**Universidade de Aveiro** Departamento de Biologia
**Ano 2019**

**JOANA ISABEL DE ÓRFÃO CORREIA**

# ON CAPTORHINIDS: ANALYSIS OF MORPHOLOGICAL CHARACTERS WITH PARTICULAR ATTENTION TO SKULL SCULPTURING

# ANÁLISE DE CARACTERES MORFOLÓGICOS DE CAPTORRINÍDEOS COM PARTICULAR ATENÇÃO À ESCULTURA CRANIANA

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Dissertação apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Mestre em Ecologia Aplicada, realizada sob a orientação científica do Doutor Rui Castanhinha, Professor Auxiliar Convidado do Departamento de Biologia da Universidade de Aveiro

# DECLARAÇÃO

Declaro que este relatório é integralmente da minha autoria, estando devidamente referenciadas as fontes e obras consultadas, bem como identificadas de modo claro as citações dessas obras. Não contém, por isso, qualquer tipo de plágio quer de textos publicados, qualquer que seja o meio dessa publicação, incluindo meios eletrónicos, quer de trabalhos académicos.

“Perhaps I am just a hopeless rationalist, but isn't fascination as comforting as solace? Isn't nature immeasurably more interesting for its complexities and its lack of conformity to our hopes? Isn't curiosity as wondrously and fundamentally human as compassion?” – Stephen Jay Gould, 1993.

**o júri**

| | |
|---|---|
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**palavras-chave**

Evolução, Paleontologia, Filogenia, Morfologia, Anatomia, Escultura cranial, Captorhinidae.

**resumo**

Os captorrinídeos são um grupo já extinto de répteis Paleozóicos, sendo modelos representativos dos Reptilia mais basais. Estes amniotas não-sinapsídios representam a primeira grande radiação filogenética de vertebrados terrestres. A sua anatomia craniana é conservada e os ossos do crânio têm a particularidade de serem esculpidos.

Em análises filogenéticas é comum usar-se características morfológicas dos crânios, nomeadamente a textura da superfície externa dos ossos do crânio (escultura craniana). No entanto e no caso dos captorrinídeos, não existe um consenso relativo à definição e classificação desta característica, e autores diferentes referem-se ao mesmo estado de caracter com expressões distintas. Adicionalmente, a tecnologia actual permite a identificação de estruturas previamente não descritas na escultura dos ossos, requerendo nomenclatura nova e standardizada, de modo a que possam ser usadas como caracteres filogenéticos.

Neste trabalho é apresentada uma redescrição detalhada dos caracteres mais usados na literatura mais recente em reconstruções filogenéticas de captorrinídeos. É também proposta uma redefinição da terminologia relativa à escultura dos ossos cranianos, os estados de caracter correspondentes são ainda revistos e redefinidos. São também definidos e propostos novos caracteres morfológicos.

Foi ainda elaborado um portfolio com ilustrações e esquemas que permitem apresentar visualmente todos os caracteres aqui utilizados nas diversas espécies de captorrinídeos.

Estes novos dados permitiram gerar novas análises filogenéticas que incluem captorhinomorfos de 23 espécies actualmente descritas. Compara-se também os resultados obtidos com os dados filogenéticos mais recentes existentes na literatura.

Foi usado s*oftware* de análise e manipulação de imagem (Krita e FIJI) para isolar redes de polígonos que representem a escultura craniana. Os dados resultantes foram analisados no *software* RStudio, onde se procedeu a uma análise estatística de modo a detectar diferenças nos padrões da escultura craniana.

Adicionalmente, a metodologia aqui desenvolvida pode ser facilmente aplicada a qualquer outro tipo de investigação em animais actuais ou extintos que também apresentem ossos craniais esculpidos, revelando novos dados sobre as implicações evolutivas e paleoecológicas desta curiosa e fascinante característica.

**keywords**

Evolution, Palaeontology, Phylogeny, Morphology, Anatomy, Skull sculpturing, Captorhinidae.

## abstract

Captorhinids are an extinct group of Palaeozoic eureptiles, being model representatives of basal Reptilia. These non-synapsid amniotes represent the first major radiation of terrestrial vertebrates. They have a conservative skull anatomy with the presence of conspicuous skull sculpturing.

Morphological skull features are extensively used in phylogenetic analysis, particularly external cranial bone surface texture (skull sculpturing). However, in captorhinids there is no consensus on the definition and classification of this trait, and different authors use different words to describe similar character states. In addition, current technology provides new information from previously undescribed structures in bone texture that require proper nomenclature definition in order to be used in phylogenetic analyses.

Here we present a deep redescription of all captorhinid phylogenetic characters used in recent literature. All characters and character states and figured in a visual portfolio to be used as a guide in future studies. We also propose a redefinition of skull sculpturing terminology, standardize correspondent character states, and define multiple new characters.

This new data allowed to generate new phylogenetic analyses that include 23 of the captorhinomorphs species currently described. We also compare our findings with the most recent available phylogenetic data.

We used image analysis *software* (Krita and FIJI) to isolate bone texture networks and individual polygons. The resulting data was analyzed on RStudio, where we performed statistical tests to find differences in skull sculpturing patterns.

The methodology here developed can be easily applied for any other research on extant or extinct animals that also present sculpturing in their skull, bringing new light into the evolutionary history of this extremely curious evolutionary novelty.

# Index

# Table of figures

## List of tables

# 1. Introduction

## a. The protagonist

The skull is one of the most complex bone structures of the body. Not only does it hold the central nervous system, but also houses major sensory organs while supporting multiple muscles (Anderson & Khalid, 2018). Gregory and Hellman state that the skull is one of the main features used in tetrapod phylogenetic analyses because they present complex specializations that result from the past needs of adaptation to very diverse habitats and lifestyles (Gregory & Hellman, 1939). Other authors note that in areas such as comparative anatomy and palaeontology, there are many cases of taxonomists using only morphological cranial characters when describing a new taxon (Castanhinha, 2014). In fact, the skull has been described to evolve as a set of different modules (Goswami & Polly, 2010; Esteve-Altava, 2016) and it is not only an extremely complex structure but also very diverse throughout phylogeny (Young, Brusatte, Ruta & de Andrade, 2010). As such, the skull provides a special opportunity to analyse the constraints that developmental processes impose on evolutionary changes and vice-versa (Hanken & Thorogood, 1993). In sum, particularly in palaeontology, cranial traits are extremely relevant, not only because they offer precious information for taxonomic classification but also for phylogenetic analyses testing evolutionary hypotheses (Hanken & Hall, 1993; Bhullar, Marugán-Lobón, Racimo, Bever, Rowe, Norell & Abzhanov, 2012).

## b. Why are captorhinids relevant?

Captorhinomorpha is a paraphyletic group that encompasses two distinct clades of non-synapsid amniotes: Captorhinidae (or captorhinids) and Protorothyrididae (Albright, 2003) (Figure 1). Captorhinidae is a clade of Palaeozoic vertebrates that represent the first major radiation of Eureptilia adapted to terrestrial environments (Modesto, Lamb & Reisz, 2014), and are considered to be model representatives of basal Reptilia (Sumida, Dodick, Metcalf & Albright, 2010) (Figure 2). They lived from Late Pennsylvanian to Late Permian, until the Permian-Triassic extinction event, 252 million years ago (Brocklehurst, 2016). This makes them the longest-lived reptile clade in the Palaeozoic.

One of their most defining features is their skull anatomy: their craniums are consistently prominent, large, and have evolved conservatively (Modesto, Scott, Berman, Müller & Reisz, 2007; Brocklehurst, 2016). As such, most publications have focused on interpreting cranial material (Seltin, 1959; Heaton, 1979).

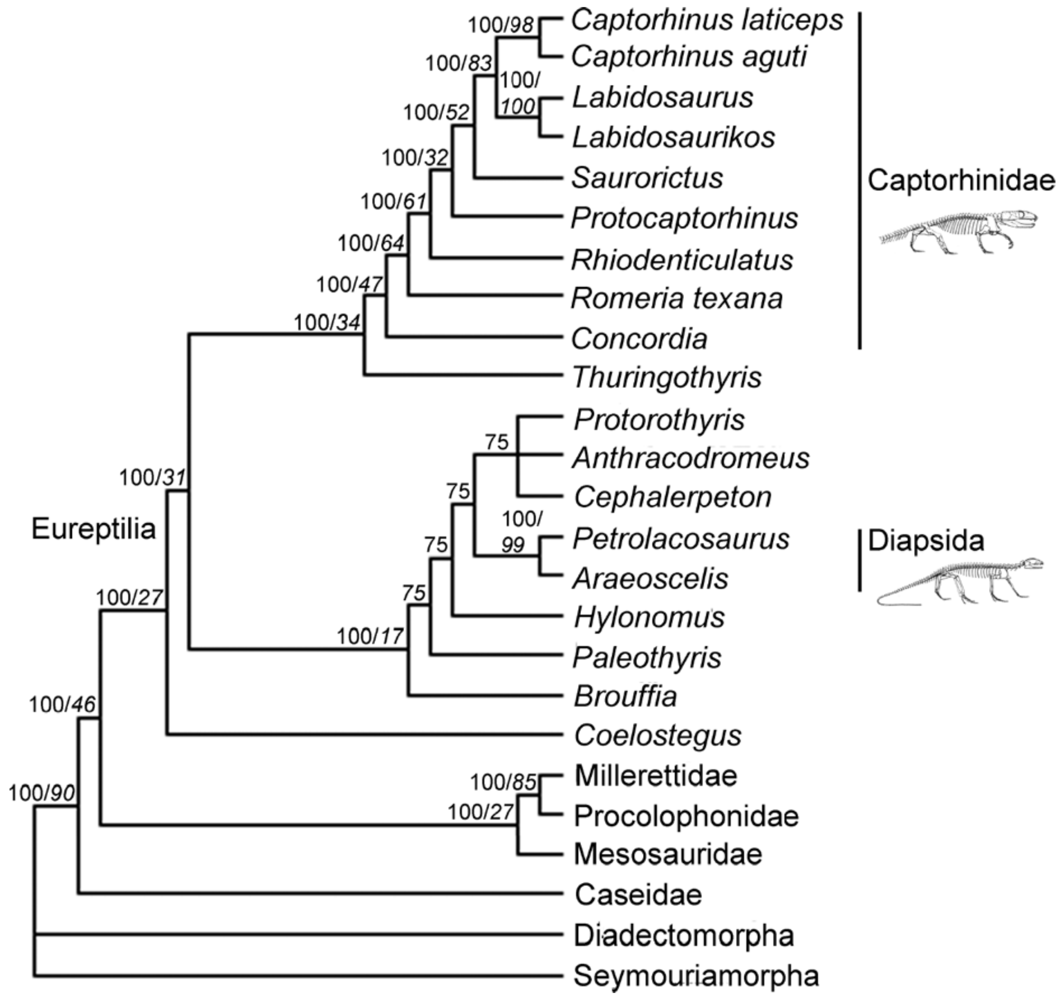


*Figure 1: Majority rule (50%) consensus tree of the parsimony analysis of eureptiles. Left/single numbers indicate the frequency of occurrence of the respective node among the different trees; italic numbers on the right are bootstrap values (included only for the nodes that are present in all the parsimony trees). Only captorhinids and diapsids are monophyletic. In Müller & Reisz, 2006.*

The Captorhinidae diagnostic features include (Heaton & Reisz, 1980; deRicqlès & Bolt, 1983; Dodick & Modesto, 1995): a) low, flat dorsal surface profile forming nearly a 90º angle with the posterior border of the skull, b) a posteroventrally angled premaxilla, c) lateral maxillary flexure, or swelling of the cheek region, d) distinctively textured dermal bone surfaces, e) loss of tabular bone.

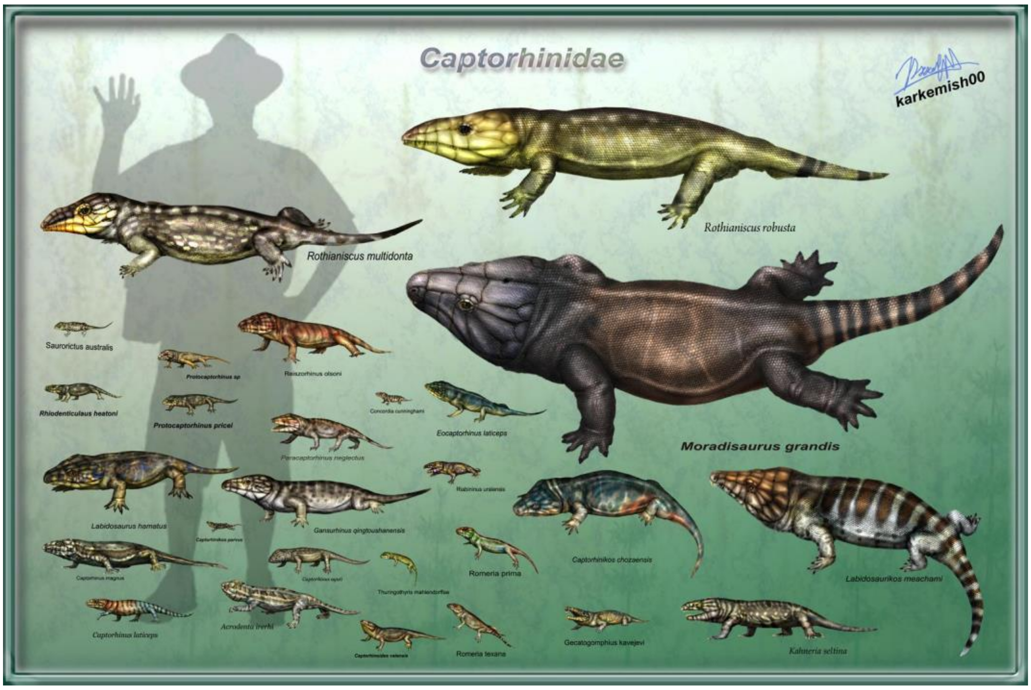


*Figure 2: Paleoart reconstruction of described captorhinomorphs, scaled. Eduardo Camargo, 2012.*

Captorhinids had diverse diets; the earliest were fauniverous/insectivorous, having adapted to a herbivorous diet in subsequent evolutionary stages (Heaton, 1979; Modesto, Scott & Reisz, 2018), where they became one of the first clades of terrestrial herbivorous reptiles (Reisz & Fröbisch, 2014). During the Early Permian, they were cosmopolites, probably due to their evolutionary success based on diversification (LeBlanc, Brar, May & Reisz, 2015). These eureptiles occupied several habitats spread all the way from equatorial southwest Laurasia to temperate areas of Pangea (Figure 3) (Modesto et al., 2007; Reisz, Liu, Li & Müller, 2011).

