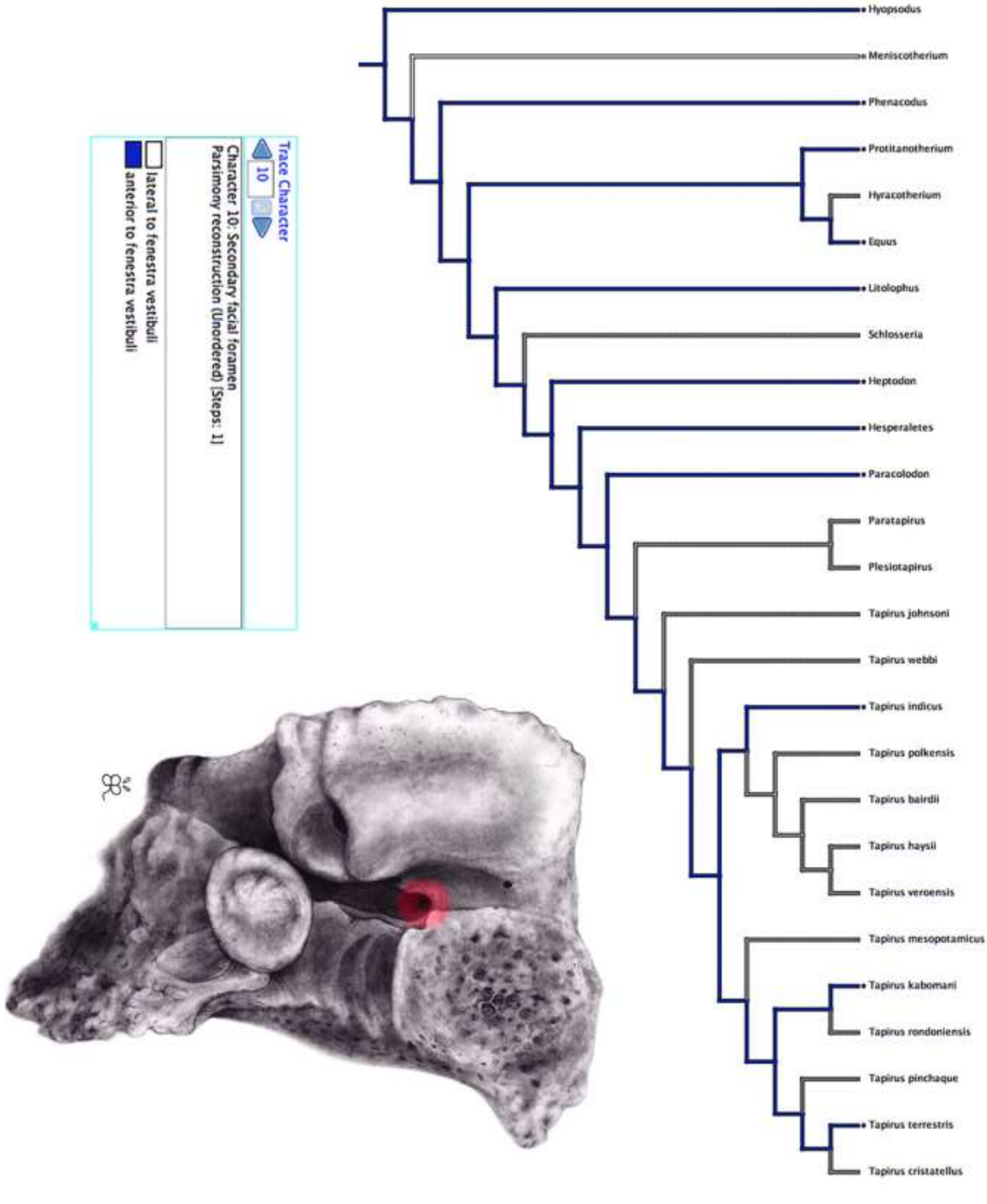

Figure 18.J) Character 10 – Secondary facial foramen - represented in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, by the quadrates above the branches. The character "Secondary facial foramen" is anterior to fenestra vestibuli in the illustration.
The taxa with missing data is in GRAY and present a dot between its name and its tree branch.

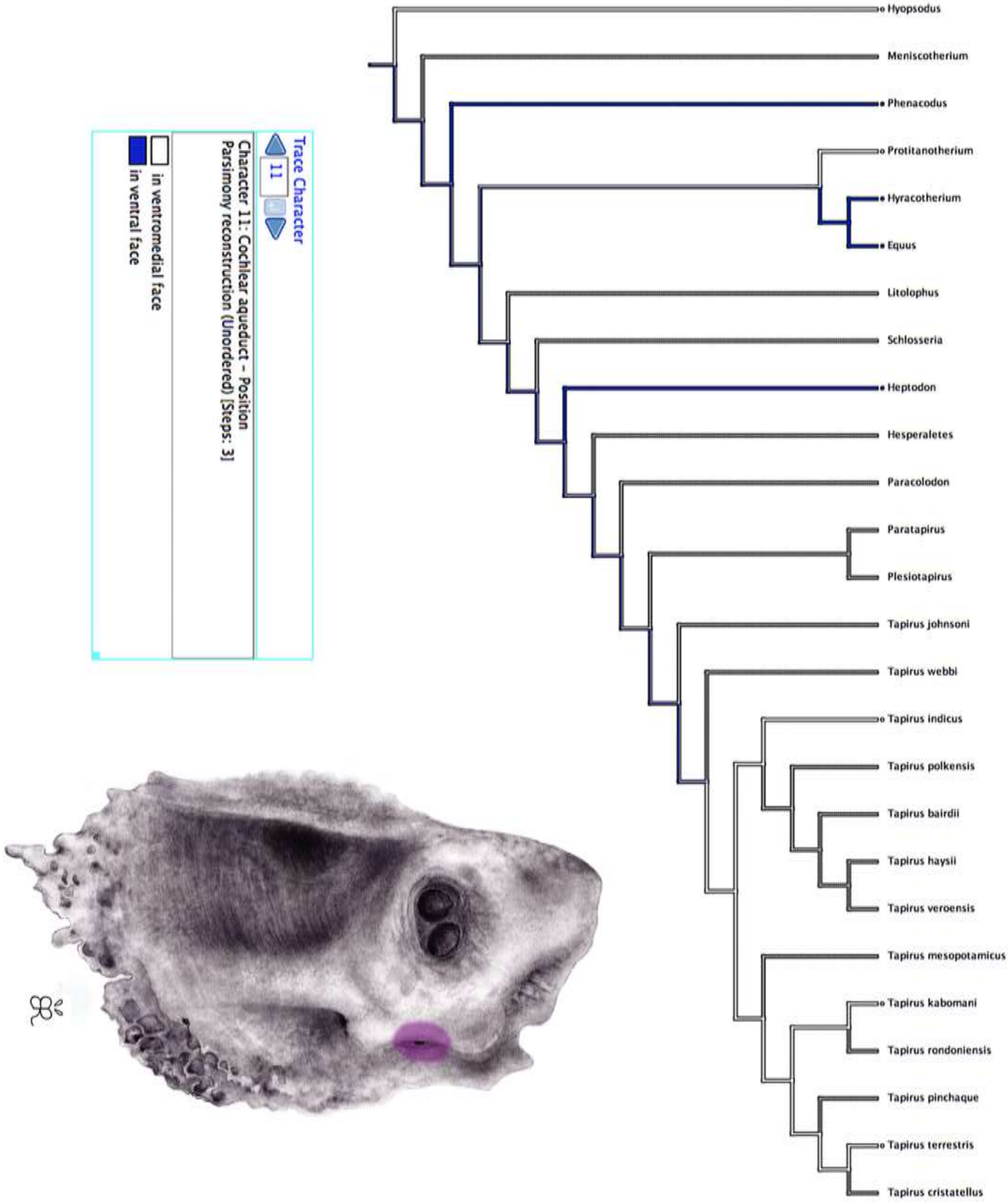

Figure 18.K) Character 11 – Cochlear aqueduct (position) - represented in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, by the quadrates above the branches. The character "Cochlear aqueduct (position)" is in ventromedial face in the illustration. The taxa with missing data is in GRAY and present a dot between its name and its tree branch.

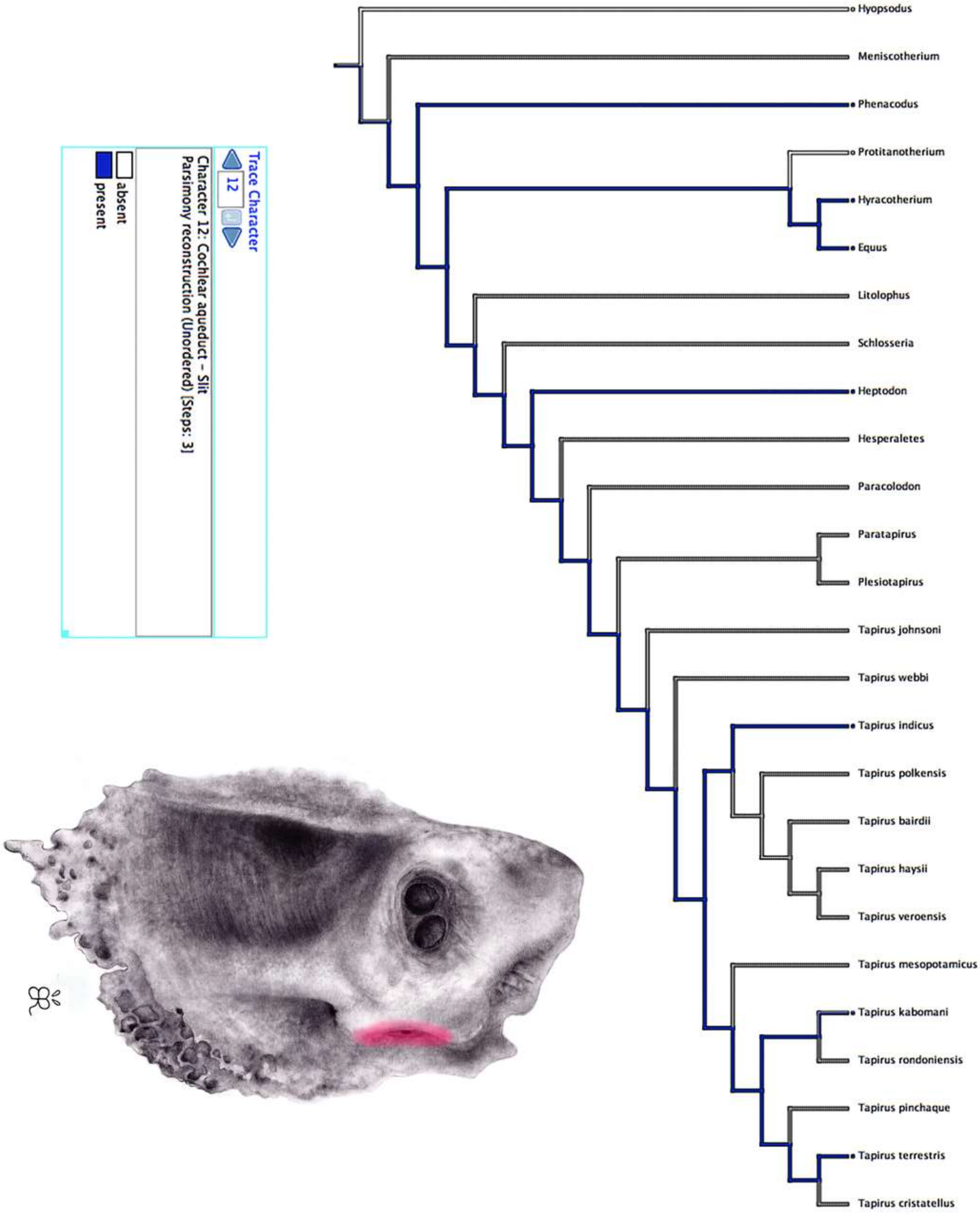

Figure 18.L) Character 12 – Cochlear aqueduct (slit) - represented in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, by the quadrates above the branches. The character "Cochlear aqueduct (slit)" is present in the illustration.
The taxa with missing data is in GRAY and present a dot between its name and its tree branch.