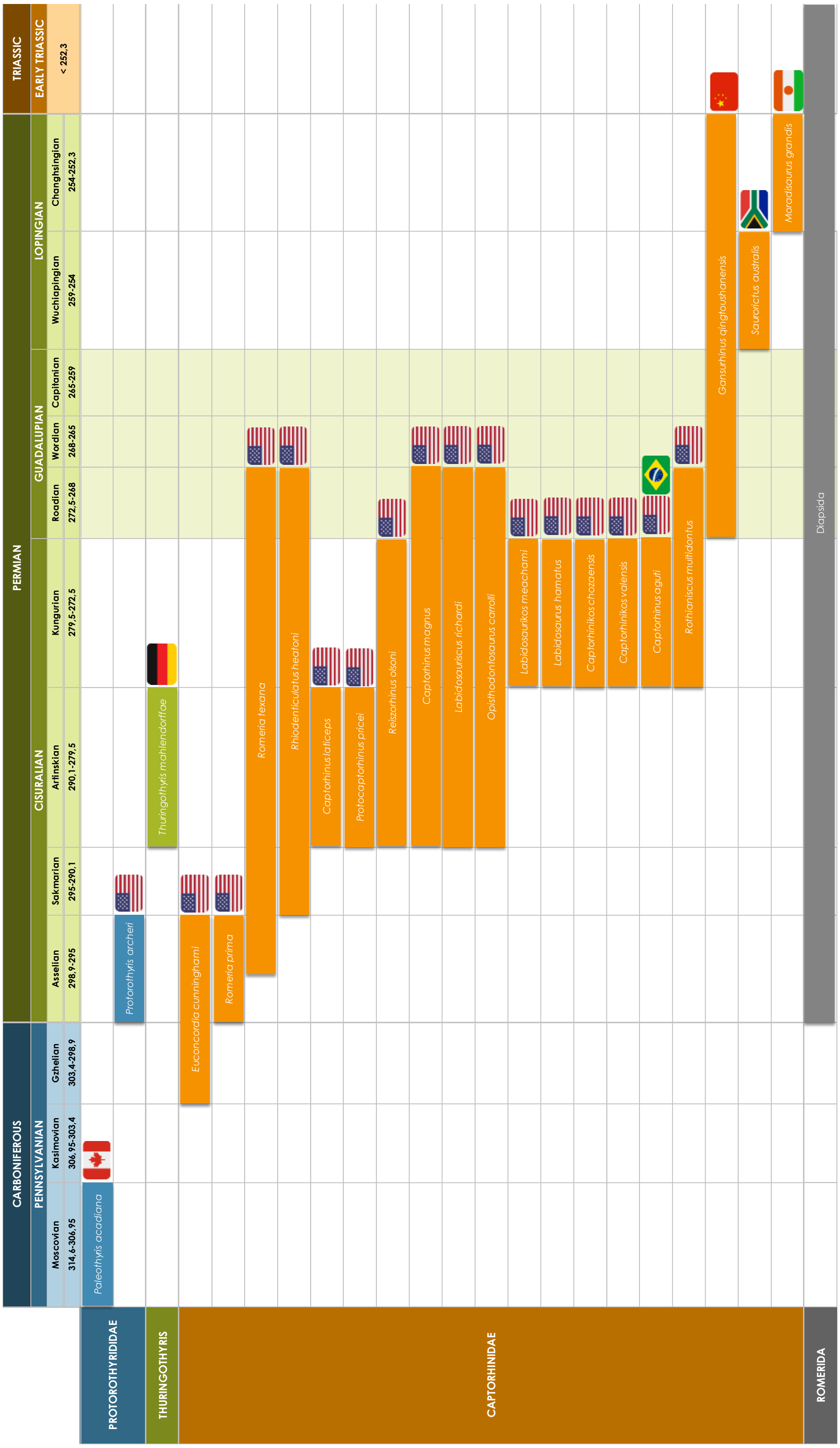


Figure 3: Captorhinomorph geological timeline information. Flags represent countries where the holotype of the respective species was discovered.

### c. Skull sculpturing: a conspicuous character

Throughout the years, several authors have used multiple osteological/morphological characteristics when describing the cranium of captorhinids in order to identify clades at different levels. One cranial character commonly used is the presence of skull sculpturing (ornamentation), namely in the following bones: premaxilla, nasal, lacrimal, prefrontal, frontal, postfrontal, postorbital, jugal, parietal, squamosal, quadratojugal, supratemporal, postparietals, dental (Case, 1911; Modesto, Scott & Reisz, 2018; Seltin, 1959).

The character states for skull sculpturing are not well-defined. This issue gets more complex as authors describe the skull sculpturing in different ways.

Some, like Müller et al., describe the sculpturing of the skull roof in a general way: “strongly reduced dermal sculpturing of the skull roof […] absence of significant [skull roof] dermal sculpturing.” (Müller, Berman, Henrici, Martens & Sumida, 2006).

Others prefer to assess “cranial texture” individually, bone-by-bone, like Sumida et al.: “Little may be made of the dermal sculpturing from the [holo]type, but CM 81785 indicates that it was very well developed (…) The pattern of dermal sculpturing [on the lacrimal] suggests that a well-developed centre of ossification was located just rostral to the anteroventral margin of the orbit […] postparietal surface is smooth except for a groove that divides it […] [the] surface [of the jugal] demonstrates clearly a pattern of elongate grooves radiating from the posteroventral margin of the orbital […] the occipital exposure of the squamosal was devoid of sculpturing […] Dermal sculpturing on the holotype [lower jaws] is faint, but it is clear and well developed in CM 81785 […] the angular and other laterally exposed elements of the mandible in CM 81785 demonstrate [sculpturing] clearly. Significantly, the sculpturing extends onto the medial surface of the angular” (Sumida et al., 2010).

Other authors define skull sculpturing by comparison, for example when describing *Labidosaurikos meachami* (Dodick & Modesto, 1995). In other species, e.g. *Captorhinus aguti* and *Captorhinus magnus* (Modesto, 1998; LeBlanc & Reisz, 2015) the published information is scarce regarding cranial sculpturing. Finally, there are also important issues that may result from erosion, taphonomy deformation or event preparation artefacts

(Berman & Reisz, 1986). As an example, in *Romeria prima*, the absence of skull sculpturing is “almost certainly the result of mechanical preparation, [not indicating] […] a lack of sculpturing in the living animal.” (Carroll & Clark, 1973).

What is very clear is that the surface of cranial bones of captorhinids presents a very conspicuous and understudied trait: the sculpturing.

### d. Morphological characters and phylogenetic analyses

As previously mentioned, palaeontological studies are usually restricted to the use of morphological characters to perform phylogenetic analyses. By their nature, the analysis of this type of characters involves a sequence of methodological decisions and implicit assumptions, unlike analyses of molecular data (Wiens, 2001). Wiens presents as examples of these assumptions and decisions choosing whether intraspecifically variable characters can be included, how authors decide to code within-species variation, and the way researchers decide (or not) to weigh different types of morphological characters relatively to each other (Wiens, 2001). However, as Wiens states, “practitioners of morphological characters tend not to be explicit about their methodology, specifically how morphological characters are selected, and how states are defined, delimited, coded and ordered” (Wiens, 2001). There are three fundamental problems of character analysis: vague character state definitions, arbitrary character state delimitation, and ordering of character states (Wiens, 2001). We noticed that some characters commonly used in captorhinids phylogenetic analyses had these exact problems. As such, we attempted to overcome these issues following a standardized method described in Chapter 2, using some suggestions proposed by Wiens. In the end, we obtained an updated and more complete character list. Studies based on this new matrix are expected to yield a more robust phylogenetic signal while helping to improve reproducibility in the future.

It was also clear during this project that the task of identifying bone structures and assessing morphological character states is challenging, especially without published visual representations of the existing variability within each character state. Hence, we constructed a portfolio (Appendix 10) containing visual representations of all morphological characters considered and their respective character states. This will also help to solve possible ambiguous interpretations that might occur in the future.

Skull sculpturing is present in multiple captorhinids and might prove itself crucial in phylogenetic analysis. However, to our knowledge, there is no comprehensive publication testing this hypothesis and the anatomical descriptions present in the literature can be confusing and ambiguous (see Methods section). In order to tackle these issues, we started by conducting a comprehensive literature review and combined it with a thorough study of captorhinid cranial morphology using not only graphical image manipulation techniques but also statistical analyses to test multiple hypotheses (see Methods section). In the Discussion and Conclusions sections, we combined these results and generated new captorhinid phylogenies that may shed light into the evolutionary trajectory of several conspicuous morphological traits and help researchers better distinguish between notably similar species.

## 2. Methodology

In order to redefine the concept of skull sculpturing, we compiled all available literature on captorhinomorphs and searched for keywords related to this characteristic. We then compiled this descriptive information for 23 species. We opted to only use the expression "skull sculpturing" in this text, which we deem as the most appropriate (see Section 4. b).

At the same time, we collected all available images where skull sculpturing could be identified and prepared them to be sorted and analysed. We analysed them using graphical image software, where we were able to identify different characteristics of skull sculpturing, and then conducted a statistical analysis to identify differences between parts of the cranium (Section 2.a.).

We compiled the most updated list of morphological characters used for phylogenetic analysis in captorhinids (Modesto et al., 2018) (Appendix 1). Upon careful reading, some characters had issues which required refinement, redefinition, recoding or had to be removed. As such, we decided to build a visual portfolio with all current morphological cranial characters, displaying each problematic character and respective proposed solution (see Appendix 6). The methodology used is described in Section 2. b., with a more detailed description per character in the Results chapter.

Of all described captorhinids, only 20 species have been regularly included in phylogenetic analyses: *Euconcordia cunninghami, Rhiodenticulatus heatoni, Romeria prima, Romeria texana, Protocaptorhinus pricei, Saurorictus australis, Captorhinus aguti, Captorhinus magnus, Captorhinus kierani, Captorhinus laticeps, Captorhinikos valensis, Captorhinikos chozaensis, Labidosaurus hamatus, Labidosaurikos meachami, Moradisaurus grandis, Rothianiscus multidontus, Gansurhinus qingtoushanensis, Reiszorhinus olsoni, Opisthodontosaurus carrolli* and *Labidosauriscus richardi* (Müller & Reisz, 2006; Modesto et al., 2018; deBraga, Bevitt & Reisz, 2019). *Captorhinikos* sp., *Gansurhinus*, *Labidosaurikos*, *Moradisaurus* and *Rothianiscus* comprise the subfamily Moradisaurinae. We opted to add two Protorothyrididae species as they have been extensively used in literature as outgroups: *Protorothyris archeri*, *Paleothyris acadiana* (Müller & Reisz, 2005). Finally, we included the species *Thuringothyris mahlendorffae,* considered a sister taxon to Captorhinidae (Müller & Reisz, 2005). There are more species of captorhinids that have been described, but we opted not to include them because some are considered *nomen dubium*, others have not been thoroughly studied, some are described based on very few fragmented specimens, and others (namely *Riabinius* sp., *Riabinius uralensis* and *Gecatogomphius kavejevi*) were published in Russian (a language we are not proficient in).

### a. Skull sculpturing analysis

The shape and pattern of cranial bone surface (skull sculpturing) is a complex morphological character which is hard to analyse, although it is commonly used in anatomical descriptions as seen in the previous section (see Section 3 a. for more examples). This is due not only to the lack of understanding of its biological significance but also to the different approaches and terms used by different authors. Hence, we started by compiling all available images of skull sculpturing in captorhinids.

We imported images to Krita (an open-source image editing *software*), where we traced the skull sculpturing features, resulting in images of the reticulate present in each skull (Figure 4). This allowed for a clearer overview of all skull sculpturing features and facilitated the standardization of nomenclature and the character score of this trait.

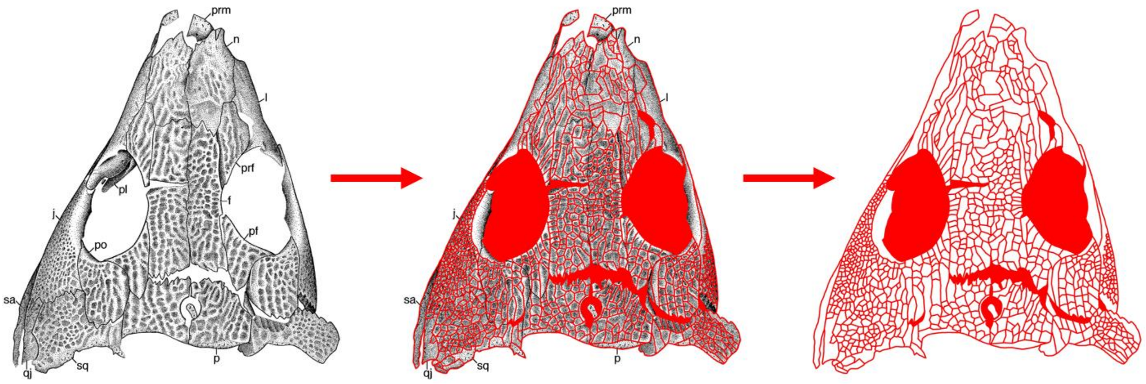
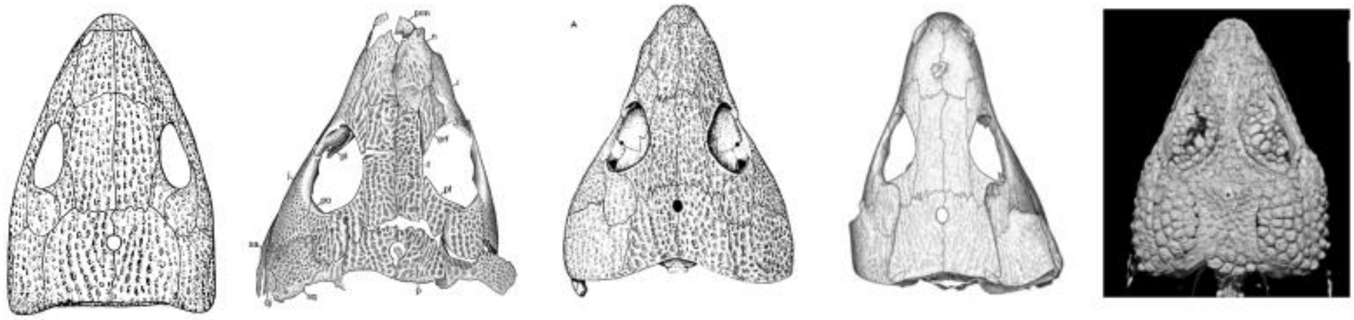


*Figure 4: Dorsal view of* Captorhinus aguti*, originally in Modesto 1998. Steps of skull sculpturing drawing process.*

Multiple images had an incomplete portrayal of the skull sculpturing or represented damaged/incomplete skulls. Therefore, we performed a detailed analysis of the more complete skulls, selecting the images with better quality (*Protocaptorhinus, Captorhinus aguti, Captorhinus laticeps, Captorhinus kierani*). We also included an extra skull from an extant lizard species (*Xenosaurus newmanorum*, of the Xenosauridae family; in Bhullar 2011) to this graphical treatment and used it as a reference, as its anatomy is resembling of captorhinids, specifically the presence of skull sculpturing (see Figure 5).



*Protocaptorhinus pricei*, in Olson 1964

*Captorhinus aguti*, in Modesto 1998

*Captorhinus laticeps*, in Heaton 1979

*Captorhinus kierani*, in deBraga et al. 2019

*Xenosaurus newmanorum*, in Bhullar 2011

*Figure 5: Plate of all craniums subjected to statistical analysis.*

We then imported the resulting skull sculpturing networks into FIJI (Schindelin, Arganda-Carreras, Frise et al., 2012) where we extracted data regarding the number of polygons present and their size and density.

In order to assess the presence or absence of symmetry between left/right sides or anterior/posterior areas, we used RStudio to multiple statistical tests and find significant differences in sculpturing distribution (Figure 6).