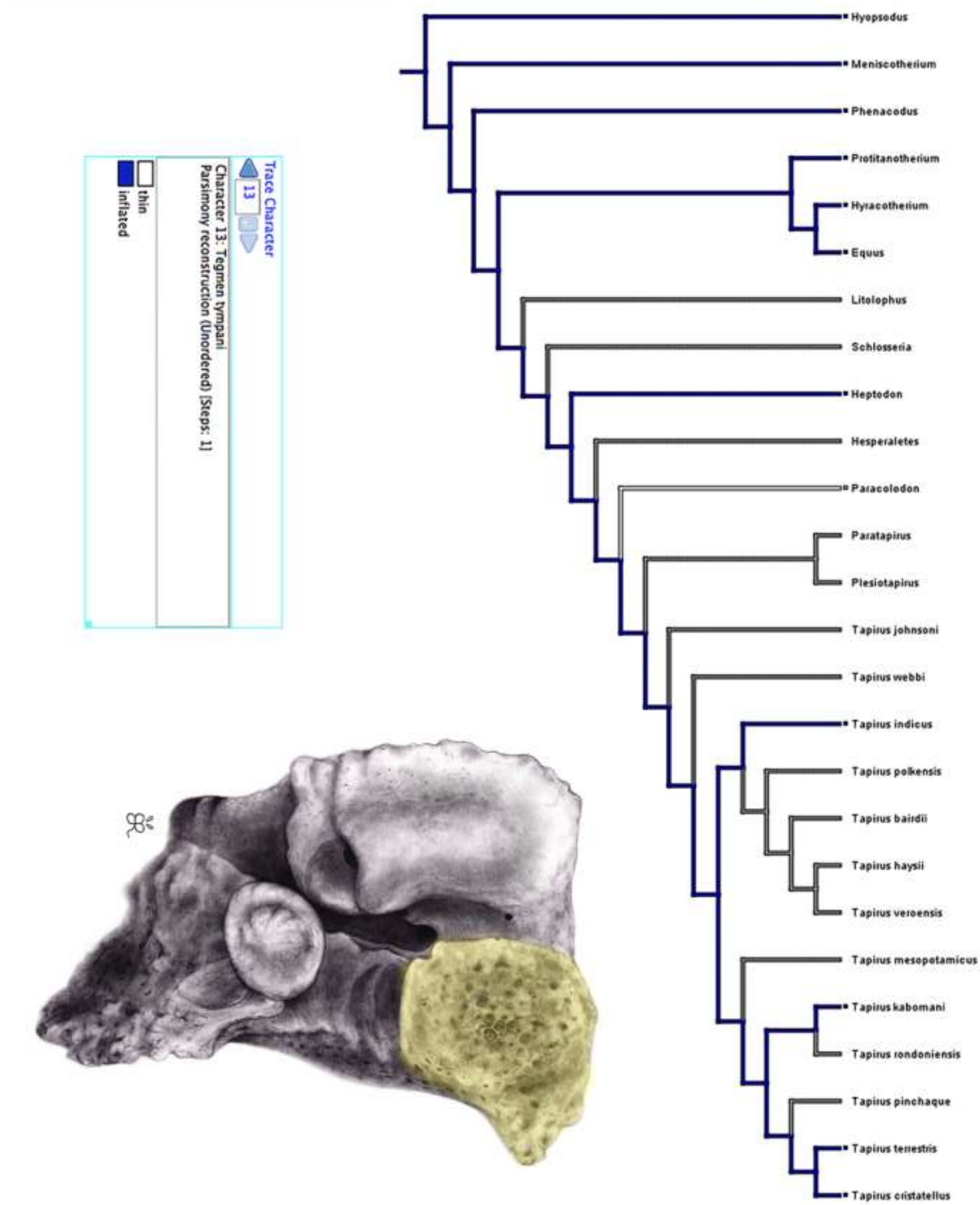

Figure 18.M) Character 13 – Tegmen tympani - represented in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, by the quadrates above the branches. The character "Tegmen tympani" is inflated in the illustration.
The taxa with missing data is in GRAY and present a dot between its name and its tree branch.

In the two additional analysis made in this study, the petrosal data didn't alter the topology of Cozzuol et al. (2013, 2014) (see Cozzuol et al., 2013, 2014). This result will be discussed in the next session of this study, in "Discussion".

5- DISCUSSION

5.1 Anatomic description of the petrosal of the genus *Tapirus*

Most of the structures described in the petrosal of *Tapirus* are variable in the same species. Because of that, it is difficult to differentiate with certainty one species from other using only the petrosal. However, there are some patterns, as the tendency of a V-shape epitympanic wing of *T. terrestris* with a more regular border and a smooth promontorium surface (Fig. 13.A), which is shared by the specimens of this species. But it is worth to mention that, despite some specimens of *T. kabomani* also showing a V-shape epitympanic wing, none of them present the pattern of such a smooth promontorium surface plus more regular epitympanic wing border, as seen is most specimens of *T. terrestris* (Fig. 14.A).

Among the genus *Tapirus*, the petrosal presents a similar size. The size of all the analyzed petrosal bone is very similar, even with the considerable size variation of skull and body size between species. *Tapirus indicus*, as mentioned in the "Introduction" session, is the largest of the five extant tapirs, but its petrosal, although the most robust and square-shaped, have similar size to the petrosal of *Tapirus kabomani*, the smallest species (Fig. 13, 14, 15). Besides that, all *Tapirus* present the promontorium flattened at some level and without any trace (sulcus and/or grooves) of arteries. The arrangement of the fenestra cochlea and fenestra vestibuli, and the sulcus that extends from fenestra vestibuli to facial sulcus, are similar in all specimens. Among the most variable characteristics of *Tapirus*, the format of the aperture of the internal acoustic meatus vary from circular to elliptical, and from regular to irregular, with part of its border extending like a bridge (Fig. 13.A, 14.A, 15.A). The subarcuate fossa is also very variable both in size and depth. In this character, as seen in hiatus Falopii position, it is possible to see a variable gradient of character states among the tapir petrosals (Fig. 13.B, 14.B, 15.B). The tegmen tympani vary not only in how much it extends ventrally but also in ossification degree (independently of the age of the animal, and varying from very dense to all pneumatized - almost hollow) (see Fig. 14.A, MN 57069). And, at last, the extension of the crista parotica and its posterior process is very different among the specimens, and can be minimum, as a small irregularity in crista parotica surface, or long, meeting the process of the crista interfenestralis.

5.2 Character mapping

On the choice of the thirteen characters in the matrix (Table1), Cifelli (1982) stated that the characters selected were previous mentioned in the literature as significant characters to investigate systematic variation inside perissodactyla and related groups, and also might be useful to study groups inadequately treated before or even not treated. Cifelli's (1982) matrix was used as base for this study, in the first place, because it was the only matrix using morphological data of petrosal in Perissodactyla. There are other morphological matrices for Perissodactyla, some of them composed also or entirely by cranio-dental characters, as in Colbert (2006) and Thewissen and Domning (1992). However, only few features of the petrosal are used as characters, like its position in the cranium and/or its relation with other cranial structure. Also, as expected, since in some analyzed fossils the petrosal is partially missing, there are some characters that could not be observed. To make them comparable with the remaining material and well documented petrosal included here, maximizing the quantity and quality of the results obtained from the analysis is a difficult task and demands a careful choice of characters to be included, always questioning if the chosen set of characters could reflect the evolution of a structure within the group, as well as the evolution of the group itself. The characters of Cifelli (1982) allowed this analysis, since they were primarily used to study only extinct taxa and could be easily found also in the petrosal of the living taxa included in the present study. According to the applicability of Cifelli's characters and states of character in the new set of taxa incorporated here, some characters were excluded or modified in the matrix (see below the complete discussion about each excluded, modified and maintained character). The states of character of the taxa with missing data were predicted by parcimony in Mesquite.

As mentioned previously in this study, unlike Perissodactyla, there are many studies focused on the inner ear of Artiodactyla. Many of them include matrices, as seen in Luo and Gingerich (1999) for the evolution of the basicranium of Mesonychia to Cetacea, Spaulding (2009) for Cetacea, Orliac (2012) for Suoidea and O'Leary (2010) for Artiodactyla in general. However, those matrices present more characters that cannot be traced in the majority of the specimens included in this study, most because the information about the characters was not available in the description and/or in the photo of the petrosal from the literature. Also, those matrices were compiled to study the evolution of Artiodactyla and related groups that occurred in a totally different context of that for Perissodactyla, using characters and characters states comparable to study the evolutive history of Artiodactyla (the ear of cetaceans, for example, is modified to hearing e balancing in aquatic environment). However, the use of those characters used in Artiodactyla studies to discuss very well documented groups and/or recent Perissodactyla groups can possibly yield interesting conclusions, as the resulting matrix will be more detailed and complete, and as already tested, the petrosal is an important source of phylogenetic information in artiodactyls.

The states of character are discussed in the following text and shown in the following figures. Each character were colored in the figures by the colors previuos used on the matrix (Table 2), in the schematic illustration (Fig. 17) and in the results figures (Fig. 18).

The "Transpromontorial sulcus" (Fig. 19.A) was modified from the "Promontorial sulcus" character of Cifelli (1982) and referred in the same manner as in *Tapirus* petrosal description, following O'Leary (2010) nomenclature. According to MacIntyre (1972), the presence of the 3 promontorial sulcus (the promontorial artery sulcus, sulcus for stapedial artery and medial carotid sulcus) is one of the primitive trissulcate petrosal patterns of all eutherians. In all ungulates it would have been lost, except for primitive Artiodactyla (Coombs & Coombs, 1982; Novacek and Wyss, 1986), and it would be absent in the Artiodactyla + Perissodactyla common ancestor (O'Leary, 2010). In that way, Wible (1986) and Bai et al. (2017) observed that the promontorium of Perissodactyla usually have a smooth surface without any of those sulci. However, as seen in O'Leary (2010) study in which the sulcus (or groove) is observed in, at least, one representative of all the major artiodactyl clades, there are some perissodactyl taxa that also have this character, also not corroborating with the statement that the presence of transpromontorial sulcus would be a primitive state.

The discussions about the presence or absence of those 3 promontorial sulcus and how its distribution varies among the eutherians are also due to the fact that in some cases more than one artery runs through the promontorium by the same sulcus (as seen in Holbrook, 1999), which may complicate the issue. However, it is important to mention that soft tissues as arteries may or may not leave its marks on the bone, and because of that, the absence of one or more sulcus on the promontorium surface cannot be treated as synonymy of the absence of soft structure (Wible, 1986; O'Leary, 2010). Therefore, in this study, only the sulcus of promontorium artery was considered as transpromontorial sulcus and the position of the sulcus in the promontorium is not discussed (as seen in Bai et al. 2017 regarding *Paracolodon*). The transpromontorial sulcus is present only in the extinct taxons *Hyopsodus*, *Paracolodon*, *Schlosseria*, *Hesperaletes* and *Meniscotherium*. Tracing the most parsimonious way, *Hyopsodus* and *Meniscotherium*, the two most basal genera on this phylogeny, retains this sulcus. However, immediately after *Meniscotherium*, the ancestral of *Phenacodus* and all the other taxa had lost the sulcus. In this way, both *Paracolodus* and *Schlosseria*, which also possess the sulcus, would have acquired it independently. The petrosal of *Tapirus cristatelus* is broken and the promontorium is one of the missing structures. However as none other known *Tapirus* petrosal present the transpromontorial sulcus, it was predicted that the transpromontorial sulcus is also absent in *T. cristatellus*.

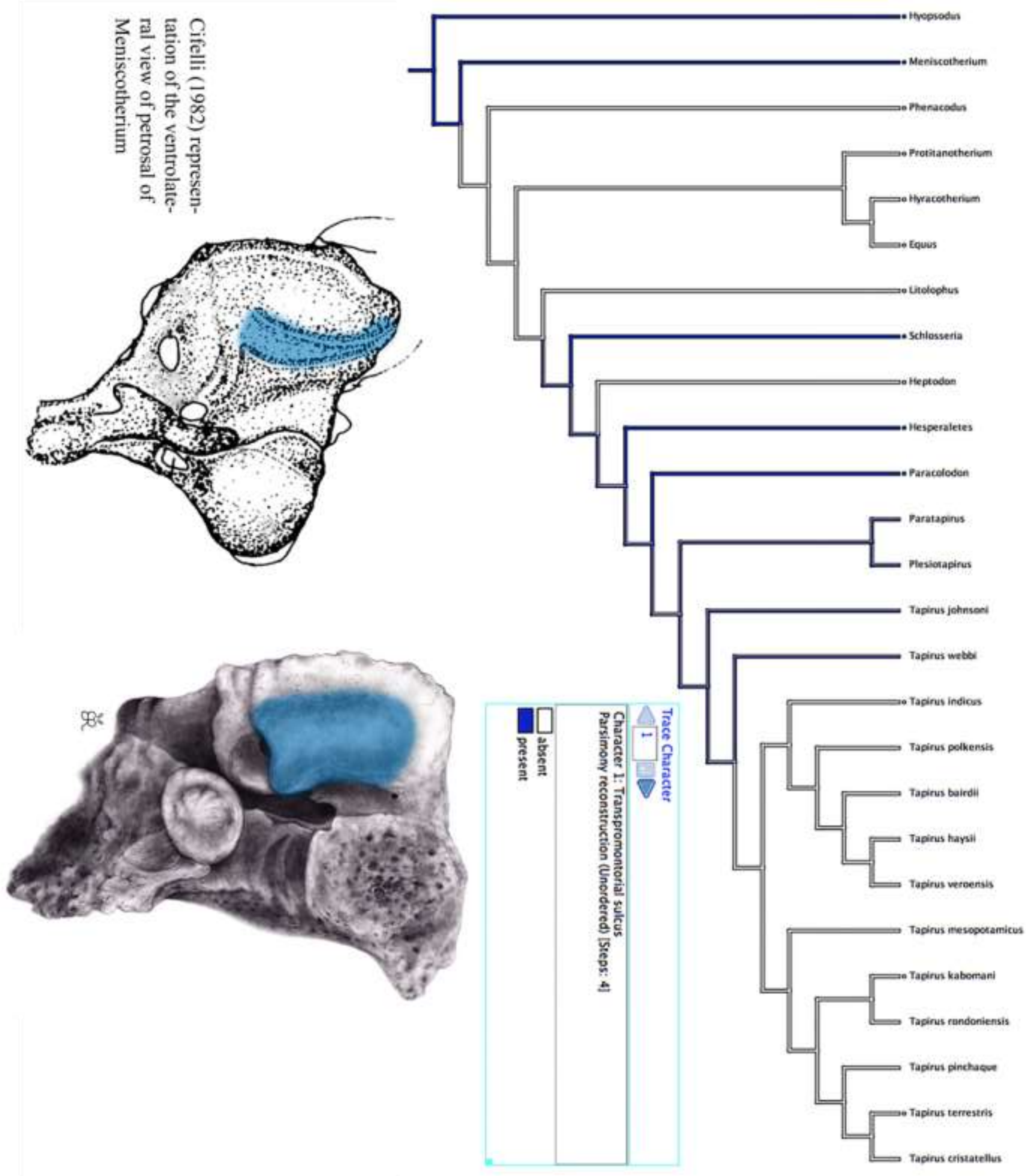

Figure 19. A) Character 1 – Transpromontorial sulcus – distributed in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, and predicted in the taxa with missing data.

The "Caudal tympanic process" character (Fig. 19.B) is modified from the "Tympanic process" of Cifelli's (1982) matrix. In Cifelli (1982), it is a single character (it was not separated in two as it was made in the present study), with four character states and each state of character present two types of information, apparently not related one to another (long, ventral; short, dorsal; long, dorsal; absent). Since these character states seems to be not related, I separated this character in two, according to the information that each one brings: extension and position. The information about its presence or absence was not included in the matrix because all the taxa considered in this study present the caudal tympanic process. According to Cifelli (1982), it was primitively short, and when it is long, it can reaches the posterior process of crista parotica, fusing to it and creating a bone bridge ventral to the facial sulcus. The long caudal tympanic process, exceeds mediolaterally the posterior process of crista parotica (see the dotted circle in fig. 19.B), and is present only in the representatives of the Hippormorpha lineage - *Protitanotherium*, *Hyracotherium* and *Equus* - and in *Tapirus cristatellus*. There are no information about this character for *Heptodon, Schlosseria, Litolophus* and *Hesperaletes*, but it is parsimoniously predicted that these taxa didn't had it either. All the other taxa have a short caudal tympanic process, not exceeding mediolaterally the posterior process of crista parotica (see the dotted circle in fig. 19.B). *T. cristatellus* does not has the posterior process of crista parotica, the structure used as reference to this character. However, as this process extends laterally from the crista parotica and the caudal tympanic process of *T. cristatellus* extends far away the crista parotica itself, the caudal tympanic process of this taxon would also extend far away from the posterior process of crista parotica if it had this later structure. It seems more likely that *T. cristatellus* probably have acquired this feature independently.

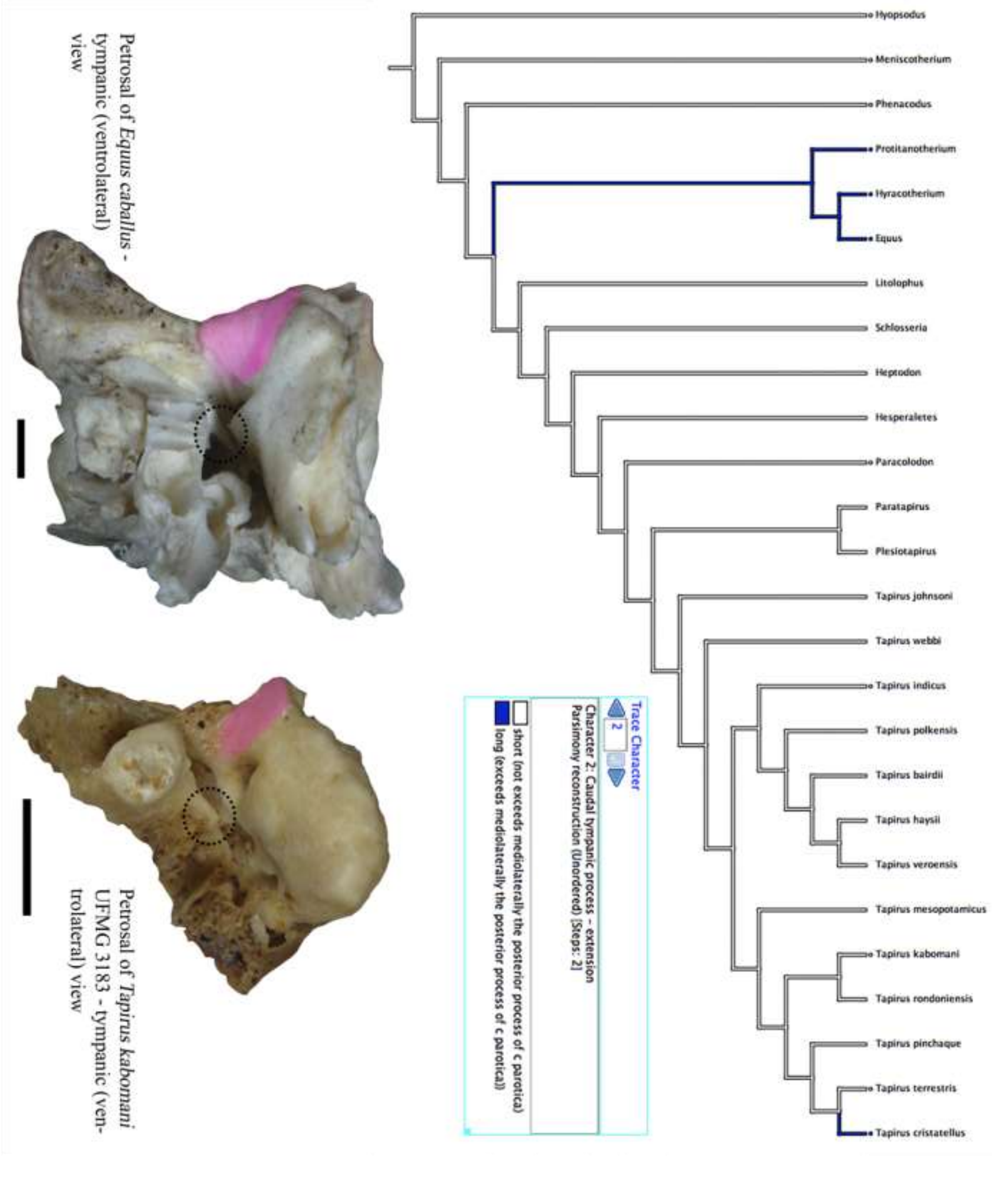

Figure 19.B) Character 2 – Caudal tympanic process (extension) – distributed in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, and predicted in the taxa with missing data. The posterior processo of crista parotica is demonstrated by the dotted black circle.

The position of the caudal tympanic process (Fig. 19.C) is related to its "ventral" or "dorsal" development in relation to fenestra cochleae. When the caudal tympanic process is ventral to the fenestra cochleae, it obstructs it partially or completely in posterior view. However, the fenestra cochleae is fully seen when the caudal tympanic process is dorsally positioned. According to Cifelli (1982), the ventral position of the caudal tympanic process, formerly considered a derived state of marsupials, is also found in some eutherians. Therefore, it could be a primitive character state. In the matrix of the present dissertation the position of the caudal tympanic processes of *Heptodon*, *Protitanotherium*, *Litolophus*, *Hesperaletes*, *Schlosseria* and *T. cristatellus* are unknown. *Paracolodon* and *T. indicus* presents its structure located ventrally to the fenestra cochleae. On the other hand, in *Hyopsodus*, *Hyracotherium*, *Meniscotherium*, *Phenacodus* and *Equus*, it is dorsal to the fenestra cochleae. Finally, at last *Tapirus terrestris* and *T. kabomani* present both states of character. The absence of information about this character in some taxa makes it difficult to be traced in the phylogeny used here, and consequently to predict the character state in taxa with missing data based on character mapping. However, according to the analysis, it is possible to infer that the more basal taxa in this phylogeny presented the caudal tympanic process dorsal to the fenestra cochleae and in some moment later it turned ventral, as seen from *Paracolodon* onwards until the polymorphic *Tapirus*.

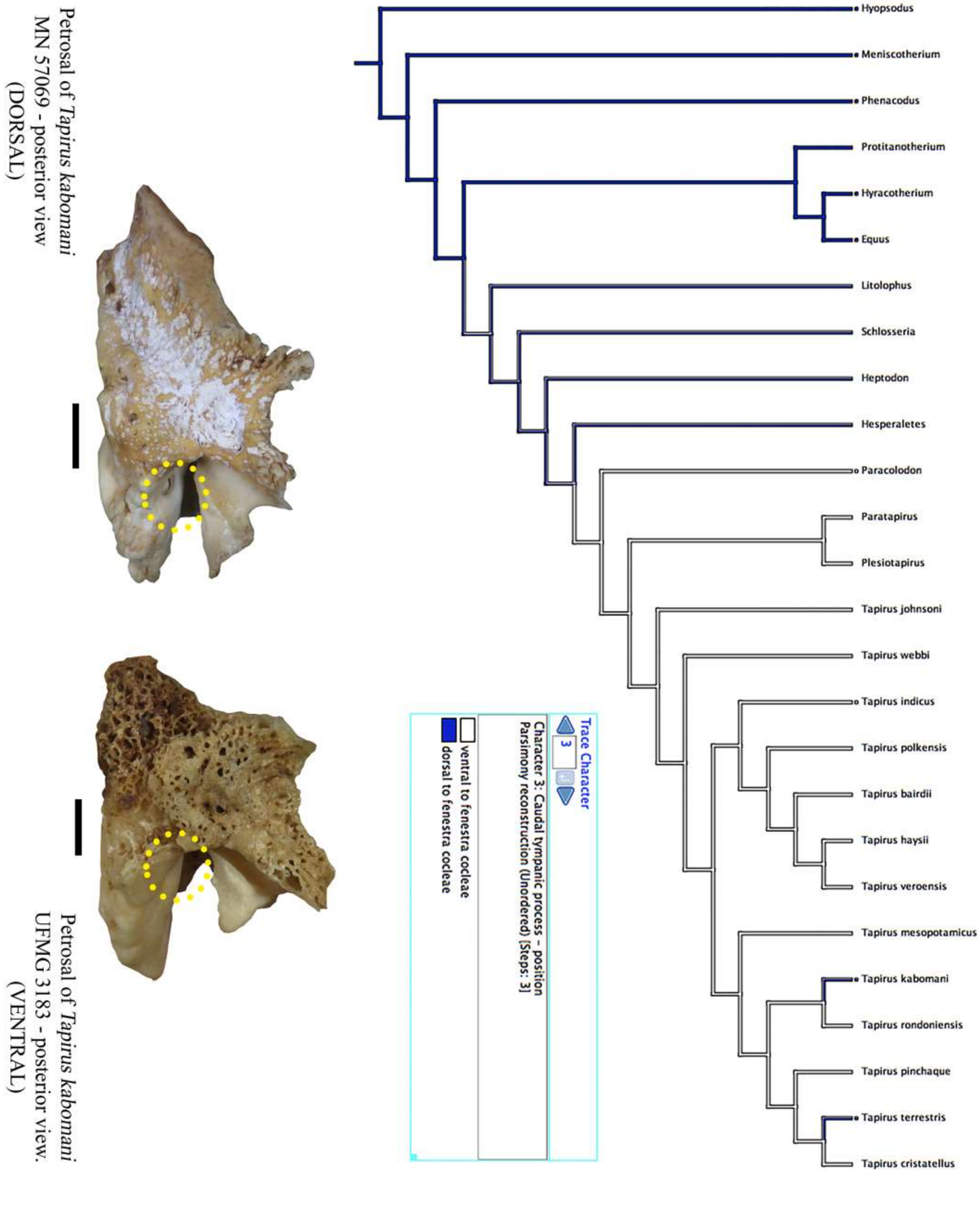

Figure 19. C) Character 3 – Caudal tympanic process (position) – distributed in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, and predicted in the taxa with missing data.

The "hiatus Falopii" (Fig. 19.D) is related to its position in the petrosal, terminally in the anterior edge of petrosal or ventral in the tympanic face of the petrosal (inside the fossa for tensor tympani). According to Cifelli (1982), the later character state is usually seen in early perissodactyls, but it is not in derived mammals. In early equoids and tapiroids it is generally ventral and there are good chances of it being a synapomorphy of some high level of group of Perissodactyla. However, Bai et al. (2017) mentioned that the hiatus Falopii of *Tapirus* was located anterior to the tegmen tympani, that is terminally in the anterior edge of petrosal. In the matrix, the character state of *Paracolodon*, *Schlosseria*, *Hyracotherium*, *Hesperaletes* and *T. cristatellus* is unknown. *Heptodon*, *Litolophus*, *Meniscotherium* and *T. indicus* present a ventrally located hiatus Falopii, while *Equus*, *Phenacodus*, *Protitanotherium* and *Hyopsodus* have a terminally located one. *Tapirus terrestris* and *Tapirus kabomani* have both character states. According to the matrix, as *Phenacodus* and *Protitanotherium* present a terminally located hiatus Falopii, *Meniscotherium* probably acquired a ventrally located hiatus Falopii independently. Although there is no information about this character in *Hyracotherium,* as *Equus* and *Hyopsodus* present a terminally located hiatus Falopii, it is parsimoniously understood that all Hippomorpha group share this character state, contradicting Cifelli's statement. However, except for the polymorphic taxa *Tapirus terrestris* and *Tapirus kabomani*, all the others tapiromorph representatives would parsimoniously present a ventral hiatus Falopii, as mentioned by Cifelli (1982).