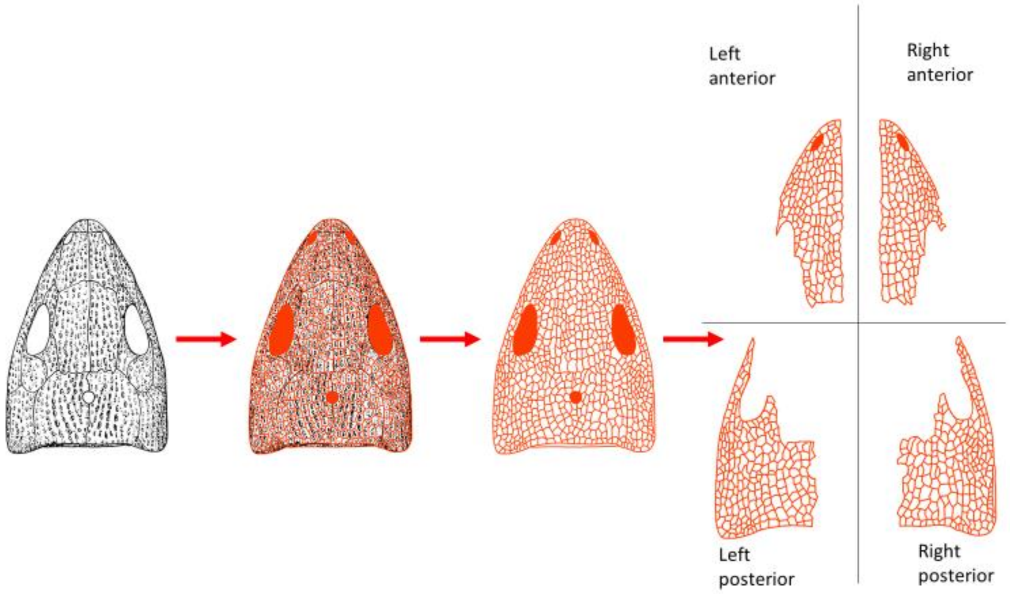
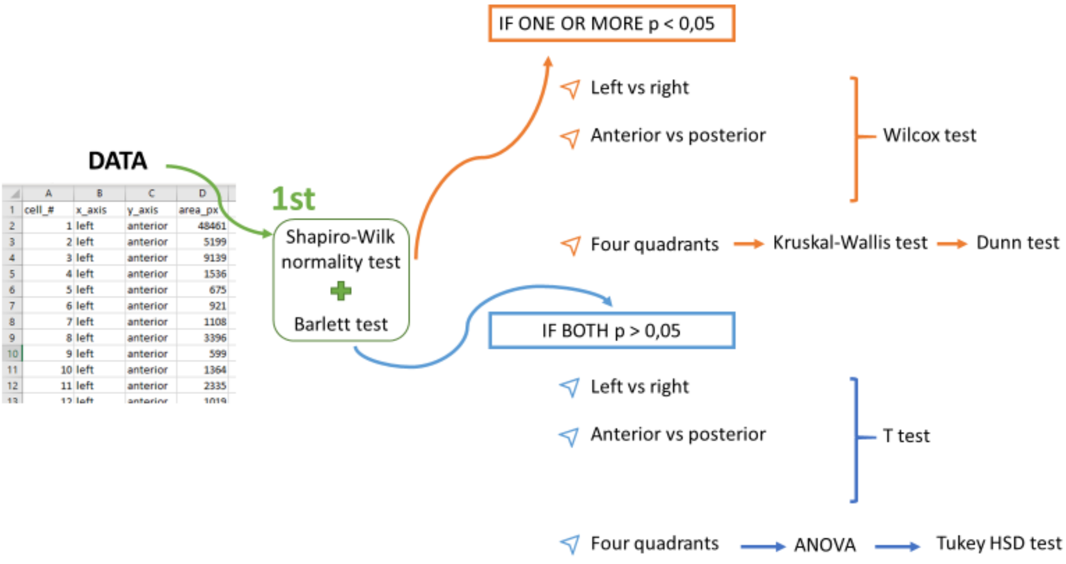


*Figure 6: Diagram of image manipulation process in Krita.* Protocaptorhinus pricei*, in Olson 1964.*

Left-right sides were split sagittally according to the medial suture across the skull. The anterior part of the skull includes premaxilla, maxilla, nasal, frontal and lacrimal bones. The posterior part of the skull includes parietal, postparietal, postorbital, postfrontal, squamosal, quadratojugal, and jugal bones. This division follows the definition of the temporal bone series in primitive tetrapods made by Romer (Romer & Parsons, 1986). If the craniums were distorted, we superimposed the left and right halves and deleted what was present only on one side, removing the excess.

First, we ran a Shapiro-Wilk test in order to assess the normality of the data, followed by a Bartlett test for testing the variance (when necessary). If the data values were parametric, we performed a T-test or ANOVA. Otherwise, we ran a Wilcox signed-rank test or a Kruskall-Wallis test for non-parametric data values. When comparing two sets of data, if T-test or Wilcox test yielded a probability value (p-value) less than 0,05, we considered the samples to be significantly different; when comparing more than two sets of data, if the ANOVA or Kruskall-Wallis tests yielded probability values less than 0,05, we considered the samples to also be significantly different. In this last case, we ran a post-hoc test (Tukey HSD test or Dunn test, respectively) in order to determine which data sets were significantly different. Below is reproduced a scheme of the statistical analysis process for more clarity on the subject (Figure 7). The results are present in the Results chapter and discussed in the Discussion chapter.



|  | A | B | C | D |
|---|---|---|---|---|
| 1 | cell_# | x_axis | y_axis | area_px |
| 2 | 1 | left | anterior | 48461 |
| 3 | 2 | left | anterior | 5199 |
| 4 | 3 | left | anterior | 9139 |
| 5 | 4 | left | anterior | 1536 |
| 6 | 5 | left | anterior | 675 |
| 7 | 6 | left | anterior | 921 |
| 8 | 7 | left | anterior | 1108 |
| 9 | 8 | left | anterior | 3396 |
| 10 | 9 | left | anterior | 599 |
| 11 | 10 | left | anterior | 1364 |
| 12 | 11 | left | anterior | 2335 |
| 13 | 12 | left | anterior | 1019 |

*Figure 7: Workflow of statistical analysis performed*

### b. Morphometry

As previously mentioned, in order to run a phylogenetic analysis, a matrix comprised of several characters and their correspondent states is required. In the case of fossil species, these characters are exclusively morphological and can range from the presence or absence of a certain bone, to the ratio between two measurements, the number of teeth or the position of a foramen.

Basal states were coded as 0 and derived states as 1, 2 or 3.

The resulting matrixes were run on version 4 of PAUP* (Swofford, 2003), which generates phylogenetic trees using the single most parsimonious tree of strict consensus or predefined majority rules.

We used the most recent phylogenetic character list for captorhinids currently published as a starting point (Modesto et al., 2018), which can be found in Appendix 1 of this dissertation. This matrix comprises 75 characters (Appendix 2). Of these, 65 (87%) pertain to cranial characters (of which 12 pertain to teeth) and 10 (13%) to post-cranial characters. The characters can be divided into quantitatives and qualitatives. Only 12 out of the 75 characters are quantitative, referring either to a proportion between two measurable dimensions of one or more structures (e.g. length and/or height of the cranium/of a specific bone/of a bone process/of a contact between bones/of a foramen), or to an angle between two structures. The remaining characters are qualitative, referring to the presence or absence of a specific structure, to the position or format of that structure, or refer to the proportions between two structures in a not-measurable way (i.e. "lateral process of opisthotic bone short").

In the work here presented we only analysed cranial characters. As such, there will not be any comments or changes in post-cranial characters.

When analysing the character list, it was obvious that certain characters had issues that could hinder not only their precision and accuracy, but also undermine further research: a) by authors who are not familiarized with this group of fossils, b) that do not have direct access to specimens, or c) introduce different levels of uncertainty depending on the characters chosen to perform an analysis.

The main problems with cranial characters found were the following:

- Double characters: characters that codified more than one aspect or more than one structure at the same time. Example: (40) Jugal/ectopterygoid: ectopterygoid present and alary process absent (0); ectopterygoid absent and alary process present, but no higher than the midpoint of the suborbital process of the jugal and distinct from the orbital margin (1); ectopterygoid absent and alary process present and positioned dorsally on the medial surface of the jugal, flush with orbital margin (2) (Modesto et al., 2018).

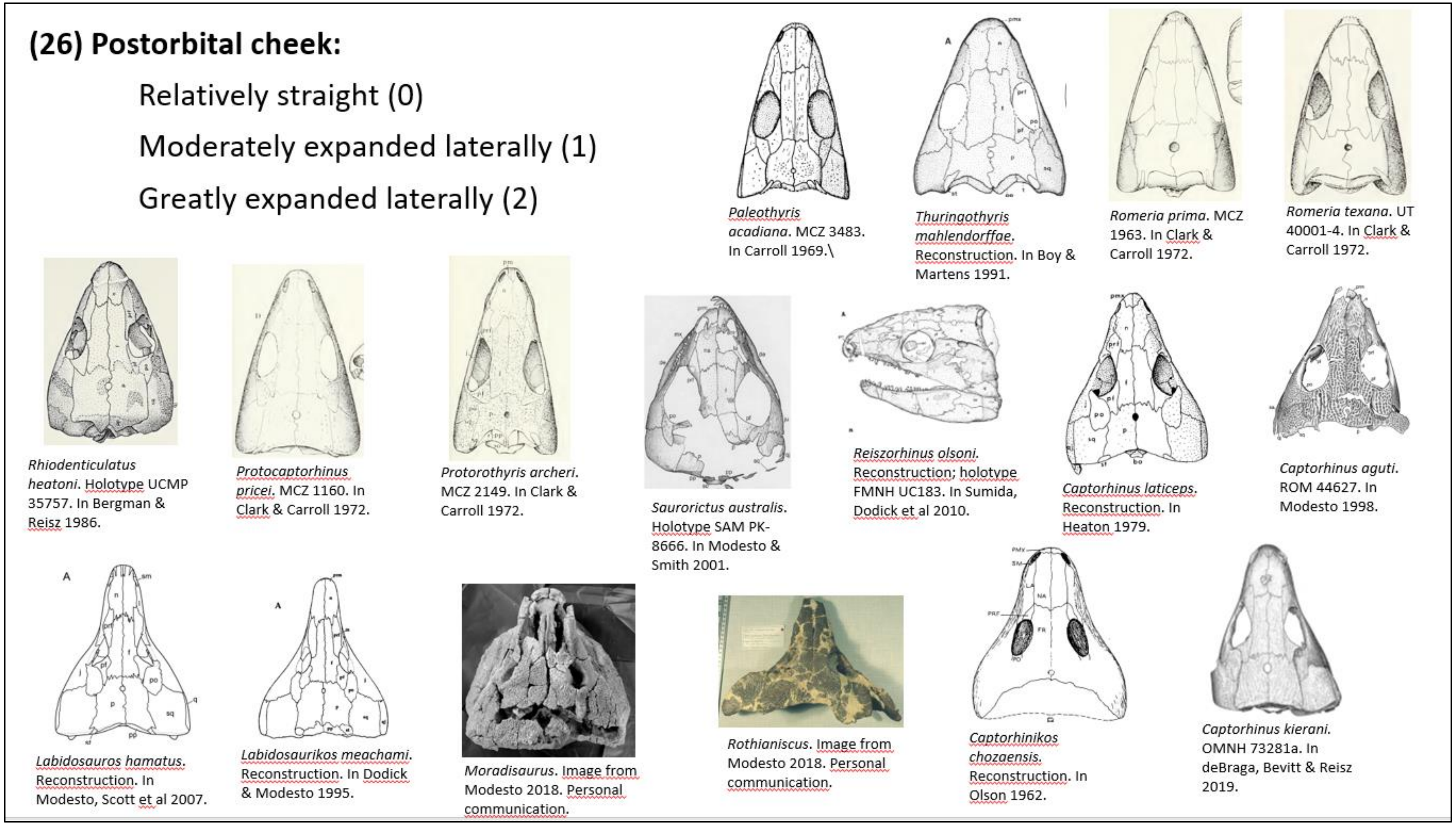
- Characters that are difficult to identify: characters that refer to a conspicuous structure that is hard to identify in skeletal remains, or of difficult access (for instance, require detailed CT scanning). Example: "(53) Supraoccipital: lateral ascending processes account for half or less height of the bone (0); lateral ascending processes account two-thirds or more height of the bone (1)” (Modesto et al., 2018).

- Qualitatives traits that should be quantitatives: characters that refer to a dimension that is measurable but do not assign any numerical threshold. Example: (13) Lacrimal: suture with jugal small (0); well developed (1). (Modesto et al., 2018).

- Non-informative characters: characters that are coded as (?) for most species or that are mostly coded the same way across all species. Example (Figure 11): (55): Exoccipital: lateral process on dorsal ramus absent (0); lateral process present (1). (Modesto et al., 2018).

- Lack of consensus: usually these characters are interpreted differently by different authors (i.e. uncertainty about which part of a structure is being referred). Example: (51) Stapes: distal process short (0); distal process elongate (1). (Modesto et al., 2018).

As such, we did a complete review of the cranial character list (Appendix 3, resulting in the matrix presented in Appendix 4). Some characters were removed, others were redescribed, and some others were replaced. This will be discussed in-depth in the Results and Discussion chapters. After identifying a problematic character, we either removed it or replaced it with a new proposed character. If the character was useful but not well defined, we modified the description. In order to help with these modifications and decisions, we constructed plates of available images in which the character could be observed (Figure 8 for an example regarding character 26).



**(26) Postorbital cheek:**

Relatively straight (0)

Moderately expanded laterally (1)

Greatly expanded laterally (2)

*Paleothyris acadiana*. MCZ 3483. In Carroll 1969.\

*Thuringothyris mahlendorffae*. Reconstruction. In Boy & Martens 1991.

*Romeria prima*. MCZ 1963. In Clark & Carroll 1972.

*Romeria texana*. UT 40001-4. In Clark & Carroll 1972.

*Rhiodenticulatus heatoni*. Holotype UCMP 35757. In Bergman & Reisz 1986.

*Protocaptorhinus pricei*. MCZ 1160. In Clark & Carroll 1972.

*Protorothyris archeri*. MCZ 2149. In Clark & Carroll 1972.

*Sauroríctus australis*. Holotype SAM PK-8666. In Modesto & Smith 2001.

*Reiszorhinus olsoni*. Reconstruction; holotype FMNH UC183. In Sumida, Dodick et al 2010.

*Captorhinus laticeps*. Reconstruction. In Heaton 1979.

*Captorhinus aguti*. ROM 44627. In Modesto 1998.

*Labidosauros hamatus*. Reconstruction. In Modesto, Scott et al 2007.

*Labidosaurikos meachami*. Reconstruction. In Dodick & Modesto 1995.

*Moradisaurus*. Image from Modesto 2018. Personal communication.

*Rothianiscus*. Image from Modesto 2018. Personal communication.

*Captorhinikos chozaensis*. Reconstruction. In Olson 1962.

*Captorhinus kierani*. OMNH 73281a. In deBraga, Bevitt & Reisz 2019.

*Figure 8: Plate of all dorsal views available for all species of captorhinids considered.*

New characters and modifications of existent characters went through the following process: firstly, we measure the elements needed for that specific character in every species. To identify thresholds that could be used to set character states we exclude the outliers and identify the largest gap within the value distribution. We used the midpoint of that value as a threshold to divide the species into two groups and create categories that corresponded to the new character states. The group that included the outgroup (*Protorothyris archeri*) was assigned the character state (0). On some characters, if the second-largest gap was equal to or above 75% of the largest gap we defined a third group and assigned character state (2) to it.

### c. Phylogeny

We started by using an initial character list comprised of 75 different characters, with 65 pertaining to skull morphology (Modesto et al., 2018; see Appendix 1 and 2).

Of these, 15 (out of 65) were considered problematic and removed, resulting in the character list and matrix present in Appendix 3 and 4.

Then, a new species (*Captorhinus kierani*) was coded and added to the previously mentioned matrix, resulting in the matrix present in Appendix 5.

After the process mentioned in Section 2. b. (further discussed in Section 3. b. and Section 4. a.), a new matrix with a total of 89 characters was generated. This matrix and its correspondent character list comprise Appendix 7 and Appendix 8.

Another 11 new characters, concerning exclusively to skull sculpturing, were added to the matrix present in Appendix 8, resulting in a new matrix with a total of 100 characters, and a new recommended morphological characters list (Appendix 9 and Appendix 10 respectively).

A complete visual portfolio for all characters is available on supplementary material in digital format, to be used as a guide (Appendix 11).

# 3. Results

This chapter is divided into three sections.

In the first section, we present a literature review of all mentions of skull sculpturing in captorhinomorphs. This section will allow the reader to have an overview of the different terms and ways authors use to refer to this character.

The second section is dedicated to the morphological characters used for phylogenetic analysis of captorhinids, where all changes made to the character list of Modesto et al. 2018 are described, character by character, finishing with the updated character lists, matrixes, and corresponding phylogenetic trees.

The third section focuses on skull sculpturing. Here we list the new characters proposed to evaluate this feature, the resulting character matrix, the corresponding phylogenetic tree and the results from the statistical analysis.

## a. Skull sculpturing in captorhinomorphs

***Protorothyris archeri***

Initially described by Price in 1937 (Price, 1937), Clark and Carroll later revised both the generic and specific diagnosis of the species (Clark & Carroll, 1973). They based the diagnosis on the holotype specimen MCZ 1532 and another referred specimen (paratype), all found in Cottonwood Creek, Moran Formation, Lower Permian of Texas, U.S.A. (Clark & Carroll, 1973). In the paper, they state that skull bones of *Protorothyris archeri* are “marked by uniformly distributed shallow pits” (Clark & Carroll, 1973). They add that the “cheek region and skull roof are uniformly sculptured with a pattern of evenly distributed pits and grooves” (Clark & Carroll, 1973). The authors also compare this sculpturing pattern with the one present in the other Pennsylvanian romeriids[1], which is more pronounced in *P. archeri* (Clark & Carroll, 1973). Clark and Carroll describe the nasal, lacrimal, maxilla, premaxilla and quadratojugal bones as nearly smooth. The external surface of the lower

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[1] Old denomination for a group of captorhinomorphs that lived from Early Pennsylvanian to Early Permian. Also known as Romeriidae. Comprised of several species including *Protorothyris* sp.; considered an invalid subgroup of Protorothyrididae according to Reisz 1980.

jaw is not sculptured (Clark & Carroll, 1973). Although the paper presents images of skull reconstructions, it is dubious whether the skull sculpturing is present (Clark & Carroll, 1973).