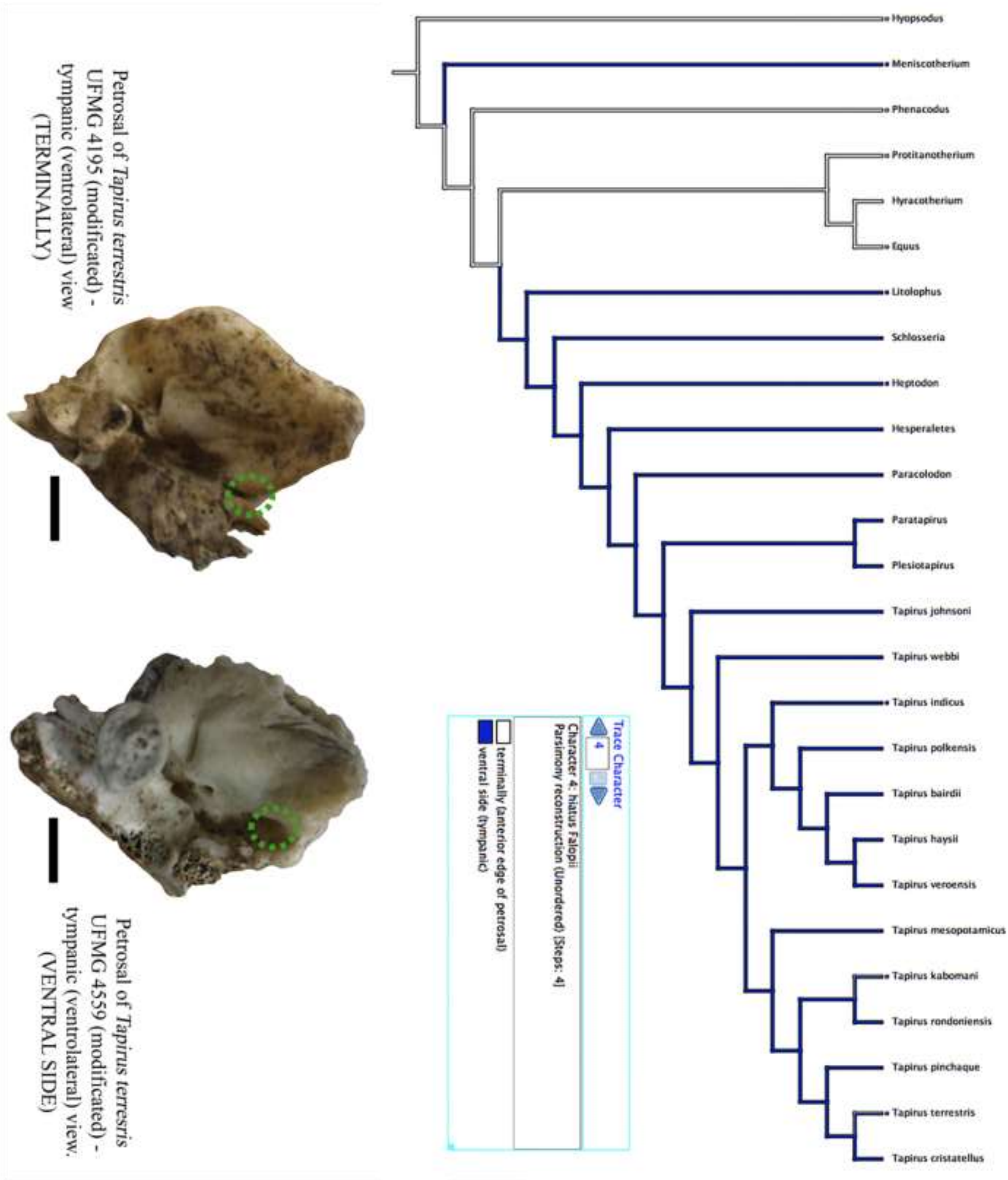

Figure 19. D) Character 4 – Hiatus Falopii – distributed in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, and predicted in the taxa with missing data.

The sulcus for stapedial artery (Fig. 19.E) is one of the 3 previous mentioned primitive promontorial sulcus of eutherians (MacIntyre, 1972). Cifelli (1982) called this character "Stapedial sulcus", but here I followed the nomenclature of O'Leary (2010). In Cifelli (1982), *Hyopsodus* was apparently the only condylarthra without the stapedial sulcus. According to him, perissodactyls and other mammals later reduced or lost the stapedial artery, so that the sulcus would have been lost either. According to Wible (1987) the presence of the stapedial artery is a homoplastic character since it was acquired independently many times among eutherians, and its absence could put Cetacea, Perissodactyla and other ungulates together, separating Artiodactyla from them, since its Early Tertiary representatives present the sulcus. According to Geisler & Luo (1998) the sulcus was absent in extant Perissodactyla, so as in extant Artiodactyla and Cetacea. O'Leary (2010) analysis pointed to the absence of the sulcus as a synapomorphy of Artiodactyla and Perissodactyla. In the matrix, the character state of the sulcus for stapedial artery of *Protitanotherium, Hesperaletes* and *T. cristatellus* is unknown. The character cannot be verified in *T. cristatellus,* since its entire promontorium was broken and missing. In *Heptodon*, *Hyopsodus*, *Paracolodon*, *Litolophus*, *Hyracotherium*, *Equus* and *Tapirus* the sulcus is absent. The sulcus is found only in *Phenacodus*, *Meniscotherium* and *Schlosseria*, corroborating the hypothesis of a perissodactyl ancestor without sulcus for stapedial artery. It would be independently acquired three times in *Meniscotherium*, *Phenacodus* and *Schlosseria*. However, Thewissen (1990) contested Cifelli (1982) about the presence of stapedial sulcus in *Phenacodus*. According to him, the area indicated to be Cifelli's sulcus for stapedial artery is "irregular in texture and not depressed in two specimens available to him" and the sulcus is "typically smooth and depressed". Because of that, it is not safe to affirm that what Cifelli (1982) considered as sulcus for stapedial artery in *Phenacodus* was, in fact, this character.

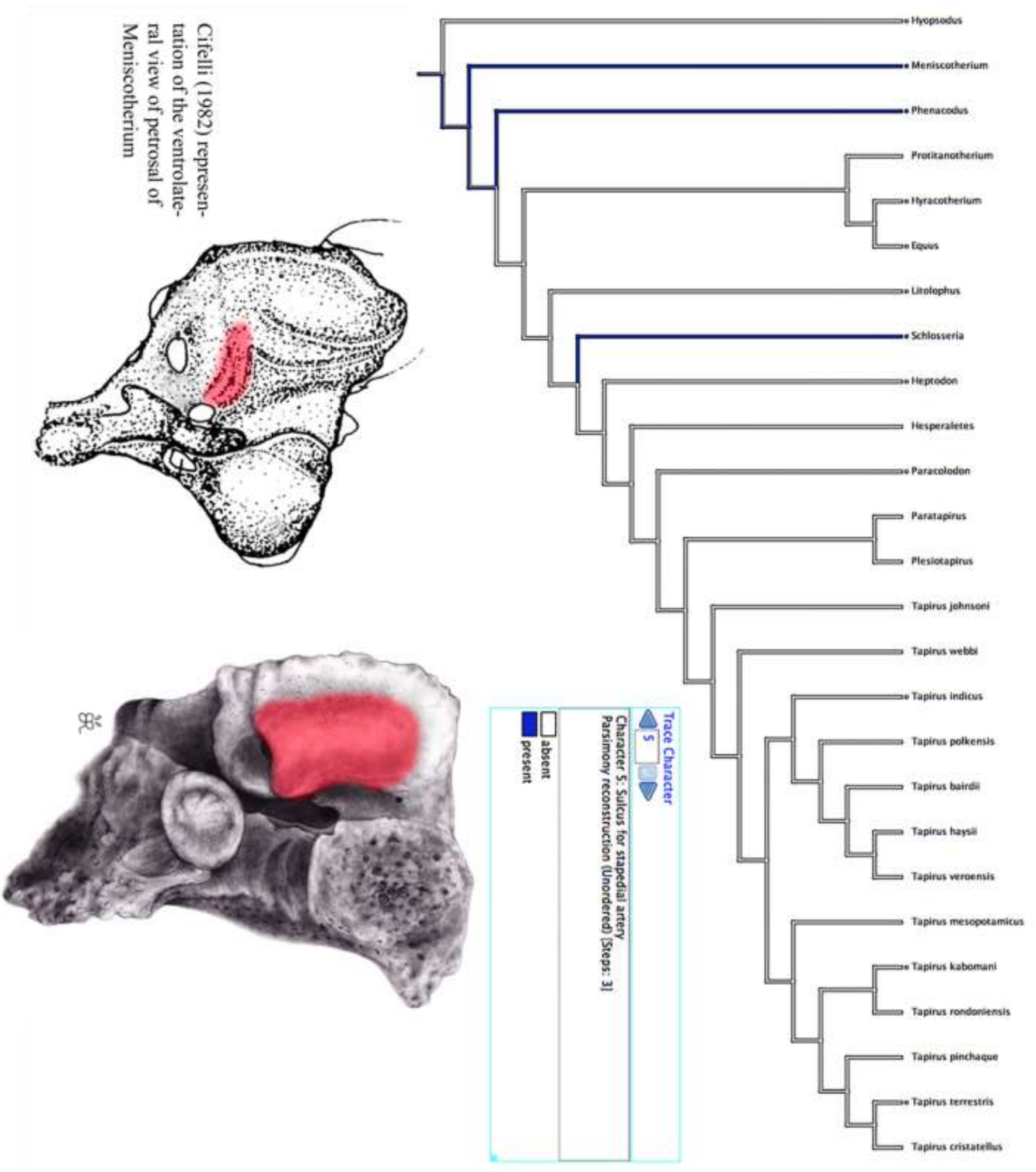

Figure 19.E) Character 5 – Sulcus for stapedial artery – distributed in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, and predicted in the taxa with missing data.

The promontorial surface character (Fig. 19.F) was used by Cifelli (1982) with that same spelling, however the states of this character was modified from smooth, rugose, ribbed and ridged to smooth or not smooth in this work. The character states were modified because it was not clear in Cifelli's and in the literature in general what is considered to be rugose, ribbed and ridged. Also, as mentioned in Wible (1986), the perissodactyls usually present a smooth-surface promontorium, without marks or grooves for arteries. However, it is important to mention that different authors consider different concepts of promontorium surface. Wible (1986) consider smooth a petrosal without any traces or marks. In turn, some taxa of Cifelli (1982), as *Hyopsodus*, present sulci on the promontorium and its surface is still considered to be smooth. Here I used the surface of the petrosal independently of the presence or absence of promontorial vessels marks. In the matrix, the promontorial surface of *T. cristatellus* is unknown, as in *Hesperaletes*, since part of the petrosal is missing. *Schlosseria*, *Phenacodus*, *Meniscotherium* and *Hyracotherium* present a not smooth promontorium surface, while all the other taxa present a smooth promontorium. The analysis of this character is emblematic, because the number of evolutionary changes needed to reach this promontorial surface scenario is the same considering an ancestor with smooth surface promontorium, as well as a not smooth surface one.

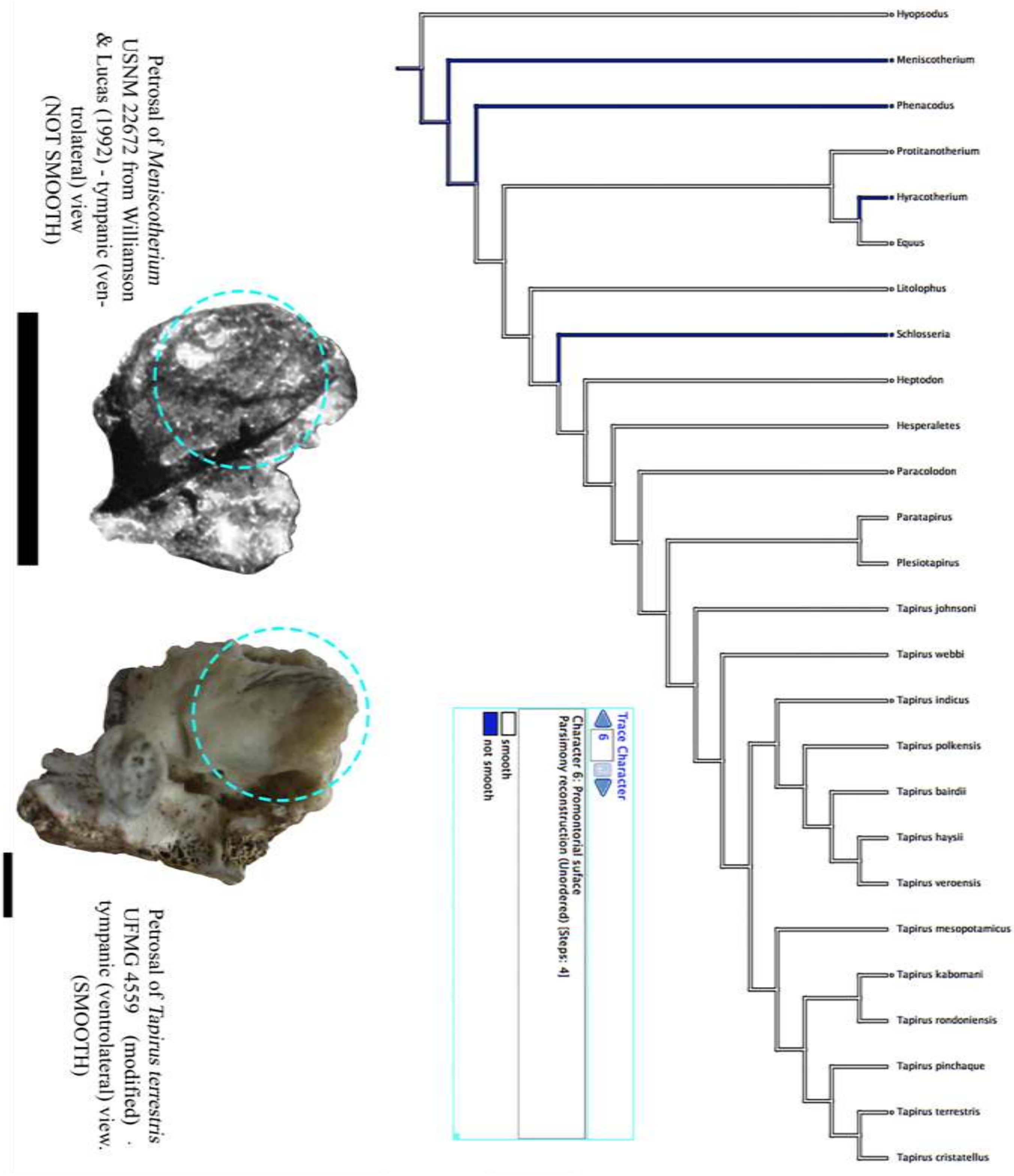

Figure 19.F) Character 6 – Promontorial surface – distributed in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, and predicted in the taxa with missing data. The petrosal UFMG 4559 was mirrored to standardize the petrosal size).

The subarcuate fossa character (Fig. 19.G), as the promontorial surface, maintain the same spelling used by Cifelli (1982), but it was separated in two different characters: the first is related to its depth - shallow or deep - and the other is related to its size - small and wide. The use of the character as Cifelli (1982) (characters states: deep, very deep and pocket, deep and pocket, absent, very shallow) can complicate the analysis, since it put together states of characters that may not be related one to another. Also, if these two categories of characters are mixed, it is not possible to understand the evolution of the character among taxa that share one of the character states, but not the other. In the present study, the absence of the subarcuate fossa was referred as non-existent and placed together with the shallow state of character because, as in O'Leary (2010), all depression was supposed to be considered and the state of absence of subarcuate fossa would be considered only when the fossa was convex, as in cetaceans. Therefore, petrosals with a non-existent subarcuate fossa would present a extremely shallow one, but not a convex one. The depth of the subarcuate fossa is related with the vestibular aqueduct, both in the cerebellar face of the petrosal. It can be shallow (same level as vestibular aqueduct in dorsal view) or deep (vertex of concavity deeper than vestibular aqueduct in dorsal view) compared one to another. However, although it is easily visualized in some taxon, this character is defined as unknown in others, mostly the fossil ones, in which the petrosal is attached to the skull and the cerebellar face, arranged within the cranial cavity, is difficult to be visualized. According to Cifelli (1982), the primitive subarcuate fossa was probably deep (MacIntyre, 1972). However, O'Leary (2010) stated that perissodactyls have a shallow subarcuate fossa. The subarcuate fossa of *Heptodon*, *Hyracotherium*, *Meniscotherium*, *Phenacodus*, *Litolophus* and *Paracolodon* are unknown. *Protitanotherium*, *Hesperaletes*, *Tapirus indicus* and *T. terrestris* have a shallow subarcuate fossa and *Schlosseria*, *Hyopsodus*, *Equus*, *T. cristatellus* and *T. kabomani* have a deep one. The character mapping points to a relation of primitiveness and derivativeness as suggested by Cifelli (1982). About its size (Fig. 19.H), the analysis was made comparing the size of subarcuate fossa to the size of the external aperture of the internal acoustic meatus. In this way, only *Protitanotherium*, *Equus* and *T. terrestris* present a wide fossa, which is more than 2x larger than the internal acoustic meatus, among the analysed taxa. So, parsimoniously, the Hippomorpha clade probably acquired this character state independently from *T.*

terrestris, and the subarcuate fossa of the ancestor was probably small (approximately the same size of the internal acoustic meatus).

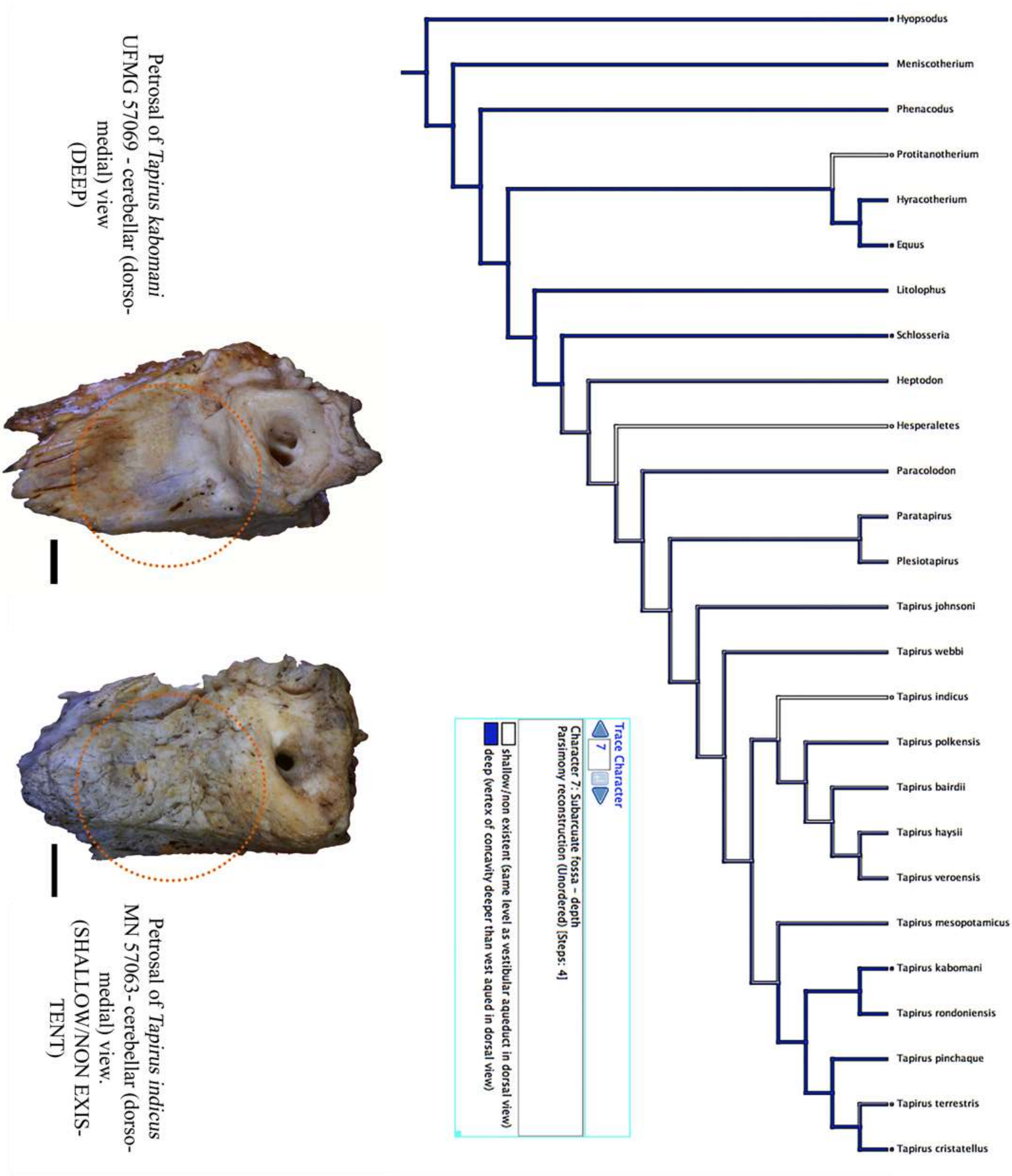

Figure 19.G) Character 7 – Subarcuate fossa (depth) – distributed in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, and predicted in the taxa with missing data.

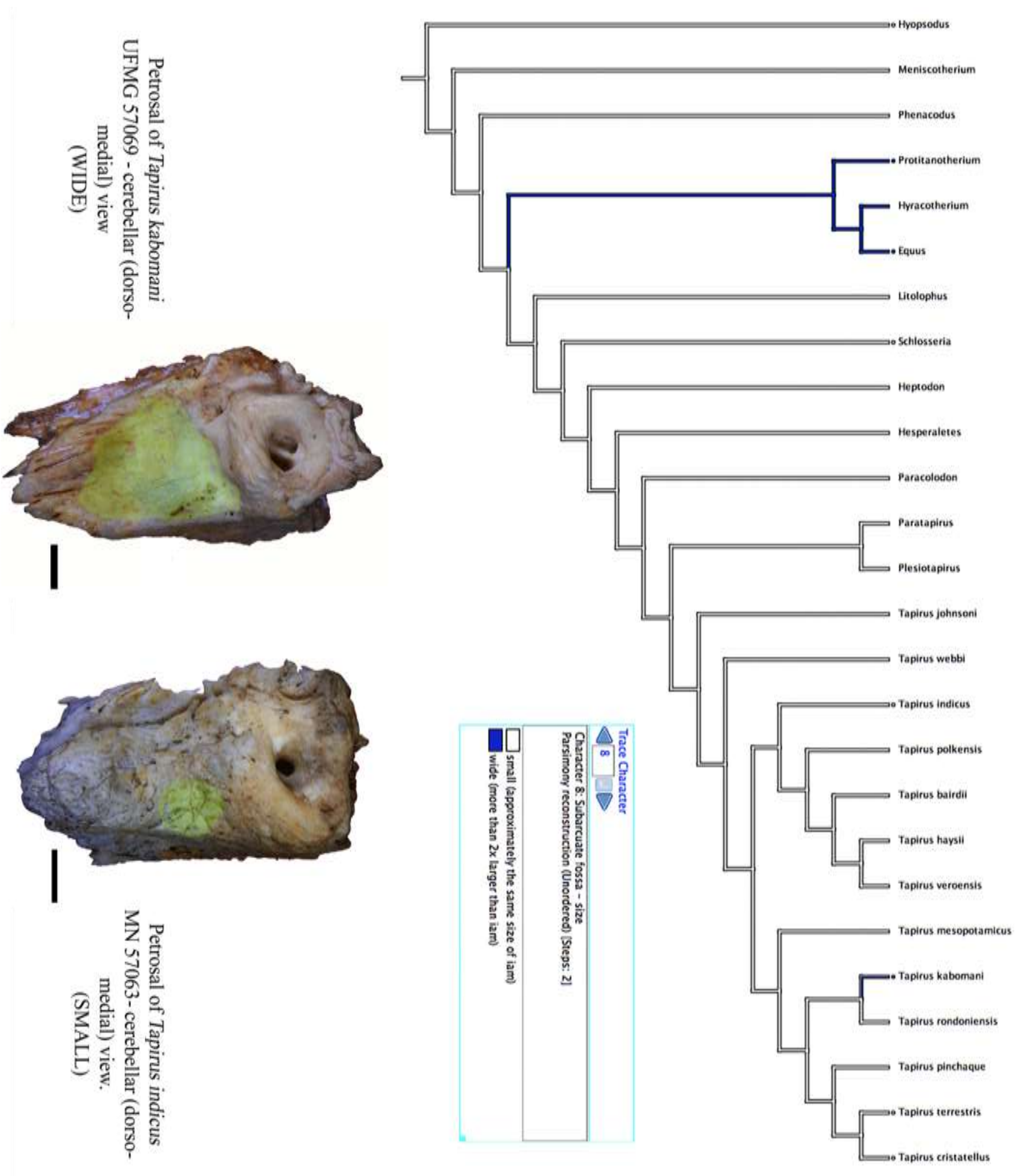

Figure 19.H) Character 8 – Subarcuate fossa (size) – distributed in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, and predicted in the taxa with missing data.

The epitympanic recess (Fig. 19.I) is considered by Cifelli (1982) a small and poorly defined depression primitively. He considered two character states to this character: small and large. However, since Cifelli didn't explored and/or explained exactly what it was considered each of the character states, their distinction remained obscure. In the absence of a proper explanation, the character was modified based on the figures of Cifelli (1982) in which the epitympanic recess was portrayed. In the present study, the size of the epitympanic recess was defined compared to other petrosal structures - small (extending from tympanohyal, but not reaching secondary facial foramen) or large (extending from tympanohyal and reaching the secondary facial foramen). As seen in the matrix, there is no information about this character in *Protitanotherium*, *Schlosseria*, *Hesperaletes*, *Litolophus*, *Paracolodon*, *Hyracotherium* and *Meniscotherium*, while all the others presents an small epitympanic recess. The choice of keeping this character in the matrix is doubtful, but there are many taxa without information about the epitympanic process, therefore it would be precocious to consider with confidence this character as uninformative and remove it from the matrix.