### *Paleothyris acadiana*

This species of romeriid captorhinomorph was first described in 1969 by Carroll (Carroll, 1969). The holotype of *Paleothyris acadiana* is specimen MCZ 3481, comprised of an almost complete skeleton, found at the Dominion Coal Co. strip mine nº 7, Morien group, Carboniferous of Nova Scotia, Canada. Carroll refers that "The bones of the skull roof, particularly the parietals, are marked by delicate pitting radiating from the centres of ossification" (Carroll, 1969). "The frontals […] are marked by linear striations. In MCZ 3483 [a paratype] the maxilla is almost smooth, but others [paratypes] show pitting of variable extent and degree. […] The premaxilla is regularly pitted." (Carroll, 1969). The referred author included images of skull reconstructions, but it is unclear if the skull sculpting is represented or not (Carroll, 1969).

### *Thuringothyris mahlendorffae*

*Thuringothyris mahlendorffae* is a sister taxon of Captorhinidae described by Boy and Martens in 1991. The holotype (MNG 7729) was found at the Bromacker Quarry in the Tambach Formation, Lower Permian of Germany (Boy & Martens, 1991). The authors mention that the sculpturing of the roof "is only partially preserved" (Boy & Martens, 1991). "As far as still recognizable, it consists of flat, irregular, radially extending valleys and intervening furrows." (Boy & Martens, 1991). The article also provides an illustration of the skull roof where dermal sculpturing is omitted, rendering it useless for further skull sculpturing analysis (Boy & Martens, 1991). There are no mentions of the presence or absence of skull sculpturing in the mandibular rami of the specimen (Boy & Martens, 1991).

New specimens were recovered in this area (Müller et al., 2006). As such, Müller et al. redescribed the skeletal anatomy of *T. mahlendorffae* in 2006 (Müller et al., 2006). Starting with the systematic palaeontology of *Thuringothyris*, the authors refer the "strongly reduced dermal sculpturing of the skull roof." (Müller et al., 2006). This lack of dermal sculpturing is reinforced in the description of the skull roof: “Notable features of the skull […] include […] the absence of significant dermal sculpturing.” (Müller et al., 2006). This paper has a photograph of the dorsal view of the skull case of the holotype, being easy to confirm the absence of skull roof sculpturing (Müller et al., 2006).

***Euconcordia cunninghami***

Müller and Reisz describe *Euconcordia cunninghami* in 2005 as the oldest known member of the Captorhinidae clade, under the designation *Concordia cunninghami* (Müller & Reisz, 2005). This taxon was known based on two remains from the Hamilton Quarry, Greenwood County, Upper Pennsylvanian of Kansas, U.S.A., one being the holotype (KUVP 8702a & b), and the other a referred specimen (KUVP 96/95) (Müller & Reisz, 2005). In the description of the skull roof, the authors mention the existence of a “distinct pattern of sculpturing, similar to that seen in small captorhinids, even though it appears less well developed than in other well-known forms such as *Captorhinus*.” (Müller & Reisz, 2005). The postparietal is described as lacking “any dermal ornamentation or sculpturing.” (Müller & Reisz, 2005). The authors distinguish the anterior and posterior parts of the supratemporal, “The anterior portion of the [supratemporal] bone […] is slightly sculptured, whereas its posterior part […] has a smooth surface”, adding that the “temporal part of the squamosal is gently sculptured” (Müller & Reisz, 2005). Regarding the lower jaw, the authors state that “most of the external surface of the mandible is smooth and lacks extensive dermal sculpturing, a condition that is not due to preparation.” (Müller & Reisz, 2005). The article is accompanied by several images, including a drawing of the holotype skull in which the sculpturing is represented. In addition, this skull sculpturing is also visible in LeBlanc & Reisz, 2015.

Finally, in 2016, as *Concordia* was then preoccupied with an extant hippolytid crustacean, *Concordia cunninghami* was renamed as *Euconcordia cunninghami* (Reisz, Haridy, & Müller, 2016). The authors redid its systematic palaeontology, emending the initial diagnosis by Müller and Reisz in 2005. The paper presents the same photograph of the holotype skull that LeBlanc and Reisz published in their 2015 paper, but in colour and higher resolution, allowing us to have a much clearer idea of how the skull sculpturing is

(Reisz, Haridy, & Müller, 2016). The presence of a "sculptured lateral surface of the dentary and surangular bones" is mentioned again (Reisz, Haridy, & Müller, 2016). The rest of the amends and updates present in the redescription pertain mainly to dental morphology and palate, with nothing else being said about the dermal sculpturing of the skull (Reisz, Haridy, & Müller, 2016).

### ***Romeria prima***

Initially named *Romeria primus*, this species was first described in "Romeriid reptiles from the Lower Permian", by authors Clark and Carroll, in 1973. Its holotype (MCZ 1963) is comprised of a skull and some postcranial material, found in Cottonwood Creek, Moran Formation, Lower Permian of Texas, U.S.A. (Clark & Carroll, 1973). They state that the skull was very smooth but not by the absence of sculpturing. Instead, Clark and Carroll deem it to be "almost certainly the result of mechanical preparation, [not indicating] […] a lack of sculpturing in the living animal." (Clark & Carroll, 1973). For this reason, the images of reconstructions present in the paper are not useful for assessing skull sculpturing (Clark & Carroll, 1973).

### ***Romeria texana***

*Romeria texana* was first described in 1937 by Price (Price, 1937). In 1973, Clark and Carroll evaluated its specific diagnosis (Clark & Carroll, 1973). The holotype (MCZ 1480) was found at Archer City Bonebed 1, Putnam Formation, Lower Permian of Texas, U.S.A. (Clark & Carroll, 1973). The authors also used as a referred specimen individual UT 40001-4 from the same horizon and locality. Like *R. prima*, the specimen "shows almost no sculpturing of the dermal bones, [it being] almost certainly the result of polishing in the course of mechanical preparation" (Clark & Carroll, 1973). However, a "pattern of shallow, scattered pits can be dimly perceived", raising questions about the real level of sculpturing of this cranium (Clark & Carroll, 1973). Similarly, the surface detail of lower jaws of the holotype had also been blunted during extraction and/or preparation of the remains (Clark & Carroll, 1973). The other referred specimen is a juvenile "preserved in a very resistant ironstone matrix" (Clark & Carroll, 1973). Its bone surface "was almost destroyed during preliminary preparation", so the authors were not able to draw further observations on the sculpturing of the skull. Just like for *R. prima*, the images of reconstructions present in the paper are not useful for assessing skull sculpturing (Clark & Carroll, 1973).

### ***Protocaptorhinus pricei***

Clark and Carroll described the new genus *Protocaptorhinus* and the new species *Protocaptorhinus pricei* in 1973. The holotype specimen MCZ 1478 was found in Rattlesnake Canyon, Admiral Formation, Lower Permian of the U.S.A. (Clark & Carroll, 1973). The authors describe the skull roof as being "deeply sculptured with uniformly distributed oval pits" (Clark & Carroll, 1973). They also mention that its "surface is deeply pitted, more like *Captorhinus* than earlier romeriids, although the individual pits are noticeably wider than in that genus [*Captorhinus*]" (Clark & Carroll, 1973). This is a clear example of a comparison being used to describe the state of a morphological character. The last reference to sculpturing regards the sculpturing of the dentary, which the authors deemed "lightly sculpted" (Clark & Carroll, 1973). There is no information in the captions of the reconstruction images present in the paper regarding the representation of skull sculpturing (Clark & Carroll, 1973).

Olson published a paper in 1984 in which he reviewed the description of the captorhinomorph *Pleuristion brachycoelus* made by Case in 1902. Olson declared it *nomen nudum* and reassigned all materials used for its description to *Protocaptorhinus pricei* as described by Carroll and Clark (Olson, 1984). This material included *P. brachycoelus* holotype (KU 351a), composed of three vertebrae, and referred specimen FMNH PR 678, which includes a skull and lower jaw (Olson, 1984). Both were discovered in Orlando, Logan County, Lower Permian of Oklahoma, U.S.A. (Olson, 1984). The author also used previously undescribed material on his analysis, from older collections and new remains collected since 1965 (Olson, 1984). On the comparison of character states between *P. pricei* and the material analysed, Olson mentions: "sculpturing of skulls in the Orlando captorhinomorph is less uniform than that figured and described for *P. pricei* […] Pits are somewhat elongated and arranged linearly in the interorbital region" (Olson, 1984). The text directs the reader to several figure drawings of the skull and jaw material, in which the sculpturing is well-evident (Olson, 1984). There are also photographs of remains in lateral and dorsal views where skull sculpturing can be discerned (Olson, 1984). The specimen used for these is UCLA VP 3621, which the author later uses as the basis for a description and discussion about dermal ossifications present in *P. pricei* (Olson, 1984). Olson notes that these ossifications are long and ribbon-like, adding that they are “closely associated with […] the dermal surface of the skull and jaws, where they occur in patches” (Olson, 1984). He also mentions that the “patches on the skull and jaws show no identifiable orientation relative to the long axes of these structures. Where not directly associated with bones the dermal ossifications are infolded and tend to form clumps and elongated bundles.” (Olson, 1984). Olson described the width range of these osseous ribbons as being between 1,5 to 3,0 mm, with a constant thickness of 0,5 mm, adding that the “fact that the thin ossifications occur throughout the nodule and are associated with various parts of the skeleton indicates that the full body, including the head and jaws, were covered by them.” (Olson, 1984). After studying cross-sections of these structures under a polarizing microscope, the author found “distinct marginal bands. In addition, an opaque band passes along the surface of the external dense layer but is absent on the internal one. Optical properties of the minerals […] indicate that the mineralization is primarily calcitic; the long axes are divided into a series of […] equidimensional segments, [...] Pore-like canals pass through the ossifications, normal to the long axes. The passages are flanked by a dense mineral, similar to that of the marginal bands, but less uniform. In places, along the outer surfaces of the ossifications, the dark band passes over the openings of the canals but in others it does not.” (Olson, 1984). Olson finishes the description of skull sculpturing characteristics by stating that “the segmental structure may be of biological origin but again it may be due to mechanical post-mortem actions. Although intriguing, origin of the detailed structure remains problematical.” (Olson, 1984). Olson proposes some biological and ecological hypothesis for the existence of this dermal sculpturing in captorhinids, such as the suggestion that this “the osseous cover may have served to retard excessive water loss”, or that “the canals may have carried fluids, perhaps moisturizers or nutrients to the skin overlying the ossifications.” (Olson, 1984).

### ***Rhiodenticulatus heatoni***

In 1986, Berman and Reisz described a specimen (UCMP 35757) as the holotype of a new genus and species of a captorhinid, *Rhiodenticulatus heatoni* (Berman & Reisz, 1986). The authors based this description on skulls and partial postcranial skeletons found in the Cutler Formation, Early Permian of New Mexico, U.S.A. (Berman & Reisz, 1986). Initially described by Williston (Williston, 1916) as *Puercosaurus obtusidens* (FMNH 743 and FMNH 745), the appearance of more remains in Lower Permian deposits in the same area required a re-examination of the type specimens (Berman & Reisz, 1986). Berman and Reisz discovered that besides the circumstances making *P. obtusidens* a *nomen dubium*, the other specimens collected were unique and well-preserved enough to be referred to as a new genus and species: *Rhiodenticulatus heatoni* (Berman & Reisz, 1986). In the description of the skull, the authors refer that "most of the superficial features of the skulls, such as sculpturing, have been lost due to weathering and excessive preparation" (Berman & Reisz, 1986). Nothing is said about the sculpturing of the mandibular rami either (Berman & Reisz, 1986). The article has some illustrations of the skull roof, with certain areas in greyscale that seem to indicate the type of sculpturing present (Berman & Reisz, 1986).

### ***Saurorictus australis***

Described in 2001 by Modesto and Smith, *Saurorictus australis* is a species of captorhinid from the Late Permian of the South African Karoo (Modesto & Smith, 2001). The authors based the species description in a single specimen from the Western Cape Province, SAM PK-8666, which is comprised of a very complete skull with some postcranial fragments (Modesto & Smith, 2001). Due to being preserved in hard mudstone, there was a "loss of much of the skull table and portions of other roofing elements" (Modesto & Smith, 2001). However, "sculpturing on other areas of the skull roof has escaped extensive weathering, judging from the left, protected side of the skull." (Modesto & Smith, 2001). Namely, the "jugal, the postorbital, and the squamosal are very lightly sculpted with the distinctive ridge-and-pit ornamentation seen in […] skulls of other captorhinids." (Modesto & Smith, 2001). The article provides images/reconstructions of the specimen in dorsal and both lateral views (Modesto & Smith, 2001). Even though it is not mentioned either in the captions or text, it seems like the grey patterns present in the drawings are representative of the skull sculpture of the holotype (Modesto & Smith, 2001).

### *Captorhinus laticeps*

Williston in 1909 described a new species of captorhinid (FMNH UC 642) from the Clyde Formation, Baylor County, Texas, U.S.A., naming it *Pariotichus laticeps* (Williston, 1909). Upon reviewing this family two years later, Case synonymized it with *Captorhinus isolomus* (Case, 1911).

Subsequent work considered this *Captorhinus* species to be the same as *Captorhinus aguti* (Seltin, 1959). In 1973, Carroll and Clark note that the specimen described by Williston had single-rowed teeth (Clark & Carroll, 1973), suggesting that it did not pertain to the genus *Captorhinus*. At the time *Captorhinus* were assumed as always having multiple teeth rows. Eventually, this specimen would become the holotype of *Eocaptorhinus laticeps* by work of Heaton, published in 1979.

*Captorhinus laticeps* was also initially named *Labidosaurus oklahomensis* by Seltin in 1959. The holotype was specimen MUO 3-1-S7 (now OUSM 15022), a well-preserved cranium, from the McCann Quarry, Wellington Formation, Kay County, Early Permian of Oklahoma, U.S.A. (Seltin, 1959). The assignment of *L. oklahomensis* to the genus *Labidosaurus* is not very surprising, as the specimens available to the author seemed to be more similar to *Labidosaurus hamatus* than *Captorhinus* (Seltin, 1959). In fact, Seltin states that "This species superficially resembles *Captorhinus* very closely." (Seltin, 1959). The analysis of this author is more focused on the maxillary and denture area, and general dimensions of the specimens (Seltin, 1959). Nothing is said about its skull sculpturing (Seltin, 1959). The reconstructions of the skull in dorsal and ventral view present in the paper do not show any detail about that characteristic either (Seltin, 1959).