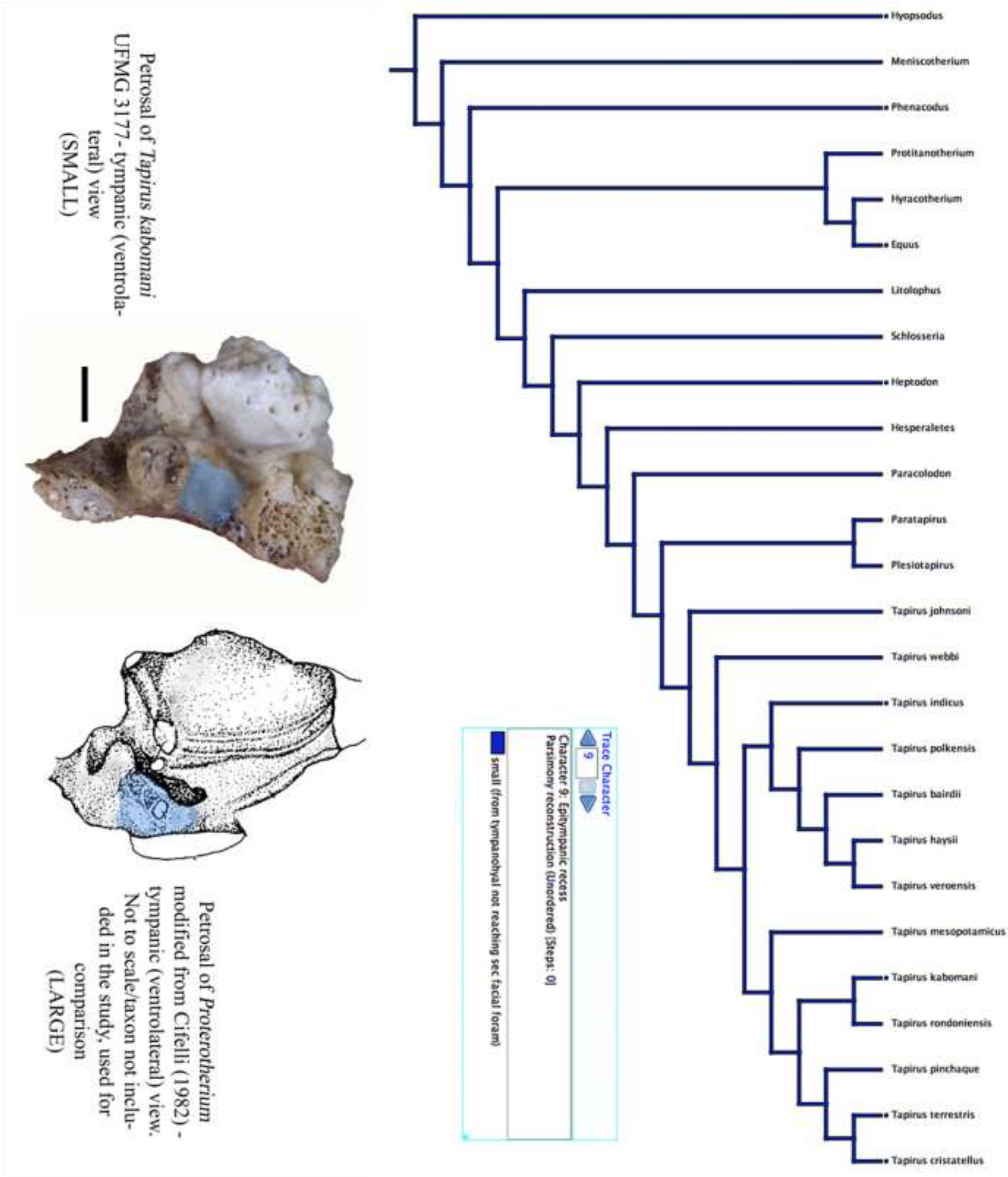

Figure 19.I) Character 9 –Epitympanic recess – distributed in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, and predicted in the taxa with missing data.

The secondary facial foramen (Fig. 19.J) is used as in O'Leary (2010) and modified from the Cifelli (1982) character "tympanic aperture of the facial canal". In the two mentioned studies this character is analysed in the same way, its position in relation to fenestra cochlea and, mainly, to the fenestra vestibuli. Cifelli (1982) used the character states - at fenestra ovalis (the same as fenestra vestibuli), anterior to fenestra ovalis, far anterior to fenestra ovalis - in which the state "at fenestra ovalis" is equivalent to "lateral to the fenestra". As the difference between "far anterior to" and "anterior to" was not clear in Cifelli's study, the character states were modified to "anterior to fenestra vestibuli", covering any "anterior location" of the secondary facial foramen, regardless of how anterior it is from fenestra vestibuli; and "lateral to fenestra vestibuli". In the analysis, the character state of *Paracolodon*, *Hyracotherium* and *Tapirus cristatellus* is unknown, and only *Meniscotherium* presents the secondary facial foramen lateral to fenestra vestibuli. As all the other taxa show this character anteriorly located, it is parsimonious to interpret that probably the ancestor already had the secondary facial foramen located anterior to fenestra vestibuli passing on this feature to almost all its descendants, except for *Meniscotherium* which lost it.

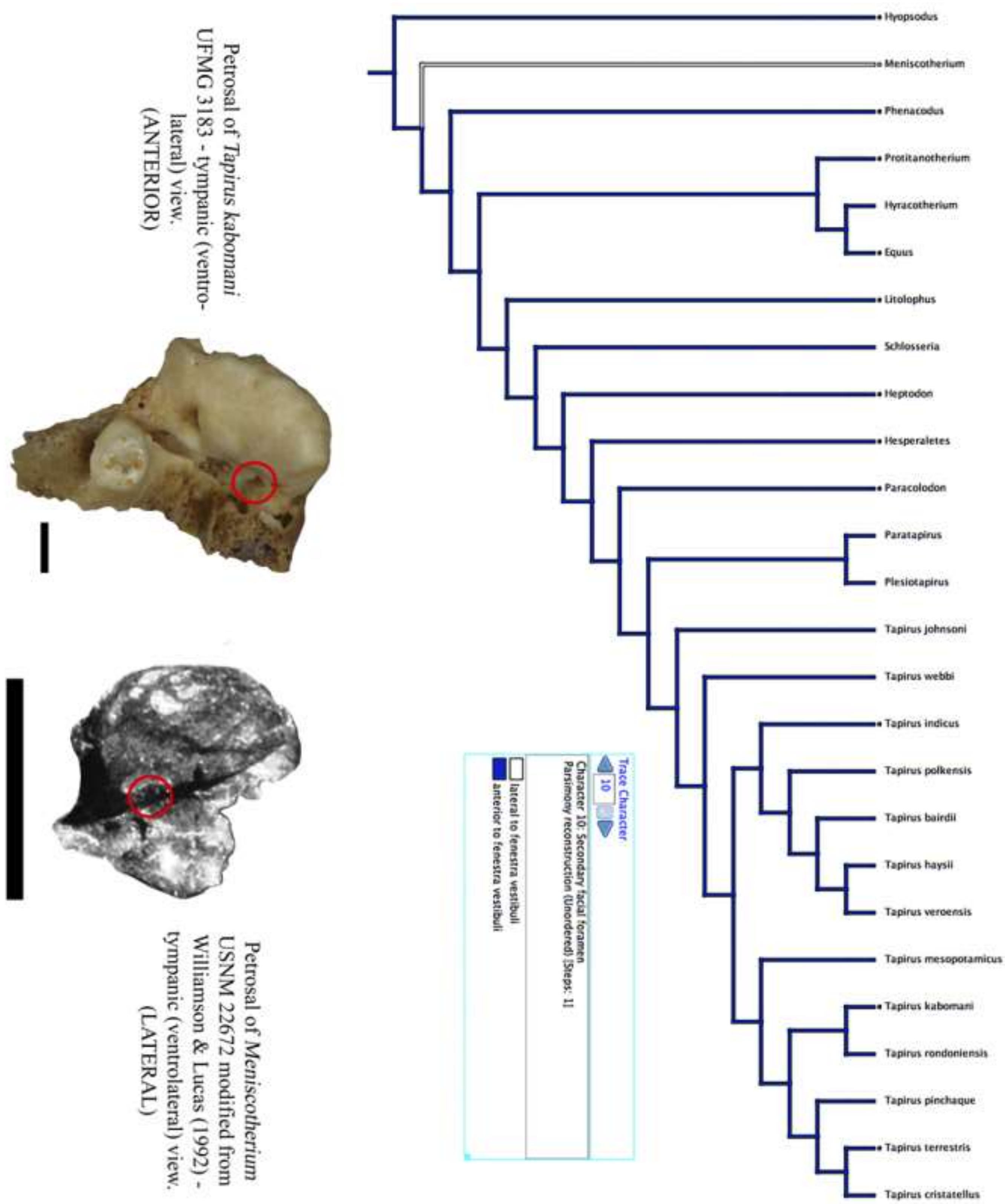

Figure 19.J) Character 10 – Secondary facial foramen – distributed in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, and predicted in the taxa with missing data. The petrosal USNM 22672 was obtained from a broader picture including all the surrounding cranial structures.

The cochlear aqueduct character is similar to O'Leary (2010) and was modified from the single character of Cifelli (1982), aquaeductus cochleae. In Cifelli's matrix it was considered the position of the cochlear aqueduct into the jugular notch - dorsal, ventral (slit), ventral, mid-way. However, as position and format were not associated one to another, the character was separated in "Cochlear aqueduct - Position" and "Cochlear aqueduct - Slit", the later is related with the presence of a slit depression where the cochlear aqueduct lies within, instead of a rounded and irregular one. The character "mid-way" was considered ambiguous and was removed from the matrix. According to Cifelli (1982), the cochlear aqueduct seems to be primitively located dorsally to the jugular notch and close to or at the cerebellar face of the petrosal. In *Phenacodus* and primitive perissodactyls it would open more ventrally into the jugular notch. In *Phenacodus*, as in Eocene tapiroids and equoids, the cochlear aqueduct would be placed inside that slit depression. The modified character "Cochlear aqueduct - Position" (Fig. 19.K) comprises 2 character states: "in ventral face" and "in ventromedial face". The first refers to the aqueduct seen from the ventral face of the petrosal; and the later to the aqueduct seen from the ventromedial (cerebellar) face of the petrosal. The character state of *Paracolodon*, *Schlosseria*, *Litolophus*, *Hesperaletes*, *Meniscotherium* and *Tapirus cristatellus* is unknown. *Heptodon*, *Hyracotherium*, *Phenacodus* an *Equus* present a ventrally positioned cochlear aqueduct; and in *Protitanotherium*, *Hyopsodus* and the other *Tapirus* it is ventromedial. The ventromedial cochlear aqueduct of *Hyopsodus* corroborates Cifelli's (1982) hypothesis about the primitiveness of this state of character. However, the other hypothesis about the ventral cochlear aqueduct of the primitive perissodactyls cannot be verified, since there are many missing data in this critical point of the phylogeny. About the character "Cochlear aqueduct - Slit" (Fig. 19.L), it is unknown to *Meniscotherium*, *Litolophus*, *Hesperaletes* and *Paracolodon* and only the cochlear aqueduct of *Hyopsodus* and *Protitanotherium* is not positioned within a slit-like depression. This result agrees with Cifelli statement about the slit depression in equoids and tapiroids. The only difference between the result of this analysis and Cifelli (1982) is the ceratomorph *Scholosseria*, the condylarth *Meniscotherium*, *Litolophus* and *Hesperaletes*, also presenting this character state, but more basal in this phylogeny than tapiroids. It is important to remenber that this mentioned difference doesn't invalidate Ciffeli's hypothesis, it would be only more inclusive, covering higher groups in the phylogeny that were not included in his analysis.

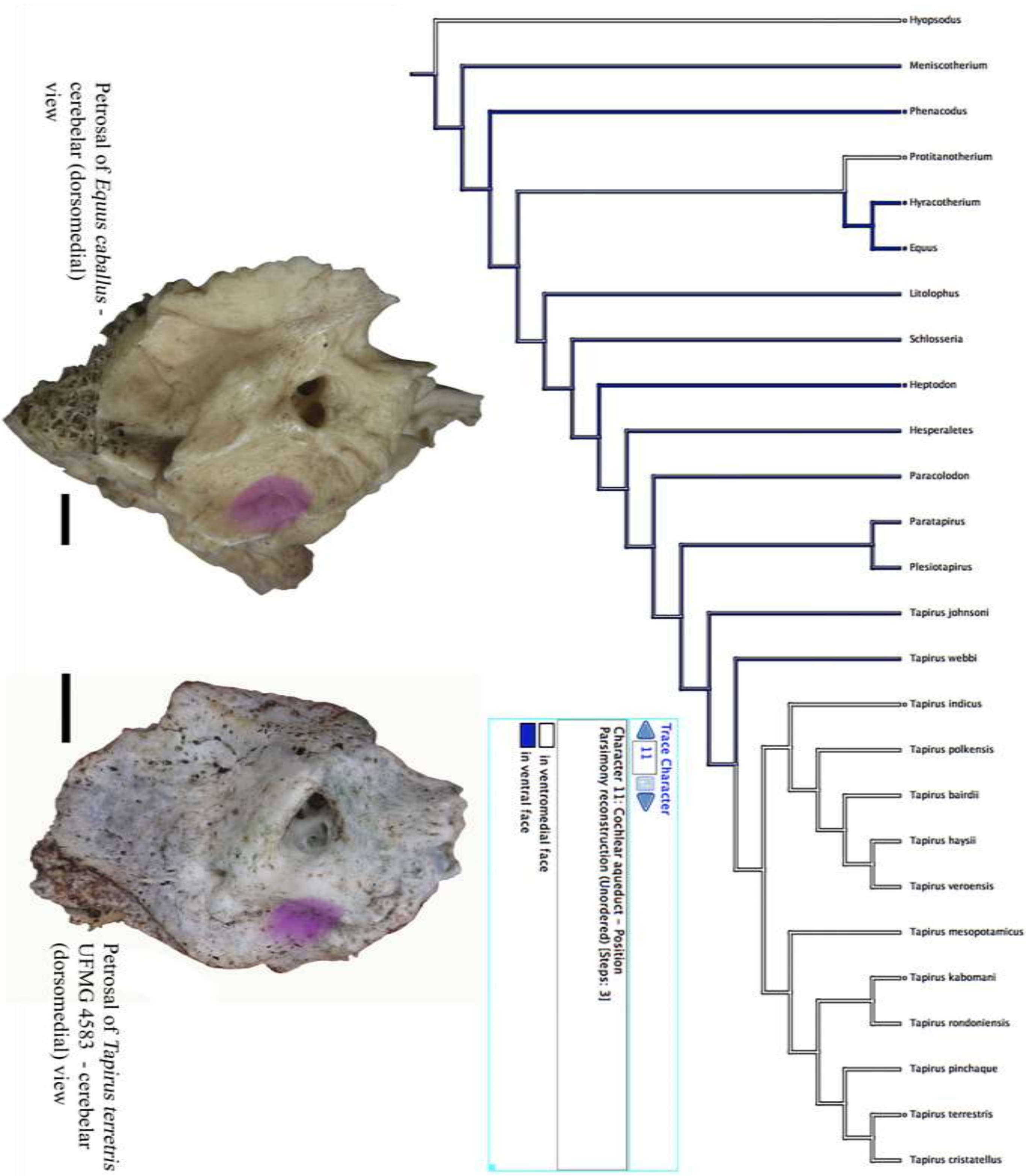

Figure 19.K) Character 11 – Cochlear aqueduct (position) – distributed in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, and predicted in the taxa with missing data.

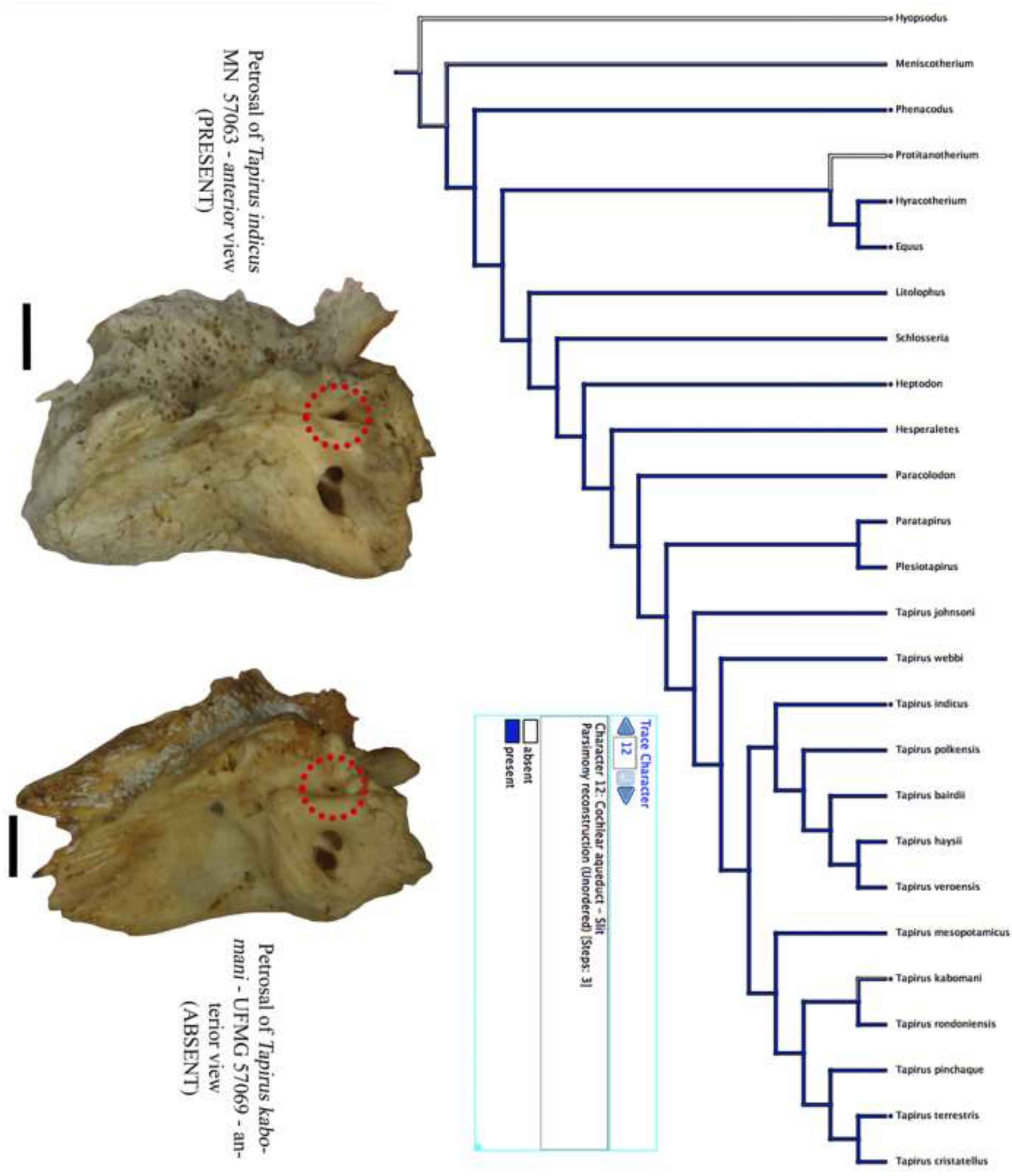

Figure 19.L) Character 12 – Cochlear aqueduct (slit) – distributed in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, and predicted in the taxa with missing data.

The tegmen tympani character (Fig. 19.M) was simplified from Cifelli's (1982) character states - thin; thin, dorsal; inflated, ventral; roofs the epitympanic sinus - to "inflated" or "thin". In O'Leary (2010) the features of tegmen tympani were distributed in 7 different characters, as shape, inflation, degree of inflation, anterior process, size of the anterior process, apex of the anterior process and vascular groove on the anterior process. However, as some taxa were analysed by photographs and/or limited descriptions made by other authors, the information is very limited to be verified in such degree of detail as O'Leary did. According to Cifelli (1982), some condylarths non-artocyonids, primitive equoid and tapiroid perissodactyls have the tegmen tympani, among other features, inflated and pneumatized. But this inflation seems to be a feature of all ungulates, except of artiodactyla and arctocyonid condylarths, and not only of the previous mentioned groups. In the matrix, except of the unknown tegmen tympani of *Schlosseria*, *Hesperaletes, Litolophus* and *Paracolodon,* all the others are inflated. This result corroborates the first hypothesis of Cifelli about the condylarths non artocyonid, primitive equoid and tapiroid perissodactyls. The unknown character state of the anteriorly cited taxa doesn't interfere in Cifelli's first hypothesis. Since tapiromorph non-tapiroids are not included in it, the current analysis became more incluse.

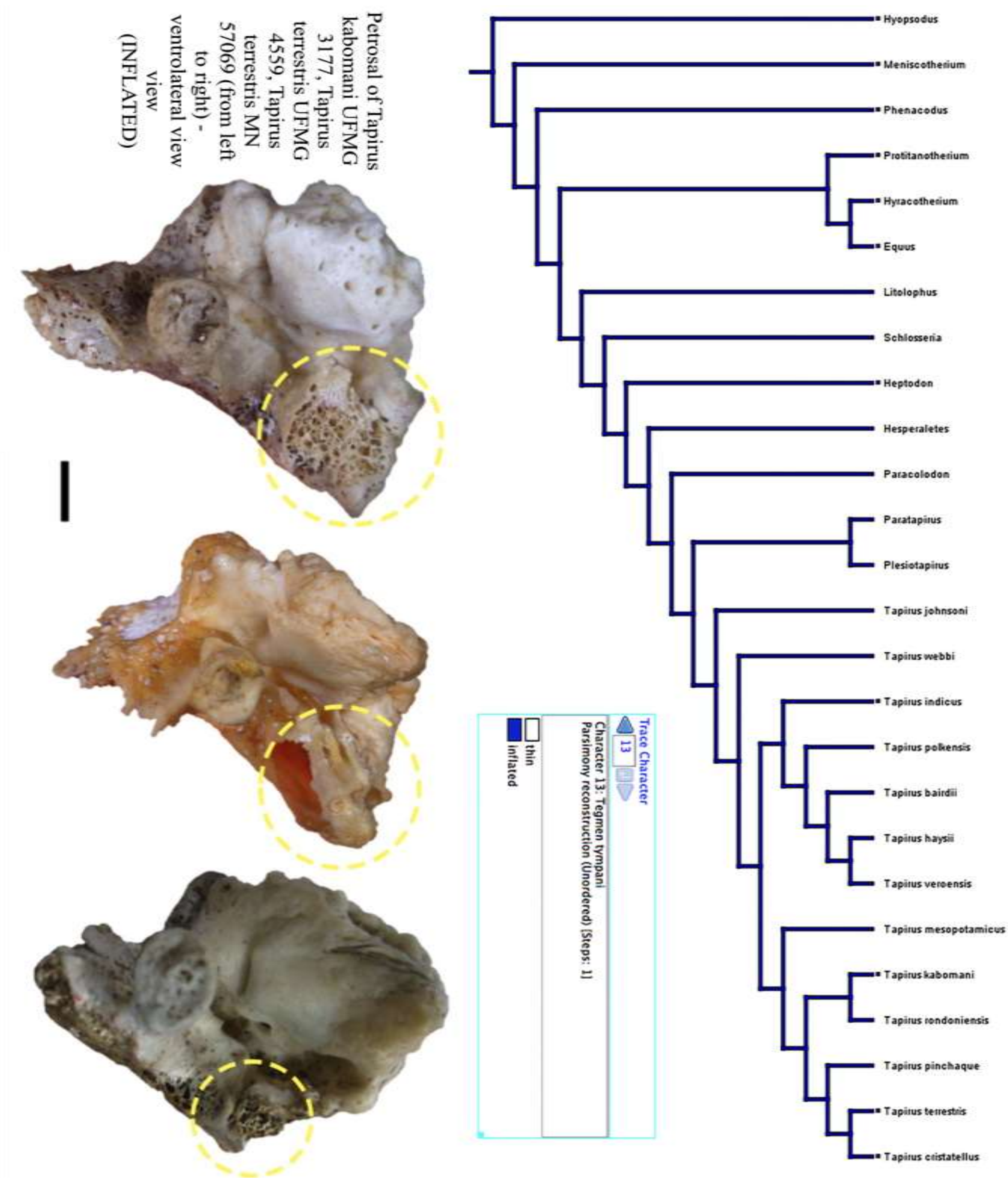

Figure 19.M) Character 13 – Tegmen tympani – distributed in the phylogeny composed by the union of Holbrook and Lapergula (2011) to perissodactyls, Colbert (2005) to tapiromorphs non *Tapirus*, Bai et al. (2017) to *Paracolodon*, Cozzuol et al. (2013) to *Tapirus* and Perini (2010) and Halliday et al. (2016) to condylarths, and predicted in the taxa with missing data. The petrosal MN 57069 and UFMG 4559 were mirrored to standardize the petrosal size.

The tympanohyal character of Cifelli (1982) was not included in the analysis, because he used the term (tympanohyal) to refer to different structures from one petrosal illustration to another. However, as the character “tympanic process”of Ciffeli (1982) matrix was related to the "tympanohyal" and its character states were dependent of it, the character was maintained in the present study but modified to “caudal tympanic process – extension”. In the absence of a name in the literature related to the structure in which Cifelli (1982) considered as tympanohyal in most of the figures, a new term was created, the "posterior process of crista parotica", to be used as reference to the extension of the “caudal tympanic process” character, since it is a process that extends posteriorly from the crista parotica. Besides that, the term "tympanohyal" was used by O'Leary (2010) to designate a different structure.

5.3 Additional analysis

The petrosal data didn't alter the topology of Cozzuol et al. (2013, 2014) (see Cozzuol et al., 2013, 2014), however it does not imply that these characters supports the referred topology. The topology could be preserved, also, because the information about the new characters constrains was insufficient to alter the well-supported phylogeny of Tapiridae, with all the resulting missing data created with the combination of both matrices. Also, because the petrosal characters considered in the present study should maybe be reviewed and updated, considering the particularities of the group studied, or the petrosal itself doesn't reflect the evolution of the group and should not be included as only source of information in phylogenetic analysis of this clade. Yet, other characters are needed to complement and strengthen the analysis. It is valid to mention that both analysis were remade using implied weighing, estimating values of the K constant of implied weight ranges were found through the script Mirande (Marcos Mirande, 2009). However, even using implied weighing the result of the analysis didn't change from the previous analysis.

6- CONCLUSION

Despite the petrosal of *Tapirus* sharing some common features among all species, it was not found a single distinct pattern in the description and comparison that could be used to diagnose the genus. However it is possible that a gradient of the variation seen among *Tapirus* could be established and a set of characters could be considered to possibly find a diagnosis pattern to discriminate species of the genus. The distribution of some characters along the phylogeny used in the present study agrees with some hypothesis found on the literature related to the Perissodactyla. However, although none of analysis results completely denied what is found in the literature, other characters still generates inconclusive results. In consequence, some analysis made using these "inconclusive" characters can also produce inconclusive results, as seen in the not included analysis mentioned previously in the "Results" section of this study. The reason why the result of the analysis was inconclusive can probably be explained by the use of few taxa, and some of them (as *T. cristatellus*) very polymorphic, by the occurrence of all the missing data of some groups included in the analysis and the use of "inconclusive" characters.

Yet, the petrosal of Perissodactyla is still very little studied, and little used in phylogenetic studies. Most studies, even describing the skull, rarely describe the petrosal, and when describes it, most descriptions are incomplete. Also, most of the studies don't focus in recent taxa, and some species, as modern rhinoceros have never being described. Another big problem about studying Perissodactyla petrosal is that most of the general knowledge about this bone is based on Artiodactyla studies, even though some facts applicable to artiodactyls, cannot be used to perissodactyls. For example, O'Leary (2010) mentioned in her *Tapirus terrestris* description the presence of a supposed tympanic bulla. However, although this structure is widely distributed in Artiodactyla (the focus of her study), it is not usually mentioned in Perissodactyla descriptions, and indeed, it was never seen in personal observations or mentioned for *Tapirus*. Besides that, in the few perissodactyl studies that the petrosal is included, the terminology used is confusing, since some authors use the same term to refer to different structures, or on contrary, they use different terms to refer to the same structure. Yet, some of them don't agree with the presence or absence of a character, as seen in the "sulcus for stapedial artery" of *Phenacodus*, described as present by Cifelli (1982), but contested by Thewissen & Domning (1992). Anyway, it is important to emphasize that the current diversity of this group is relictual and the petrosal of extant, as well as the petrosal of extinct representatives of the order, still remain poorly known and/or portrayed.