It is Heaton, in his 1979 paper "Cranial anatomy of primitive captorhinid reptiles from the Late Pennsylvanian and Early Permian Oklahoma and Texas", that states both *Labidosaurus oklahomensis* and *Pariotichus laticeps* as being conspecific (Heaton, 1979). Additionally, he proposes the designation *Eocaptorhinus* for the new genus, in order to include all captorhinids that are identical to *C. aguti* except for the single tooth row

(Heaton, 1979). *Eocaptorhinus* was then defined by Heaton as synonymous with *P. laticeps* (Williston, 1909) and *L. oklahomensis* (Seltin, 1959), amongst others (Heaton, 1979). Heaton analyses the specimens originally used by Seltin for his description of the new genus and species *Eocaptorhinus laticeps*, as "they are so well preserved that […] it has been possible to see all surfaces of cranial elements in enough detail that foramina and muscle scars can be identified." (Heaton, 1979). On the systematic description of the *Eocaptorhinus* genus, the author refers to the heavy sculpturing in the skull that is present in adults. It is "distinguished from *Protocaptorhinus* by its […] coarse heavy sculpturing (in adults)", and from *Captorhinus* by "much coarser but equally well-delineated sculpturing" (Heaton, 1979). The specific diagnosis of this species is the same as the genus (Heaton, 1979). There are no mentions about the sculpturing of the skull on its short description (Heaton, 1979). Heaton then proceeds to describe the skeleton exhaustively, starting with the skull. The author states that "the entire external surface of the dermal skull roof is ornamented by a coarse, vermiculate, ridge-and-pit sculpture pattern […] that is less well developed in juveniles" (Heaton, 1979). Later, he adds that the "anterior surface of the rostral body is heavily sculptured with deep, irregular pits that communicate with a system of fine internal canals." (Heaton, 1979). Regarding the maxilla, Heaton notes that its "medially convex posterior ridge has a smooth surface pierced by numerous very fine pits" where it contacts with the palatine (Heaton, 1979). There also appear to be "shallow sculpture pits on the lateral surface of the maxilla, [that are] not as strongly developed as on the lachrymal or the skull table elements", with a similar pattern occurring on the interior surface of the maxilla (Heaton, 1979). Heaton describes the lateral surface of the lacrimal of *E. laticeps* distinguishing between posterior and anterior areas: "Posteriorly, [it] is sculptured with deep pits and prominent ridges; anteriorly, the sculpturing is less pronounced. Each pit is pierced by one or more fine pores" (Heaton, 1979). The plane of the lacrimal-maxillary suture is ventrolaterally smooth but ventromedially grooved and ridged (Heaton, 1979). On the posterior end of the suture between the lacrimal and prefrontal, there is a thickened area along the orbital margin that has its surface heavily scarred by sharp, bony ridges (Heaton, 1979). The author restates the presence of "numerous deep grooves and ridges on the sutural surfaces of both […] lachrymal and prefrontal" further (Heaton, 1979). The ventral surface of the nasal is smooth, unlike the exterior; the lateral surface of the anterior plate of the prefrontal is "heavily sculptured with deep pits, each pierced by one or more small pores" (Heaton, 1979). The frontal is sculptured externally "with the same pattern as the nasal" (Heaton, 1979). Heaton mentions that "both ventral contact surfaces of the parietals and the dorsal contact surfaces of the squamosals and postorbitals have extensive, laterally directed ridge-and-groove scarring" (Heaton, 1979). The posterior border of the ventral surface of the parietal is also heavily scarred along with a "[…] shelf that served as sutural contact with the ascending process of the supraoccipital medially and the postparietals posteriorly" (Heaton, 1979). The sculpturing of the parietals is of the "usual deep, pit-and-ridge type with perforating pores", with a "tendency for the pits to align themselves longitudinally except for a single, well-developed ring of pits around the pineal foramen" (Heaton, 1979). The author mentions that the parietals of *Romeria* and *Protocaptorhinus* seem to be "less heavily sculptured, but [it] is difficult to astain […] because of the severe treatment some of these specimens have received during preparation" (Heaton, 1979). The internal surface of the postparietal appears "smooth, with very light muscle scarring" (Heaton, 1979). Opposite to it, the "entire external surface of the postparietal is heavily sculptured with deep pits and irregular intervening ridges", being present on the posterior plate a "distinct pattern of three or four longitudinal rows of pits" (Heaton, 1979). Regarding the postorbital, its lateral surface is "heavily sculptured with the typical pitted pattern. The more dorsally located pits tend to become aligned longitudinally like those of the postfrontal and the parietal. Ventrally, the pits are scattered. As with other dermal skull bones, the pits are pierced by small pores" (Heaton, 1979). The external surface of the posterior plate of the jugal is also "sculpted with deep pits, all perforated by small pores." (Heaton, 1979). "The anterior process is marked by many small, shallow, vermiculate pits much like those of the maxilla.", and "the medial surface of the internal process is heavily scarred" (Heaton, 1979). The external surface of the squamosal is "heavily sculptured in the usual manner" (Heaton, 1979). The 1979 publication by Heaton is also accompanied by a big number of very detailed drawings and reconstructions of *E. laticeps*, where skull sculpting is clearly visible and identifiable (Heaton, 1979). Namely, the first twenty-three figures presented by the author provide a lot of information about the ornamentation of the skull as a single module and then separated into distinct elements (Heaton, 1979). Heaton bases his reconstructions on the holotype and/or referred specimens (Heaton, 1979). He describes the lateral surface of the mandible rami as being “sculptured extensively by shallow, vermiculate pits”, while “the unsculptured surface bears numerous prominent muscle-insertion scars” (Heaton, 1979). There is also a “large, smooth region of the lateral surface of the mandible” that appears to be related to the insertion of a broad muscle or tendon. The ventral plane of the dentary “bears a small number of deep longitudinal grooves” (Heaton, 1979). The internal surface of the Meckelian canal is pierced with foramina, and “the lateral surface of the dentary is heavily sculptured by many vermiculate pits” (Heaton, 1979). Asides some scarring that is attributed by Heaton to the insertion of certain muscles, “no other scarring is visible on the splenial” (Heaton, 1979). The author also refers that the “lateral surface of the surangular is unsculptured, except in its most ventrally exposed region”, while “the internal surface of the surangular shows no markings or perforations” (Heaton, 1979). In regard to the angular, most of its lateral surface “is sculptured by deep pits radiating from an apparent growth center located near the midpoint of the ventral edge of the bone”, while “a long […] area on the lateral surface of the most posterior projection of the angular bears no sculpturing.” (Heaton, 1979). “[…] All of the ventral and medial surfaces of the angular are [also] sculpture-free.” (Heaton, 1979).

Gaffney and McKenna, on the same year, question the validity of distinguishing *Eocaptorhinus* from *Captorhinus* based on the only relatively consistent morphologic difference between them, the number of tooth rows (Gaffney & McKenna, 1979).

Based on the extensive work previously done, Heaton and Reisz published a full skeletal reconstruction of *E. laticeps*, with the skull, limb and vertebral elements (Heaton & Reisz, 1980). Some of the images published are reconstructions and it is possible to identify the general outlines of the skull sculpturing (Heaton & Reisz, 1980).

Regarding further taxonomy changes of *E. laticeps*, Gaffney proposes a synonymy of *Eocaptorhinus* under *Captorhinus*, suggesting an independent origin for the multiple tooth rows in the latter genus (Gaffney, 1990). However, Dodick and Modesto in 1995, while analysing the phylogeny of the captorhinid *Labidosaurikos meachami,* suggested that the "origin of multiple-tooth-rows in Captorhinidae is diphyletic" (Dodick & Modesto, 1995). This made them recognise *Eocaptorhinus laticeps* and *C. aguti* as sister taxa, further recognising formally the new combination *Captorhinus laticeps*, making it synonym with *E. laticeps* (Dodick & Modesto, 1995).

### ***Captorhinus aguti***

The taxon *Captorhinus aguti* was described for the first time by Cope, 1882, as *Ectocynodon aguti*, based on specimen AMNH 4333 from Coffee Creek, 34, Arroyo Formation, Clear Fork group, Lower Permian of Texas, U.S.A. (Cope, 1882). Cope states that species of this genus have sculptured cranial bones like the genus type *Ectocynodon ordinatus*, specimen AMNH 4342 (later declared *nomen dubium* and *nomen oblitum* by Heaton in 1979) (Cope, 1882). *E. aguti* has, according to Cope, a "sculpture of the maxillary and malar bones consist[ing] of closely placed shallow fossae. On the posterior part of the frontals, there are strong ridges radiating posteriorly, and […] close together" (Cope, 1882). No images are present in this paper (Cope, 1882).

In 1896, Cope describes the species *Pariotichus aduncus* based on specimen AMNH 4332, from Coffee Creek, 34, Arroyo Formation, Clear Fork group, Lower Permian of Texas, U.S.A. (Cope, 1896a). Its cranial surface is "sculptured with shallow pits separated by rather thick ridges" (Cope, 1896a).

On a later paper published in the same year, Cope describes the new genus *Captorhinus* as part of the Pariotichidae and the species *Captorhinus angusticeps* (specimen AMNH 4438, also from Coffee Creek, 34, Arroyo Formation, Clear Fork group, Lower Permian of Texas, U.S.A). (Cope, 1896b). However, "nothing can be said of the [skull] sculpture, as the surface of the bone […] is injured" (Cope, 1896b). Cope also reassigns *E. aguti* to the genus *Pariotichus* he had previously defined in 1878 (Cope, 1878), renaming it *Pariotichus aguti* (Cope, 1896b). The author also refers to the existence of a "cranial structure partly reticulate, especially medially" (Cope, 1896b). On the same paper, Cope describes the species *Pariotichus isomolus* based on specimen AMNH 4338, from Coffee Creek, 34, Arroyo Formation, Clear Fork group, Lower Permian of Texas, U.S.A. (Cope, 1896b). Cope says it is “nearly allied to *P. aguti*” (Cope, 1896b). Namely, “in the sculpture of the superior surface of the skull, the longitudinal striae are more prominent than the transverse ones which connect them, except on the muzzle, where they are about equally conspicuous. The sculpture is finer and reticulate on the jugal and quadratojugal regions. About a dozen longitudinal ridges between the orbits. Sculpture of mandible tubercular reticulate.” (Cope, 1896b). This paper has a plate comprised of complex drawings of *P. aguti* in its natural size (Cope, 1896b). The skull, mandibular arch/premaxillary bones, and the humeri are all illustrated (Cope, 1896b). The skull sculpturing is well-evident and clearly identifiable (Cope, 1896b).

In 1910, Broom renames *Captorhinus angusticeps* as *Pariotichus angusticeps* (Broom, 1910).

Case, in 1911, transfers all characters and species assigned to the family Pariotichidae to family Captorhinidae and redefines it (Case, 1911). All *Pariotichus* species are then referred to as *Captorhinus* (Case, 1911). Captorhinidae skulls are “acuminate [and] rugose” (Case, 1911). In the revised description of the genus, Case states that the skull has a “definite reticulate sculpture” (Case, 1911). Only four species of *Captorhinus* were considered in the revised description of the genus by Case: *C. aguti*, *C. angusticeps*, *C. isolomus* and *C. aduncus* (Case, 1911). The differences between them pertain mostly to teeth sizing (Case, 1911). It is also stated that the species initially described as *Ectocynodon incisivus* defined earlier by Cope (Cope, 1888) and then renamed as *Pariotichus incivisus*, cannot be distinguished from *C. aguti* (Case, 1911). Its head sculpture is “well-defined” and “reticulated in pattern” and Case unites them under the same name (Case, 1911). The revised description of *C. isolomus* states the same as the original description regarding skull sculpturing by Cope (Cope, 1888), with additional input from the analysis conducted by Broili (Broili, 1904) of *P. isolomus*: “sculpture formed largely of more elongate lines; on the sides the presence of cross lines produced a pretty regular network” (Case, 1911). For the revised description of *C. aduncus*, the author remarks that “the sculpture of the surface is not to be distinguished from that of the other species” (Case, 1911). Finally, and for *C. angusticeps*, nothing is mentioned regarding skull sculpturing (Case, 1911). It is very important to note how Case states that *Captorhinus* is a good example of “the difficulty of making species in vertebrate palaeontology; each specimen might be considered as distinct and numerous species formed with characters given, or with a little more freedom, all might be placed in a single species” (Case, 1911). On the section dedicated to the morphological revision, Cope presents drawings of the skulls of species *C. angusticeps*, *C. isolomus* and *C. aguti* (Case, 1911). Some are more detailed, others are very simple (Case, 1911). None includes skull sculpturing (Case, 1911). At the end of the publication, there is a page with (what seem to be low-resolution) photographs of a *C. angusticeps* skull with sculpturing (Case, 1911).

Watson published in 1954 an article in which he dedicates a section to captorhinids (Watson, 1954). The author defines a new genus (*Paracaptorhinus*) and a new species (*Paracaptorhinus neglectus*) based on a skull of his own collection (DMSW R9) of unknown horizon and localization - besides the fact that it was found in Texas (Watson, 1954). This skull is somewhat damaged due to extensive weathering and Watson does not make comments regarding the existence of skull sculpturing (Watson, 1954). Even though Watson mentions several times the similarities between this specimen and the data he had on *C. aguti*, he fails to recognize they are the same species and not distinct taxa (Watson, 1954). There are several drawings of the skull of *P. neglectus* that suggest that there might be skull sculpturing, but it is ambiguous and not very clear, as it also could represent just a stylistic choice (Watson, 1954).

Seltin publishes in 1959 a paper based on a review of the Captorhinidae family, summarizing the description of all *Captorhinus* species (Seltin, 1959). His descriptions are after Case (Case, 1911) and Cope (Cope, 1882; Cope, 1896a; Cope, 1896b). Seltin analyses further the diagnostic value of the characters used to differentiate between these species (Seltin, 1959). In the case of skull sculpturing, Seltin states that it is a very difficult character “to treat quantitatively” and that “observations of specimens had shown little difference” (Seltin, 1959). The author adds that “the types of sculpture present [in examined skulls from several collections] could be derived from one type or could be variations [of it], and [that] this character does not seem to be correlated with any other character” (Seltin, 1959). Seltin then concludes that there is no evidence for more than one species of *Captorhinus*, namely *C. aguti* (Seltin, 1959). Olson and Barghusen, in 1962, state their agreement with this perspective (Olson & Barghusen, 1962). Seltin presents one simplified drawing of a *C. aguti* skull where sculpturing is not present (Seltin, 1959).

Cope described some remains (AMNH 4335, from Coffee Creek, 34, Arroyo Formation, Clear Fork group, Lower Permian of Texas, U.S.A) in 1896 as a new species, *Hypopnous squaliceps* (Cope, 1896b). In this species, the skull "surface of the […] bones is sculptured in a shallow honeycomb pattern, the longitudinal ridges predominating on the median regions posteriorly" (Cope, 1896b). The author presents one image of the skull in dorsal view and another in lateral view where this pattern is undoubtedly present (Cope, 1896b). However, Case suggests in 1911 that what Cope had initially identified as one skull are actually two skulls (Case, 1911). Drawings of the skulls accompany the text but do not show skull sculpturing (Case, 1911). As such, Cope drops the species and genus. Still, Seltin decided to list *Hypopnous* as a synonym of the genus *Captorhinus* (Seltin, 1959). Eaton disagreed and believed that those *H. squaliceps* remains were of a romeriid captorhinid (Eaton, 1964). Eaton also presents three drawings of the skull in which some skull sculpturing seems to be present but cannot be identified with complete certainty, as the matrix in which the fossil is contained is also represented (Eaton, 1964). The author classified this specimen as *Romeria* sp. (Eaton, 1964). In the same year, Baird and Carroll stated that the identification made by Eaton was in error (Baird & Carroll, 1964). In Romeriidae, "the postparietals are unsculptured and the posterior margin of the sculptured skull roof arcs forward on either side of the midline" (Baird & Carroll, 1964). This did not happen in *Hypopnous*: "on the contrary, the dorsal surfaces of the postparietals are sculptured and the posterior margin of the skull roof arcs backwards on either side of the midline" (Baird & Carroll, 1964). The authors then made *H. squalidens* synonym with *C. aguti*, as they saw "no distinction between" both (Baird & Carroll, 1964). Their paper does not contain any images (Baird & Carroll, 1964).

By 1966, there was a lot of *Captorhinus* material available in several museums from Texas and Oklahoma sites (Fox & Bowman, 1966). As no complete study of the osteology of *Captorhinus* had been done until then, authors Fox and Bowman conducted one (Fox & Bowman, 1966). These authors listed the following species as synonymous of *C. aguti*: *E. aguti*, *P. aguti*, *E. incisivus*, *P. incisivus*, *C. incisivus*, *C. angusticeps*, *P. angusticeps*, *P.*

*isolomus*, *P. laticeps*, *C. isolomus*, *P. aduncus* and *C. aduncus* (Fox & Bowman, 1966). Specimen AMNH 4333 was defined as the holotype (Fox & Bowman, 1966). Regarding the sculpturing present in the dermal bones of the skull roof, the authors state that “the walls of the premaxillary incisures possess small foramina. […] The contacts of the maxillary […] have been made firm and immoveable by the complex system of grooves and ridges that blanket the articulating surfaces.” (Fox & Bowman, 1966). At the contact of the nasal with the prefrontal, “the articulation is by means of small processes and notches that are combined with a multiple tongue-and-groove system usually involving two to three horizontal ridges and grooves extending […] along the edges of the respective bones” (Fox & Bowman, 1966). Regarding the lacrimal, “the articulating surface of this region is crossed by irregular grooves and ridges that touch the maxillary and jugal” (Fox & Bowman, 1966). The contact of the prefrontals with the frontals and nasals is “by a complex system of grooves and ridges on the apposing faces of the bones. […] The articulation between the frontals is expressed in a system of grooves and ridges that radiate upward, forward, backward, and obliquely, from a point that is opposite the contribution of the frontal to the orbital rim” (Fox & Bowman, 1966). The squamosal has a flange of “unornamented bone around the posterior corner of the skull to the occiput” (Fox & Bowman, 1966). The postparietal, from a medial to notch direction is “is attached to the parietal by means of a lappet that fits under a shelf of heavily striated bone extending along the posterior edge of the parietals” (Fox & Bowman, 1966). The parietals “articulate with each other by a complex system of interdigitating processes, grooves, and ridges” (Fox & Bowman, 1966). On the mandibular rami, “the outer surface […] is […] sculptured” and it “extends upwards from the ventral edge of the jaw to the base of the teeth”, while “the medial surface is flat and free of ornamentation” (Fox & Bowman, 1966). “The external surface of the surangular possesses a vertical or near-vertical flange of unornamented bone that, with the dentary and coronoid more anteriorly, surmounts the coronoid process”, and “on the ventral edge of the jaw, the prearticular forms a groove that extends from the base of the retroarticular process forward” (Fox & Bowman, 1966). This has a total of 38 illustrations of *C. aguti*, including several views of the skull, however, few have the skull sculpturing visible (Fox & Bowman, 1966).

Heaton in 1979 published a paper where he makes a taxonomic review of the clade Captorhinidae (Heaton, 1979). The author summarizes all taxonomic changes previously reported and defines a new genus and species, *Eocaptorhinus laticeps* (Heaton, 1979). Heaton deems this species as a synonym of *Captorhinus isolomus* described by Case in 1911 and the non-*C. aguti* described by Seltin in 1959 (Heaton, 1979). This genus is distinguished from *Captorhinus* by several characters, including a "much coarser but equally well-delineated sculpturing" (Heaton, 1979). The author dedicates a section to the differentiation of *Captorhinus* and *Eocaptorhinus* but does not make any further reference to skull sculpturing (Heaton, 1979). Heaton also synonymizes *Paracaptorhinus* with *Captorhinus*, and *P. neglectus* with *C. aguti* (Heaton, 1979). No illustrations of *C. aguti* are present (Heaton, 1979).

Olson defined the species and genus *Bayloria morei* in 1941 (Olson, 1941), but other authors classify *Bayloria* as a synonym of *Captorhinus* (Reisz & Heaton, 1982). There are two illustrations of a *B. morei* skull (FMNH UC 1639) and two illustrations of a *C. aguti* skull (FMNH UR 2316), both in lateral and dorsal views (Reisz & Heaton, 1982). Skull sculpturing seems to be present but hard to identify with certainty (Reisz & Heaton, 1982).

In 1998, Modesto described new material and re-examined *Captorhinus* specimens, in order to correct and adjust earlier cranial anatomy interpretations (Modesto, 1998). He stated that regarding the right postparietal of *C. aguti* specimens, "the dorsal exposure […] is even partly sculpted by the characteristic ridge-and-pitting of the other roofing elements" and included illustrations of both the skull roof (in dorsal, dorsolateral, posterior and ventral views) and lower jaw fragments where sculpturing is evident (Modesto, 1998).

Authors LeBlanc and Reisz published a paper about the patterns of tooth development and replacement in captorhinids (LeBlanc & Reisz, 2015). Even though the paper is focused on dentition, it has a photograph of a *C. aguti* (OMNH 52329) in left lateral and ventral views, where skull sculpturing can be observed (LeBlanc & Reisz, 2015).

### ***Captorhinus magnus***

This species of single tooth-rowed captorhinid was described in 2002 by Kissel, Dilkes and Reisz. The studied remains were discovered in the Dolese Brothers limestone quarry at Richards Spur, Lower Permian of Oklahoma, U.S.A., and its holotype is specimen OMNH 55387 (Kissel, Dilkes, & Reisz, 2002). Even though the holotype is comprised only of a complete right femur, other referred specimens (OMNH 56820 and 56821) were studied to have information about the rest of the anatomy, including the cranium (Kissel et al. 2002). On the diagnosis and description, the authors refer that the "skeletal elements of *Captorhinus magnus* possess a nearly identical morphology to those" of *Captorhinus aguti* described by Fox and Bowman in 1966 and as such, "a complete description of *C. magnus* is not required." (Kissel et al., 2002). Neither the description of the cranium or of the mandibular rami have information regarding sculpturing (Kissel et al., 2002). However, the paper has one photograph of a skull in right lateral view, two photographs of a different skull in dorsal and left lateral view, and a photograph of a nearly complete left lower jaw in lateral view, where typical captorhinomorph skull sculpturing is observable (Kissel et al., 2002). There is also a drawing of a left dentary in lateral view where sculpturing is evident (Kissel et al., 2002). Still, one could assume that the skull sculpturing present in *C. magnus* is virtually identic of sister taxon *C. aguti,* also from Richards Spur (Kissel et al., 2002).

Other authors present a figure that includes a photograph of a right lateral view of what they considered to be a *C. magnus* skull (specimen BMRP 2005.3.1), where sculpturing is evident (LeBlanc & Reisz, 2015). However, authors deBraga, Bevitt and Reisz refute this classification in 2019, where they assign this specimen as the holotype of *Captorhinus kierani*. They also correct its specimen number and update it to OMNH 73218a (deBraga et al., 2019).

### ***Labidosaurus hamatus***

In 1878, Cope first describes the genus and species *Pariotichus brachyops* (Cope, 1878). Regarding the genera characteristics, the author mentions the absence of sculpturing on the cranial bones (Cope, 1878). Cope also describes the genus and species *Ectocynodon ordinatus*, having as holotype an unidentified specimen with "cranial bones sculptured, but no lyra" (Cope, 1878). Furthermore, Cope mentions the presence of a "sculpture of vertex in longitudinal series of pits of considerable irregularity" (Cope 1878). In 1882, Cope describes another species, *Ectocynodon aguti*. In this species, the "sculpture on the maxillary […] bones consists of closely placed shallow fossae" (Cope, 1882). "On the posterior part of the frontals, there are strong ridges radiating posteriorly, situated close together" (Cope, 1882). In neither paper are present images of specimen skulls. The following year, Cope establishes the *Pariotichidae* family, referring to it *Ectocynodon, Pantylus*, and *Pariotichus* (Cope, 1883). He retracts his earlier statement about the description of the latter species, writing that "the surface of the cranium has mostly been weathered away in the type of *Pariotichus*, […] and I suspect that it is really sculptured and not smooth, as I originally stated". The author also describes the new species *P. megalops*. The holotype (unidentified specimen) has a cranium "sculptured in honeycomb fashion, the ridges radiating on some of the bones [posterior part of the frontal and parietal and anterior part of the squamosal and intercalare]" (Cope, 1883). The external surface of the mandible also presents grooves, but the paper does not include any figures to show this (Cope, 1883).

Later, Cope summarizes the characters of the taxa present in Cotylosaura, including Parotichidae (Cope, 1896b). In the same article, the author analyses the genera included within Pariotichidae (Cope, 1896b). *Ectocynodon* is now united with *Pariotichus* (Cope, 1896b). Cope makes a description of the genus *Pariotichus* more extended than previous ones: "The sphenoid [of *Pariotichus aguti*] is deeply grooved on the middle line" (Cope, 1896b). Cope also describes the characters of the various other species, for example, *P. incisivus* should have a reticulated sculpturing, with and the sculpture of interorbital and parietal bones should also be reticulated (Cope, 1896b). For all other species, the cranial sculpturing should be present in "more or less longitudinal ridges" (Cope, 1896b). For *P. ordinatus*, it is further stated that the "interorbital sculpture [should show] longitudinal ridges" (Cope, 1896b). In the case of *P. isolomus*, the "cranial sculpture [should present] longitudinal ridges" (Cope, 1896b). Skull sculpturing in *P. aguti* should appear as "partly reticulate, especially medially" (Cope, 1896b). Finally, for *P. hamatus*, only characteristics not pertaining to the skull sculpturing are mentioned (Cope, 1896b). On the last pages of the paper, the author presents plates containing some illustrations of skulls and mandibles of *P. aguti* and *P. hamatus* (Cope, 1896b). For the latter taxon, only the dorsal and lateral views of the skull are available, and the skull sculpturing is difficult to identify (Cope, 1896b).

In the same year, Cope describes the species *P. aduncus* and adds it to the Pariotichidae family and points that “the [skull] surface is sculptured with shallow pits separated by rather thick ridges” (Cope, 1896a). Cope refers the species formerly described as *Pariotichus*, *P. hamatus*, to a distinct species and genus – *Labidosaurus hamatus*, genus Pareiasauridae (Cope, 1896a). He mentions in the specific description of *L. hamatus* that the “sculpture of the cranial surfaces is in shallow fossae with rather thick partitions, of smaller size than *Pariotichus aguti*, which resembles it most nearly” but no image of this species is provided (Cope, 1896a).

Case redescribes in 1899 *Pariotichus incisivus*, the species originally described by Cope as *Ectocynodon incisivus* (Case, 1899). On the original generic description in 1878, the latter author refers that *Ectocynodon* “cranial bones [are] sculptured, but [there is] no lyra” (Case, 1878). The specific definition of the species *E. incisivus* was proposed later also by Cope in 1886, where he states that “the head sculpture is well defined and is reticulated in pattern” (Case, 1886). Case makes an additional description of the *P. incisivus* cranium, where he mentions that the “character of the sculpture in the occipital and parietal regions [of the upper surface of the skull] is shown” in two figures representing the superior view of the cranium (Case, 1899). Indeed, it is easy to observe the reticulated pattern of “small foramen, superimposed with ridges in certain areas” (Case, 1899).

In 1904 Broili proposes a new phylogenetic arrangement that reassigns Pareiasauridae as a family belonging in the Cotylosauria[2] suborder (Broili, 1904). As the species only has one tooth row, the author also states that *Pariotichus* should be included in the genus *Labidosaurus*, and Pareiasauridae family (Broili, 1904). The *Labidosaurus hamatus* specimen analysed by Broili (a mounted specimen in the Alte Akademie, Munich, Germany, a skeleton from the same locality and horizon as specimen AMNH 4341

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[2] Ordinal name formerly used for primitive reptiles in the subclass Anapsida, including the stem reptiles (Williston, 1908). Proposed by Cope in 1880, but more recently reranked as an unranked clade, belonging to Batrachosauria (Laurin & Reisz 1995).

mentioned later in Case, 1911) had suffered great damage on the surface during preparation (Broili, 1904). Considerations that rely on this character must account for that fact. Nevertheless, the skull surface of the specimens seems to be rough and covered in “narrow, bead-like elevations between seams” (Broili, 1904). These interconnected granulations seem to be organized, centred in the posterior half of the skull and then feathering longitudinally to the limits of the eye sockets, sides of the skull and jaw rims (Broili, 1904). Broili adds that “the lower jaw likely has the same sculpturing on the outside as the skull cover plates do” (Broili, 1904). The 1904 paper has one illustration of the reconstruction of *L. hamatus* but the representation of skull sculpturing is neither clear or mentioned in the caption (Broili, 1904).

Later, Williston re-examines the specimen previously studied by Case in the 1899 paper and renames it from *Ectocynodon incisivus* to *Labidosaurus incisivus* (Williston, 1908). The author says that the surface of the skull is sculptured. However, no further mention of this type of ornamentation is made throughout the text (Williston, 1908). The skull illustrations provided in the article do not represent the sculpturing present in the skull and the same happens for the restoration of *L. incisivus* done by the author (Williston, 1908).

In 1911 Case redescribes the genus *Labidosaurus*, in which species *Pariotichus* (Cope 1896b), *Labidosaurus* (Cope, 1896a), *Pariotichus hamatus* (Case 1899), *Labidosaurus* (Broili, 1904) and *Labidosaurus* (Williston, 1908) were included. This redescription has specimen AMNH 4341 from Coffee Creek, Arroyo Formation, Clear Fork Group, Baylor/Willbarger County, Lower Permian of Texas, U.S.A. as its holotype both for genus and species, *L. hamatus* (Case, 1911). The original description does not mention anything about skull sculpturing. However, in the revised description, item 8 reads “skull with reticulate sculpture” (Case, 1911). The author also revises the description at species level, starting with *L. hamatus* (Case, 1911). Case assigns species *Pariotichus hamatus, Labidosaurus hamatus, Pariotichus incisivus* and *Labidosaurus incisivus* to this taxon (Case, 1911). The original description for *L. hamatus* states that the surface of the skull based on the holotype “is so much injured […] as to render it impossible to state the character of the sculpture, if any existed” (Case, 1911). However, Case also mentions that “the sculpture of cranial surface is in shallow fossae with rather thick partitions, of smaller size than in the *Pariotichus aguti*" (Case, 1911). On the appendix of Case 1911, there are photographs of several views of an *L. hamatus* skull where dermal sculpturing is easily recognisable. Specimens initially assigned to *Labidosaurus hamatus* (Broili, 1904) were reassigned to this taxon by Case (Case, 1911). Nothing is said about the skull sculpturing (Case, 1911). On the same paper, Case refers to the *Pariotichus laticeps* specimen AMNH 4338 described by Williston in 1909 to *Captorhinus isolomus,* previously described by Cope in 1896 (Case, 1911).

In 1966, Bowman and Fox state that *C. isolomus* is a subjective synonym of *Captorhinus aguti* (Fox & Bowman, 1966).

Williston in 1917 describes new remains pertaining to the genus *Labidosaurus* found near Craddock Brothers Ranch, Clear Fork Formation, Seymour, Early Permian of Texas, U.S.A. (Williston, 1917). The author bases his restoration of *Labidosaurus sp.* in specimen nº 174. (Williston, 1917). The remains include the right half of the skull and some post-cranial skeleton (Williston, 1917). The paper includes a photograph of this specimen and of specimen nº 183, "tentatively assigned to *Labidosaurus* sp. but most probably from a different genus altogether" (Williston, 1917). In the illustrations of the restoration of *Labidosaurus* sp. there is no representation of skull sculpturing (Williston, 1917). However, the photographs show some evidence of skull ornamentation in low detail (Williston, 1917).

In 1959 Seltin publishes a review of the clade Captorhinidae that includes three species of *Labidosaurus*: *L. hamatus* and *L. broilii*, respectively described by Cope in 1896 and Case in 1911, and *Labidosaurus oklahomensis*, a new species (Seltin, 1959). The latter taxon would eventually be reassigned to *Captorhinus laticeps* by Heaton in 1979 (see subsection *C. laticeps* above) (Heaton, 1979). This paper has an illustration of the dorsal and ventral views of the skull of *L. hamatus* (CNHM UR 161) but the skull sculpturing is not represented (Seltin, 1959).