Therefore, considering all these questions about the use of petrosal to study perissodactyls representatives, it is precocious to affirm, as Holbrook (1999), that, although some tapiromorph characters and perissodactyls characters are important for higher-level phylogenetic studies, the petrosal morphology "does not vary in any systematic way among tapiromorphs". Because, although this study had made a small revision of the petrosal of the Perissodactyla group, there are many important perissodactyl representatives still not sampled, some groups has extensive missing data and the characters could be reviewed. After a more complete revision, characters as the cochlear aqueduct could bring important phylogenetic information, differentiate not only high-level groups but also less comprehensive groups. Also, yet, it could not be used in this kind of studies alone, could be applied in phylogenetic studies combined with other characters (from other body structures and/or from molecular analysis) to form a more complete character matrix analysis, and be used to study character evolution. In addiction, since Holbrook (1999) many significant tools were developed and/or upgraded to improve the comprehension of the shape, as geometric morphometry 2D and 3D. When used, these recent techniques can show many things in the petrosal that were not evident without resources.

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8- SUPPLEMENTARY DATA

Appendix 1- Cranium of *Tapirus indicus* MN 57063. As the cranium was articulated with the mandibule, the ventral view was inaccessible.

Fig. 20 - Cranium of *Tapirus indicus* MN 57063. Photograph by Larissa Dumbá

Appendix 2 – Age of the *Tapirus* studied based on the dentition.

Young	No molar erupted
Young adult	M1
	M2
Adult	M3
Old adult	M3 with much wear

Appendix 3- List of species included in this study with dental age, locality and sex (when available).

	Acronyms	Age		Cranium side	Location	Sex	Extra Information
T. kabomani	UFMG 3176	M1	Young adult	right	Rio Madeira, Rondonia, Brazil		
	UFMG 3183	M3	Old adult	left	Lábria, Amazonas, Brazil		
	UFMG 3177	M2	Young adult	left	Amazonas, Brazil	Male	Holotype
	UFMG 6030	M2	Young adult	left	?		
	MN 57069	M2	Young adult	right	?		
	MN 1700	M3	Adult	right	Goiás, Brazil		
T. terrestris	UFMG 4557	M2	Young adult	left	Floresta do jamari, Rondonia, Brazil		

	UFMG 4560	M2	Young adult	left	Lábria, Amazonas, Brazil		
	UFMG 4586	M1	Young adult	left	PARNA Amazonia - Tapajós, Itaituba, Pará, Brazil		
	UFMG 4558	M3	Adult	left	Mato Grosso, Brazil		
	UFMG 4583	M2	Young adult	left	Parque Nacional do Viruá, Roraima, Brazil		
	UFMG 4559	M2	Young adult	right	Lábria, Amazonas, Brazil		
	UFMG 4195	M2	Young adult	left	Terra indígena Karitiana, Porto Velho, Rondônia, Brazil		
T. indicus	MN 57063	M2	Young adult	right	Asia		
	MACN 30351 (only in figure 8.D)	M2	Young adult	right and left	Unknown		From the Jardín Botánico y Zoológico de Asunción
T. cristatellus	MCL 5643/01	?	?	right and left	Gruta dos Brejões		

Appendix 4 – Synonym terms of petrosal characters found in the literature about Perissodactyla.

O'Leary terms used in this study	Where it was used	Other names to the same structure	Where it was used
Promontorium (Giannini et al., 2006)	Whitmore (1953); Radinsky (1965); MacPhee (1981); Cifelli (1982); Coombs & Coombs Jr. (1982); Williamson and Lucas (1992); Luo and Gingerich (1999); Mader (2009); Bai et al. (2010); Ping & Yuan-Qing (2010); Bai et al. (2017);	Promontory of the pars cochlearis	Mead and Fordyce (2009)
		Ventromedial eminence of the pars cochlearis	Luo and Gingerich (1999)
Fenestra cochleae (Giannini et al., 2006)	Schulte (1917); Whitmore (1953); Bai et al. (2017)	Round window	Mead and Fordyce (2009)
		Cochlear window	MacPhee (1981)
		Cochlear fenestra	Ping & Yuan-Qing (2010)
		Foramina for the cochlear nerve	Mader (2009)
		Fenestra rotunda	Kellogg (1936); Radinsky (1965); Coombs & Coombs Jr. (1982); Bai et al. (2010)
		Fenestra rotundum	Cifelli (1982); Williamson and Lucas (1992); Mader (2009)
Fenestra vestibuli (Giannini et al., 2006)	Cifelli (1982); Mead and Fordyce (2009); Bai et al. (2017)	Oval window	Mead and Fordyce (2009)
		Vestibular fenestra	Mead and Fordyce (2009); Ping & Yuan-Qing (2010)

		Venestra ovale	Mader (2009)
		Foramina for the vestibular nerve	Mader (2009)
		Vestibular window	Evans and Christensen (1979); Mead and Fordyce (2009)
		Fenestra ovalis	Cifelli (1982); Coombs & Coombs Jr. (1982); Radinsky (1965); Williamson and Lucas (1992); Bai et al. (2010)
Crista interfenestralis (Wible et al., 1995)	Bai et al. (2017)	Crista vestibuli	Whitmore (1953)
Transpromontorial sulcus (Wible, 1986)	Bai et al. (2017)	Promontory sulcus	Cifelli (1982); Williamson and Lucas (1992); Mader (2009)
		Promontory artery sulcus	Ping & Yuan-Qing (2010)
		Promontory groove	Coombs & Coombs Jr. (1982)

Sulcus for stapedial artery (Novacek, 1986)	Cifelli (1982); Bai et al. (2017)	Stapedial groove	Coombs & Coombs Jr. (1982)
		Promontorial stapedial artery groove	Wible & Gaudin (2004)
		Stapedial artery sulcus	Ping & Yuan-Qing (2010)
		Stapedial artery groove	Cifelli (1982); Novacek (1986)
Epitympanic wing (MacPhee, 1981)	Mead and Fordyce (2009)	-	-
Basicapsular groove (Presley, 1979)	Bai et al. (2017)	Sulcus medialis	Cifelli (1982); Novacek (1986)

Posteromedial flange (O'Leary, 2010)	-	-	-
Fossa for tensor tympani (Kellogg,1936; Fordyce, 1994; Luo and Gingerich, 1999:45) (Giannini et al., 2006)	Radinsky (1965); Cifelli (1982); Bai et al. (2017)	Fossa muscle tensor tympani	
		Fossa muscularis major	Reysenbach de Haan (1957); Coombs & Coombs Jr. (1982)
		Groove for tensor tympani	Cifelli (1982); Luo and Gingerich (1999)
Tegmen tympani (Giannini et al., 2006)	Radinsky (1965) Cifelli (1982); Coombs & Coombs Jr. (1982); Williamson and Lucas (1992); Bai et al. (2017)	Superior process	Luo and Gingerich (1999)
Anterior process of tegmen tympani (Luo and Gingerich, 1999)	-	-	-
Epitympanic recess (Giannini et al., 2006)	Cifelli (1982); Coombs & Coombs Jr. (1982); Bai et al. (2017)	Fossa for the head of malleus	Evans and Christensen (1979)
		Recessus epitympanicus	Mead and Fordyce (2009)
Facial canal (Giannini et al., 2006)	Radinsky (1965); Cifelli (1982); Williamson and Lucas (1992); Mader (2009)	-	-
Facial sulcus (Giannini et al., 2006)	Coombs & Coombs Jr. (1982); Mader (2009); Bai et al. (2017)	Facial canal	Coombs & Coombs Jr. (1982); Ping & Yuan-Qing (2010)
		Sulcus for the facial nerve	Ping & Yuan-Qing (2010)
		Sulcus facialis	Cifelli (1982)
		Groove for the facial	Radinsky (1965)

		nerve	
		Anterior part of the canal for the facial nerve	Mader (2009)
		Stylomastoid canal (only the more distal path of the facial sulcus)	Mead and Fordyce (2009)
		Aquaeductus Falopi	Coombs & Coombs Jr. (1982) Cifelli (1982;

Fossa for stapedius muscle (Giannini et al., 2006)	Bai et al. (2010)	Fossa for stapedial muscle	Radinsky (1965)
		Stapedial fossa	Ping & Yuan-Qing (2010)
		Stapedial muscle fossa	Bai et al. (2017)
		Fossa muscularis minor	Reysenbach de Haan (1957); Cifelli (1982); Coombs & Coombs Jr. (1982); Novacek (1986); Mader (2009);
Stylomastoid notch (Giannini et al., 2006)	Mead and Fordyce (2009); O'Leary (2010)	Stylomastoid foramen	Mead and Fordyce (2009)
Crista parotica (Wible and Gaudin, 2004)		Facial crest of the periotic	
		Crista facialis petrosi (van der Klaauw, 1931)	

		Crista facialis	Wible and Gaudin (2004)
Caudal tympanic process (Giannini et al., 2006) ------------------------------ Geisler and Luo (1996: fig. 3;) and Geisler and Sanders (2003: char. 225) - used this term to refer to a process that extends laterally to fenestra cochlea and medially to fossa for the stapedial muscle, from pars cochlearis.	MacPhee (1981); Geisler and Luo (1996); Geisler and Sanders (2003); O'Leary (2010) Bai et al. (2017);	Posterior cochlear crest	Fordyce (2002)
		Posterior tympanic process	Mead and Fordyce (2009)
		Tympanic process	Cifelli (1982); Coombs & Coombs Jr. (1982); Wible et al (2004)
Internal acoustic meatus (Giannini et al., 2006)	Ping & Yuan-Qing (2010)	Periotic canal/canalis perioticus	McFarland et al. (1979)
		Internal auditory meatus	Radinsky (1965); Cifelli (1982); Coombs & Coombs Jr. (1982); Mader (2009)
Foramen acusticum superius (Giannini et al., 2006)		Lateral foramen	Cifelli (1982)
		Area vestibularis utriculo-ampullaris	Mead and Fordyce (2009)
		Dorsal vestibular area	Mead and Fordyce (2009)
		Foramen for the vestibular ramus of the acoustic nerve	Ping & Yuan-Qing (2010)
Foramen acusticum inferius (Giannini et al., 2006)		Area vestibularis saccularis	Mead and Fordyce (2009)

		Ventral vestibular area	
		Medial foramen	Cifelli (1982)
		Cochlear foramen	
		Foramen for cochlear ramus of the acoustic nerve	Mead and Fordyce (2009)
		Subfloccular fossa	Ping & Yuan-Qing (2010)
Subarcuate fossa (Giannini et al., 2006)	Cifelli (1982); Mader (2009); Ping & Yuan-Qing (2010)	Cerebellar fossa	Cifelli (1982)
		-	Evans and Christensen (1979); Mead and Fordyce (2009)
Petromastoid canal (Gannon et al., 1988)	-	Aqueductus vestibulae/vestibuli	-
Vestibular aqueduct (Giannini et al., 2006)	Radinsky (1965)	-	Cifelli (1982); Mader (2009)
Mastoid plate (O'Leary, 2010)	-		-

Hiatos Falopii (Giannini et al., 2006)	Mader (2009); Bai et al. (2017)	Facial hiatus	Radinsky (1965)
		Anterior opening for the greater superficial petrosal nerve	Luo and Gingerich (1999)
Ventrolateral tuberosity (Luo and Gingerich, 1999)	-	-	-
Cochlear aqueduct (Sisson, 1911)	Radinsky (1965)	Aqueductus cochleae	Cifelli (1982); Mader (2009)

		Perilymphatic foramen	Luo and Gingerich (1999)
Secondary facial foramen (Giannini et al., 2006)	Bai et al. (2017)	Apertura tympanica canalis facialis	Coombs & Coombs Jr. (1982)
		Tympanic aperture of the facial canal	Reysenbach and Haan (1957); Williamson and Lucas (1992); Bai et al. (2010)
		Tympanic aperture of the facial nerve	Mader (2009)
		Tympanic opening of the facial canal	Cifelli (1982)
		Foramen for the facial nerve (cranial nerve VIII)	Mader (2009)
		VII, internal or external opening for the facial nerve canal	Luo and Gingerich (1999)
		Epitympanic foramen of the facial canal	Mead and Fordyce (2009)
		Foramen faciale (MacPhee, 1981)	Thewissen and Domning (1992)
Posterior process of crista parotica (New term)		Hyoid process	Coombs & Coombs Jr. (1982)
		Tympanohyal	Radinsky (1965); Cifelli (1982); Coombs & Coombs Jr., 1982
External acustic meatus (Giannini et al., 2006)	Mead and Fordyce (2009)	External auditory meatus	Coombs & Coombs Jr. (1982); Cifelli (1982); Bai et al. (2010); Bai et al. (2017)
		Meatus acusticus externus	Mead and Fordyce (2009)
		Opening for the tympanic ligament	Luo and Gingerich (1999)
		Auditorius (externus) meatus disectus	Eustachius and Lancisius (1714)
Crista transversa	O'Leary	Transverse crista/crest	Ping & Yuan-Qing (2010)

(Giannini et al., 2006)	(2010)	Crista falciformis	Gray (1918)
		Transverse septum	Luo and Gingerich (1999)
Fossa for the head of malleus (Luo and Gingerich, 1999)		Mallear fossa	Schulte (1917); Mead and Fordyce (2009)
		Facet for the malleus	Mead and Fordyce (2009)

Appendix 5 - Additional analysis results - Resulting tree with/without grouping constrains. The topology of the resulting tree was the same in both analysis.