Modesto, Scott, Berman, Müller and Reisz in 2007 redescribed the cranial skeleton of *L. hamatus* based on new, undescribed specimens (Modesto et al., 2007). The authors draw new conclusions in terms of the phylogeny of captorhinids (in the genus *Captorhinus* and clade Moradisaurinae) (Modesto et al., 2007). The finding that *L. hamatus* is more closely related to moradisaurines within *Captorhinidae* supports and backs up the idea of a diphyletic origin for multiple tooth rows in these captorhinids (Modesto et al., 2007). On the species updated description, still based on the holotype AMNH 4341, the authors mention the presence of "features [such as] the characteristic sutural patterns that are readily evident in smaller captorhinids." (Modesto et al., 2007). The sculpturing pattern observable in the nasal is "almost identical to that seen in *Captorhinus*, ranging from a simple, roughened surface with a few small pits anteriorly to short, nearly parallel furrows posteriorly." (Modesto et al., 2007). The frontal, "despite being greater in absolute size, […] is slightly less densely sculptured with the characteristic pits and short furrows as are the frontals of the various species of *Captorhinus*." (Modesto et al., 2007). The density of dermal ornamentation in the postfrontals is "slightly less than that in smaller captorhinids" (Modesto et al., 2007). The dermal sculpturing in *Labidosaurus* parietal bones "is consistent with that seen in most other captorhinids, except for the additional presence of a few pits in the parietal that are conspicuously larger than the usual ridge-and-pit excavations" (Modesto et al., 2007). This sculpturing does not extend to the postparietal bones (Modesto et al., 2007). In the squamosal, "the pattern of dermal sculpturing on the temporal portion of the bone is similar to that seen on the same bone in *Captorhinus*, except for the pits and furrows being relatively smaller than those in the larger *Labidosaurus*" (Modesto et al., 2007). The entire lateral surface of the dentary is almost completely "sculptured by fine pits, and a line of distinctly larger pits, […] parallels the dentition [and] their sizes reflect the sizes of the teeth. Close to the sutures with the splenial and the angular, the pits give rise to oblique […] furrows. On the right mandibular ramus of CM 73371, a relatively large oval pit is superimposed onto the system of furrows, which may represent the anteriormost extent of an irregular pattern of sculpturing that is largely borne by the angular." (Modesto et al., 2007). The sculpturing of the splenial "becomes a little more accentuated posteriorly but does match the sculpturing seen on the dentary and the angular." (Modesto et al., 2007). "Apart from its larger size and minor details of the dermal sculpturing, the angular of *Labidosaurus* […] resembles that of […] *Captorhinus*. Sculpturing, which is limited to the lateral surface, consists of a system of fine pits and short furrows for the most part, with one or two slightly larger randomly positioned pits that are reminiscent of the large pits present on the dentary. These larger pits tend to cluster longitudinally close to the ventral margin, and […] are accompanied by larger shallow excavations. On the left mandibular ramus […] the excavations take the form of moderately deep pits […], over which is superimposed the regular pattern of small pits and furrows. In approximately the same area on the right ramus, there is instead a more extensive trough-like excavation […] which straddles the division between the smoothly finished bone of the medial surface and the sculptured bone of the lateral surface. The floor of this excavation is for the most part flat with a roughened texture, over which is superimposed a diffuse pattern of small pits and a few furrows." (Modesto et al., 2007). This paper is accompanied by several detailed illustrations of skeletal elements, including the skull and the mandibular rami. In the reconstruction of the cranium and mandibular rami, it is possible to see in much detail the skull sculpturing mentioned earlier (Modesto et al., 2007). There is also an illustration of the partial right mandibular ramus of specimen CM 76876 where the skull sculpturing details are visible (Modesto et al., 2007).

Reisz et al. published a paper in 2011 pertaining to the existence of osteomyelitis in *L. hamatus* specimen CMNH 76876. The paper has coloured and highly detailed photographs and CT scans of the infection site, which are somewhat useful regarding bone sculpturing present in the mandible (Reisz, Scott, Pynn & Modesto, 2011).

### ***Labidosaurikos meachami***

*Labidosaurikos meachami* was first described by Stovall in 1950. This description is based on a specimen comprised of a skull and right mandible (MUO 3-1-S2, now OMNH 04331) found near Crescent, Hennessey formation of Logan County, Lower Permian of Oklahoma, U.S.A. (Stovall, 1950). The author refers to its similarity to *Labidosaurus hamatus* (Stovall, 1950). Stovall states that "the sculpturing [in the skull] is pronounced although definitely not in rows" (Stovall, 1950). The contact between the jugals and the squamosals and quadratojugals shows sutures that feather "off the squamosal and quadratojugal on top of the jugal" (Stovall, 1950). The article is accompanied by a figure in which several photographs of the skull and mandible are present in several views (Stovall, 1950). The skull sculpturing present in this specimen is well-evident (Stovall, 1950).

In “Fauna of the Vale and Choza: 9 Captorhinomorpha”, Olson describes new species *Labidosaurikos barkeri*, based on a specimen (CNHM UR 110) collected on Locality FA – Pipe site, Choza Formation, Clear Fork group, Lower Permian of Texas, U.S.A. (Olson, 1954). This specimen is comprised of a partial skeleton and includes an upper jaw and skull fragments (Olson, 1954). However, nowhere in the systematic description the author mentions the existence of skull sculpturing (Olson, 1954). Although a drawing of some skull parts accompanies the text, there is no representation of possible skull sculpturing there either (Olson, 1954).

Seltin, in “A review of the family Captorhinidae”, considers *L. barkeri* synonymous with *L. meachami* and reassigns all *L. barkeri* specimens to the former taxon (Seltin, 1959). On the analysis of the genus, the author does not mention anything about possible skull sculpturing on any of the referred specimens (Seltin, 1959). The accompanying illustration of this *L. meachami* specimen skull and dentition does not account for the bone ornamentation either (Seltin, 1959).

In 1995 authors Dodick and Modesto conduct a thorough study of *L. meachami* cranial anatomy, along with a phylogenetic analysis of the interrelationships between north American captorhinids (Dodick & Modesto, 1995). Using the same skull in which Stovall based his description of *L. meachami*, the authors reassess the diagnosis and description of the taxon (Dodick & Modesto, 1995). Dodick and Modesto mention that the skull has “strongly developed external sculpturing” (Dodick & Modesto, 1995). The dermal sculpturing of the parietal bones “most closely resembles that seen in *Labidosaurus*, with […] the presence of pits that exceed in size all other pits and grooves. These large pits are found near the parietal foramen and along the suture with the postparietal” (Dodick & Modesto, 1995). The posterior half of the postparietal is “strongly pitted as the other roofing bones” (Dodick & Modesto, 1995). The posterior process of the postfrontal is more heavily sculptured than in other captorhinids (Dodick & Modesto, 1995). The “sutures with neighbouring elements in dorsal view are […] irregular, […] [being] clearly influenced by the pattern of the sculpted pits and furrows” (Dodick & Modesto, 1995). Nothing is said about the sculpturing present in the lower jaws of the holotype (Dodick & Modesto, 1995). However, in the illustrations of the right mandible, a ridge-and-pit structure seems to be present in certain areas (Dodick & Modesto, 1995). Nevertheless, the presence of bone ornamentation on the mandibular rami is not mentioned in any caption neither in the text (Dodick & Modesto, 1995). Appendix 1 of the article presents a description of several characters used in the phylogenetic analysis (Dodick & Modesto, 1995). Character number 25 refers to the sculpturing of the skull (Dodick & Modesto, 1995). The primitive character state, meaning a sculpturing of "small honeycombing pits and grooves", is coded as (0), while the derived state consists of "pits and grooves with notably larger, randomly positioned pits on posterior skull table", is indicated by (1) (Dodick & Modesto, 1995). This is important because in Appendix 2 Dodick and Modesto present a matrix with the distribution of 39 characters and corresponding states for eight species (*Protorothyris, Romeria, Protocaptorhinus, Rhiodenticulatus, C. laticeps, C. aguti, Labidosaurus* and *Labidosaurikos*) (Dodick & Modesto, 1995). Character number 25 is correspondently coded as 0, ?, 0, ?, 0, 0, 1, 1 (Dodick & Modesto, 1995). For example, in the case of *Labidosaurikos*, the skull sculpturing state is (1), meaning it has "pits and grooves with notably larger, randomly positioned pits on posterior skull table" (Dodick & Modesto, 1995).

In 2017, Jung and Sumida re-examined a specimen (MCZ 1352) from the Arroyo Formation, Clear Fork group, Lower Permian of Texas (Jung & Sumida, 2017). This specimen is comprised of a partial maxillary toothplate and had first been previously assigned to *Trichasaurus* by Romer and Price in 1940 (Jung & Sumida, 2017). Upon further examination, Jung and Sumida considered MCZ 1352 as a juvenile specimen of *L. meachami* but do not offer any additional information regarding the skull sculpturing in this taxon (Jung & Sumida, 2017).

### ***Moradisaurus grandis***

*Morarisaurus grandis* was first described by Taquet in his paper "Première découverte en Afrique d'un Reptile Captorhinomorphe (Cotylosaurien)" dated from 1969 (in O'Keefe, Sidor, Larsson, Maga & Ide, 2005). The same author continued research on this species, publishing a paper in 1989 titled "La faune de vertébrés du Permien Supérieur du

Niger. I. Le captorhinomorphe Moradisaurus grandis (Reptilia, Cotylosauria)—le crâne" (in O'Keefe et al., 2005).

In 2005, O'Keefe, Sidor, Larsson, Maga and Ide published on the morphology and ontogeny of the hind limb of *Moradisaurus grandis* (O'Keefe, Sidor, Larsson, Maga & Ide, 2005). The authors analyse newly collected hindlimb elements from the Upper Permian Moradi Formation of Niger (O'Keefe et al., 2005). On the section dedicated to systematic palaeontology and the revised diagnosis, they mention (without figuring) the "heavy ornamentation" present in the skull of the holotype (O'Keefe et al., 2005).

### ***Rothianiscus multidontus***

The species *Rothianiscus multidontus* was first described by Olson and Beerbower in their 1953 paper "The San Angelo Formation, Permian of Texas, and its Vertebrates" (Olson & Beerbower, 1953). It was initially named *Rothia multidonta*, and its holotype (specimen CNHM UR 87, comprised of a partial skull and lower jaws) dates from the Middle Permian (Olson & Beerbower, 1953). Even though the skull top is absent for the holotype, "the skull margin, palate, and lower jaws are fairly well preserved" (Olson & Beerbower, 1953). The authors state that "both the type and the referred specimen show the lateral surface of the skull to be deeply sculptured." (Olson & Beerbower, 1953). Olson and Beerbower considered that the lower jaws of *R. multidonta* are "similar in many respects to the jaws of *Labidosaurus* and *Labidosaurikos*", but do not refer to the dermal sculpturing at any point (Olson & Beerbower, 1953). The paper includes reconstructions depicting both the skull of CNHM UR 87 and part of the left lower jaw of CNHM UR 129, but there is no clear representation of skull sculpturing (Olson & Beerbower, 1953).

Seltin, in 1959, discusses the genus and analyses the genus *Rothia* according to previously cited work by Olson and Beerbower (Seltin, 1959). The major skull features are comparable to *Labidosaurus* and *Labidosaurikos* (Seltin, 1959). On the analysis, Seltin lists the differences between *Rothia* and other species of captorhinids (Seltin, 1959). The author does not make any reference to the presence or absence of skull sculpturing in *Rothia multidonta* (Seltin, 1959). The only available image of this species is a drawing of the skull in ventral view that does not account for bone sculpturing (Seltin, 1959). Seltin adds that some remains recovered from the Flowerpot Formation, Oklahoma, might pertain to *R. multidonta* (Seltin, 1959).

In 1962, Olson and Barghusen analyse the specimens mentioned by Seltin and assign them to the *R. multidonta* taxon (Olson & Barghusen, 1962). However, all referred specimens are comprised of post-cranial remains, bearing no additional information on the skull sculpturing of this species (Olson & Barghusen, 1962).

In 1982, deRicqlès and Taquet publish "La faune de vertébrés du Permien supérieur du Nigér I", where they recombine *Rothia multidonta* into *Rothianiscus multidonta* (deRicqlès & Taquet, 1992).

Currently, the species is referred to as *Rothianiscus multidontus*, so the latin is concordant (Modesto, pers. comm.). Modesto (pers. comm.) provided us with high-quality photos of a *Rothianiscus* specimen, ID FMNH UR713, discovered in the Late Permian of the San Angelo formation in Texas, Knox County, U.S.A. Although the specimen is missing part of the anterior skull, sculpturing is clearly visible.

### ***Gansurhinus qingtoushanensis***

Described in 2011 by Reisz, Liu, Li and Müller, *Gansurhinus qingtoushanensis* is a moradisaurine captorhinid from the Middle Permian of China (Reisz et al., 2011). It was discovered near Yumen in the Gansu Province (Reisz et al., 2011). The holotype is comprised of a partial skull and some postcranial materials (Reisz et al., 2011). The authors state that the left maxillary is smooth and "seems to preserve at least part of the original surface." (Reisz et al., 2011). The article contains photographs of the holotype but does not present skull sculpturing clearly (Reisz et al., 2011).

### ***Captorhinikos valensis***

Olson makes the first description of a new genus and species *Captorhinikos valensis* (Olson, 1954). Its holotype is specimen CNHM UR 101 (now FMNH UR 101), and its remains are comprised of the anterior part of the lower jaw and maxillary tooth plate (Olson, 1954). It was found in the Vale Formation, Clear Fork Group, Early Permian of Texas, U.S.A. (Olson, 1954). However, the author does not describe sculpturing (Olson, 1954) and does not provide illustrations of the skull (Olson, 1954). There is a reconstruction of the lower jaw but it is unclear if the dermal sculpturing is represented (Olson, 1954).

Seltin, in 1959, publishes a genus and species diagnosis of *Captorhinikos valensis* after Olson (Seltin, 1959) but nothing is said about the skull sculpturing (Seltin, 1959). There is only one figure depicting a reconstruction of the upper and lower dentitions of the holotype (Seltin, 1959), but skull sculpturing is not discernible.

In 2014, Modesto, Lamb and Reisz conducted a revision of *Captorhinikos valensis* along with a new phylogenetic analysis (Modesto et al., 2014). By re-examining *C. valensis*, the authors describe its anatomy in greater detail and restate its systematic palaeontology (Modesto et al., 2014). Modesto et al. report that the lateral surface of the maxilla in specimen FMNH UR 102 “bears low, rounded, and interconnecting ridges and is punctured with numerous small foramina, a pattern of ornamentation that is seen in other small captorhinids.” (Modesto et al., 2014). The lateral surface of the mandible is described as “richly ornamented with a system of low, elongate, and rounded ridges delineated by long, narrow excavations […] quite distinct from the typical elongated pits that excavate the lateral surfaces of the dentaries of other captorhinids.” (Modesto et al., 2014). Nothing else is said of the skull sculpturing (Modesto et al., 2014). However, the paper includes photography of the left dentary of the holotype where this ornamentation is clearly visible (Modesto et al., 2014). There is also photography of the partial left maxilla of FMNH UR 102 where dermal sculpturing can also be identified (Modesto et al., 2014).

In 2005, LeBlanc, Brar, May and Reisz referred some of newly recovered material to *C. valensis*, previously known only from younger strata in Texas (LeBlanc et al., 2015). Hence, the authors amend the species initial diagnosis by Olson 1954, updating it with new information. It should be noted that the new material came from portions of dentary bones and maxillae, not from other cranium bones or elements. Furthermore, there are no references to skull sculpturing on the text. However, in a figure comprised of drawings of three partial dentaries of *C. valensis* in lateral view (respectively OMNH 77533, OMNH 55796, and OMNH 77534) some bones seem to be sculptured (LeBlanc et al., 2015).

### ***Captorhinikos chozaensis***

Similarly to *Captorhinikos valensis*, *Captorhinikos chozaensis* was described by Olson in 1954. Its holotype is the specimen CNHM UR 97 (now FMNH UR 97) and is comprised of both lower jaws and skull fragments (Olson 1954). It was found in the lower part of Choza Formation, Clear Fork group, Foard County, Early Permian of Texas, U.S.A. (Olson 1954). Just like with its sister taxon *C. valensis*, the author does not describe skull sculpturing and there is no illustration of the skeleton of *C. chozaensis* (Olson 1954).

In 1958, Vaughn publishes a paper analysing a specimen (USNM 21275) he assigns to *C. chozaensis,* from the Hennessey Formation, Lower Permian of Oklahoma (Vaughn, 1958). The similarity between the cranium of *C. chozaensis* and those of *Captorhinus* and *Labidosaurus* is again mentioned (Vaughn, 1958). On the supplementary description, Vaughn states that the "surface of the dermal skull roof is, as in captorhinids generally, ornamented with numerous small pits." (Vaughn, 1958). That is all the information on skull sculpturing included and there are no illustrations present (Vaughn, 1958).

Seltin publishes "A review of the family Captorhinidae" in 1959, where he describes and analyses the genus and the species separately (Seltin, 1959). Again, skull sculpturing is not mentioned in *C. chozaensis* (Seltin, 1959). The only image provided is a reconstruction of the lower dentition of the holotype (Seltin, 1959) with no skull sculpturing visible.

Olson, in 1962, dedicates the second part of "Permian vertebrates from Oklahoma and Texas" to his single-penned "The Osteology of *Captorhinikos chozaensis*" (Olson & Barghusen, 1962). Following work by Vaughn, Olson refers specimen CNHM UR 183 to *C. chozaensis* instead of the initially attributed *Labidosaurikos meachami* (Olson, 1962). Olson analyses new material and revaluates previous descriptions by other authors (Olson, 1962). The author states the difficulty in differentiating "*Captorhinus, Labidosaurus, Captorhinikos* and *Labidosaurikos* from features of the dorsal and lateral surfaces of the skulls and structures of the lower jaws" due to the lack of detail in the at-the-time knowledge about structural patterns (Olson, 1962). Still, the osteological study conducted by Olson is very much based on measurements, proportions, and dentition; he does not describe skull sculpturing (Olson, 1962). This anatomical trait is not displayed in the images representing cranial reconstructions (Olson, 1962).

In 1970, Olson publishes “New and little-known genera and species of vertebrates from the Lower Permian of Oklahoma”. Here, the author analyses *C. chozaensis* remains along with a revisit of already-known material (Olson, 1970). However, this analysis is more focused on the geological distribution of the species and comparison relative to the state of ossification between *C. chozaensis* and *Captorhinus parvus* (Olson, 1970). No information on bone sculpturing is given and there are no images available on the paper (Olson, 1970).

### *Reiszorhinus olsoni*

Sumida, Dodick, Metcalf and Albright, in 2010, described the new genus and species *Reiszorhinus olsoni*, based in a holotype (FMNH UC183) from Mitchell Creek, Waggoner Ranch Formation, Lower Permian of Texas, U.S.A. (Sumida et al., 2010). However, this specimen comprised of a nearly complete skull had been discovered almost a century before. Williston, in 1917, used it in his reconstruction of a *Labidosaurus* skull (Williston, 1917; Sumida et al., 2010). Clark and Carroll in 1973 mentioned this specimen and stated that it could have some relation to *Labidosaurus* but were unwilling to assign it confidently to that taxon (Clark & Carroll, 1973). In 1980, although having used it as the basis for an illustration of *Labidosaurus* teeth, Heaton along with Reisz concurred with Clark and Carroll and defended that the skull represented a new species of *Protocaptorhinus* (Reisz & Heaton, 1982). Finally, Sumida et al. showed that although a new taxon, this specimen was also distinct at the generic level, and hence described *R. olsoni* (Sumida et al., 2010). Luckily, although suffering from some deformation, the specimens (both holotype and referred specimen CM 81758) do provide “information regarding the degree of dermal sculpturing present.” (Sumida et al., 2010). CM 81758, namely, “indicates that it was very well developed.” (Sumida et al., 2010). Regarding the lacrimal, the “pattern of dermal sculpturing on CM 81785 suggests that a well-developed centre of ossification was located just rostral to the anteroventral margin of the orbit.” (Sumida et al., 2010). The authors also mention that the “occipital exposure of the squamosal was devoid of sculpturing” (Sumida et al., 2010). They add that on the lower jaws, the dermal “sculpturing on the holotype is faint, but it is clear and well developed in CM 81785.” (Sumida et al., 2010);

specifically, although "surface sculpturing has been prepared away in the holotype, the angular and other laterally exposed elements of the mandible in CM 81785 demonstrate it clearly. Significantly, the sculpturing extends onto the medial surface of the angular in this specimen as well." (Sumida et al., 2010).

### *Opisthodontosaurus carrolli*

Reisz, LeBlanc, Sidor, Scott and May describe this species for the first time in 2015 (Reisz, LeBlanc, Sidor, Scott & May, 2015). The holotype of *O. carrolli* (OMNH 77469) was found in the Richards Spur area, Early Permian of Oklahoma, U.S.A. (Reisz et al., 2015). The authors refer that many aspects of the cranial anatomy of *Opisthodontosaurus* are "indistinguishable from those of *Captorhinus*", and hence comparison between both would allow them to "focus only on those parts […] in which *Opisthodontosaurus* differs from that taxon" (Reisz et al., 2015). Curiously, the skull sculpturing is clearly different (Reisz et al., 2015). "The sculpturing in *Opisthodontosaurus* [is] significantly more subdued than in [the genera] *Captorhinus*, *Labidosaurus*, or *Labidosaurikos* and more like the sculpturing in the Carboniferous captorhinid *[Eu]Concordia*" (Reisz et al., 2015). As such, even though there is not a clear description of how the skull sculpturing is in *O. carrolli*, we can and assume that it is somewhat similar to *Euconcordia* (Reisz et al., 2015). Reisz et al. describe the sculpturing in the mandibular rami, stating that in "contrast to the rest of the dentary bone, the coronoid process does not have the typical captorhinid surface sculpturing but rather very slight ridges and valleys that extend posterodorsally." (Reisz et al., 2015). This paper has photographs and drawings of the partial skull of the holotype and another referred specimen (OMNH 77470) in lateral view, in which the sculpturing is observable (Reisz et al., 2015). There is also an illustration of the left dentary of specimen OMNH 43300 in lateral view where sculpturing is also present (Reisz et al., 2015).

### *Labidosauriscus richardi*

*Labidosauriscus richardi* is a species of captorhinid recently described by Modesto, Scott and Reisz in 2018. The holotype (OMNH 77609) was found at Richards Spur, Dolese

Bros. limestone quarry, Lower Permian of Oklahoma, U.S.A. (Modesto et al., 2018). *L. richardi* is diagnosed as a small captorhinid characterized by reduced ridge-and-pit cranial ornamentation over which is superimposed a distinctive finer system of tiny pits and furrows" (Modesto et al., 2018). In the extensive description of the skull roof, the authors address the sculpturing further (Modesto et al., 2018). The premaxilla differs from *Captorhinus* "in exhibiting ornamentation consisting of a system of fine pits and furrows, rather than the distinct honey-combing seen in *Captorhinus* and *Labidosaurus*" (Modesto et al., 2018). The external surface of the maxilla "is lightly sculpted with shallow, fine furrows" (Modesto et al., 2018). The rest of the sculpturing present in dermal bones consists of a "system of fine foramina and furrows that is superimposed over reduced ridge-and-pit sculpturing" (Modesto et al., 2018). The dentaries sculpturing is comprised "of the fine pits and grooves that were described … for skull roof elements" (Modesto et al., 2018). "Tiny pits and short grooves are concentrated anteroventrally […], and these tend to longer, posteriorly-attenuating grooves from tooth position 4 onwards. This system of fine pits and grooves is superimposed over a pattern of slightly larger pits from which issue short, mostly posteriorly-directed grooves, as well as the line of labial foramina" (Modesto et al., 2018). The paper has several pictures and photographs of the skull case and both mandibular rami where the sculpturing is clear (Modesto et al., 2018).

### *Captorhinus kierani*

Initially considered as another specimen of *Captorhinus magnus*, the holotype of *Captorhinus kierani* (formerly BMRP.2005.3.1., now OMNH 73281a) firstly appeared in literature in 2015 (LeBlanc & Reisz, 2015). This paper includes a photograph of the lateral right side of the skull, where sculpturing is evident (LeBlanc & Reisz, 2015). Nothing is mentioned about skull sculpturing (LeBlanc and Reisz, 2015).

The paper where *Captorhinus kierani* is described for the first time was published earlier this year, by authors deBraga, Bevitt and Reisz (deBraga et al., 2019). deBraga et al. update the specimen ID code and reassign it to *Captorhinus kierani* as its holotype, staging it as a sub-adult (deBraga et al., 2019). The main differences between *Captorhinus magnus* and *Captorhinus kierani* are related to teeth morphology (deBraga et al., 2019).

Nevertheless, skull sculpturing is still mentioned (deBraga et al., 2019) and it is said that the region contributing to skull roof is ornamented with a typical *Captorhinus* sculpting pattern (deBraga et al., 2019). Additionally, the authors propose that "this condition is autopomorphic for *C. aguti*, distinguishing it from *C. magnus* and *C. laticeps* where postparietals lack ornamentation and are restricted to the occipital face" (deBraga et al., 2019). DeBraga, Bevitt and Reisz had access to cutting-edge imaging technology, including neutron CT-scans and SEM. As such, the high-quality images presented are extremely detailed (deBraga et al., 2019). Besides photographs and drawings of the skull in several views, there are also images of isolated bones and an isomorphic rendering of neutron scan of the lateral skull view (deBraga et al., 2019).

## b. Morphological characters: a critical review

### Characters 1 to 6

"**(1) Premaxilla ventral margin aligned:** anteroposteriorly in lateral view (0); anteroventrally in lateral view (1)" (Modesto et al., 2018).

**"(2) Premaxilla:** alary process absent (0); alary process present on posterodorsal process (1)" (Modesto et al., 2018).

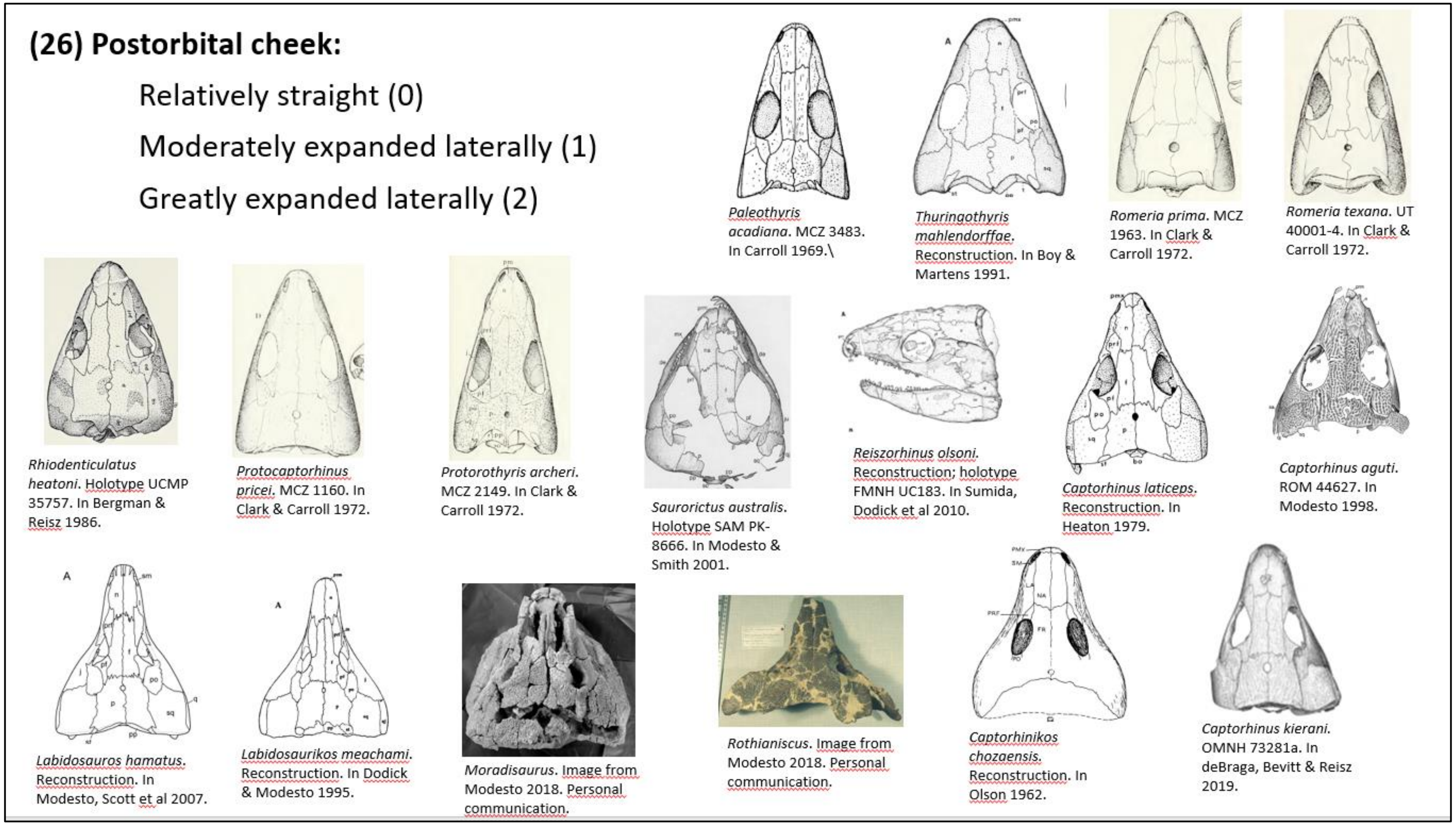
**"(3) Premaxillary dentition:** first tooth relatively small relative to maxillary caniniform (0); subequal to maxillary caniniform (1). In taxa lacking maxillary caniniforms, state 1 applies when the first premaxillary tooth is the largest marginal tooth present" (Modesto et al., 2018).

**"(4) Maxilla:** relatively straight (0); posterior end flexed laterally (1)" (Modesto et al., 2018).

**"(5) Maxilla:** posterior-most tooth positioned at level of posterior margin of orbit (0) or positioned more anteriorly (1)" (Modesto et al., 2018).

**"(6) Maxillary dentition:** tooth stations number 30 teeth or more (0); teeth number 18–26 (1); teeth number 14–17 (2); teeth number 13 or less (3). For multiple-rowed taxa, only those teeth with unobstructed profiles when viewed laterally are considered." (Modesto et al., 2018).

We maintain these characters as previously described; all character states are figured in Appendix 11 (see Figure 9 for an example).



**(26) Postorbital cheek:**

Relatively straight (0)
Moderately expanded laterally (1)
Greatly expanded laterally (2)

*Paleothyris acadiana*. MCZ 3483. In Carroll 1969.\

*Thuringothyris mahlendorffae*. Reconstruction. In Boy & Martens 1991.

*Romeria prima*. MCZ 1963. In Clark & Carroll 1972.

*Romeria texana*. UT 40001-4. In Clark & Carroll 1972.

*Rhiodenticulatus heatoni*. Holotype UCMP 35757. In Bergman & Reisz 1986.

*Protocaptorhinus pricei*. MCZ 1160. In Clark & Carroll 1972.

*Protorothyris archeri*. MCZ 2149. In Clark & Carroll 1972.

*Saurorictus australis*. Holotype SAM PK-8666. In Modesto & Smith 2001.

*Reiszorhinus olsoni*. Reconstruction; holotype FMNH UC183. In Sumida, Dodick et al 2010.

*Captorhinus laticeps*. Reconstruction. In Heaton 1979.

*Captorhinus aguti*. ROM 44627. In Modesto 1998.

*Labidosauros hamatus*. Reconstruction. In Modesto, Scott et al 2007.

*Labidosaurikos meachami*. Reconstruction. In Dodick & Modesto 1995.

*Moradisaurus*. Image from Modesto 2018. Personal communication.

*Rothianiscus*. Image from Modesto 2018. Personal communication.

*Captorhinikos chozaensis*. Reconstruction. In Olson 1962.

*Captorhinus kierani*. OMNH 73281a. In deBraga, Bevitt & Reisz 2019.

*Figure 9: Representation of states considered for character 26 (See Appendix 10)*

### Character 7

“**(7) Teeth on maxillary dental field**: none (0); less than 40 (1); 40 or more (2). Definition modified from Reisz et al. (2011) for clarity.” (Modesto et al., 2018).

Character 7 was removed given that it is not independent of characters 6 and 9; if character state 6 is (1), (2) or (3), it is necessarily character state (0) or (1) for character 7. In addition, the limits of the maxillary dental field are not clearly stated, which can lead to different interpretations.

### Characters 8 to 12

“**(8) Maxillary caniniform teeth:** present (0); absent (1)” (Modesto et al., 2018).

**“(9) Number of tooth rows in the upper jaw:** one (0); two to four (1); five (2); six or more (3)” (Modesto et al., 2018).

**“(10) Marginal dentition:** ‘cheek’ teeth recurved (0); chisel-shaped (1); bulbous and ogival (2); bulbous at base and conical above (3)” (Modesto et al., 2018).

**“(11) Maxilla:** double row of teeth extend far anteriorly on tooth row absent (0); double row of teeth extend far anteriorly on tooth row present (1)” (Modesto et al., 2018).

**“(12) Dental tooth wear:** absent (0); present, modest (1); present, saddle shaped (2).” (Modesto et al., 2018).

We maintain these characters as previously described; all character states are figured in Appendix 11.

### Character 13

“**(13) Lacrimal:** suture with jugal small (0); well developed (1).” (Modesto et al., 2018).

Instead of being qualitative, this character requires a qualitative interpretation to be scored. Furthermore, there is no clear definition of what “small” and “well-developed” mean in terms of actual numbers or proportions. Hence, we decided to replace this character with two clearly different alternatives following the methodology earlier summarized.

The first alternative refers to the angle that the lacrimal suture with jugal makes with the vertical axis (see Figure 10).

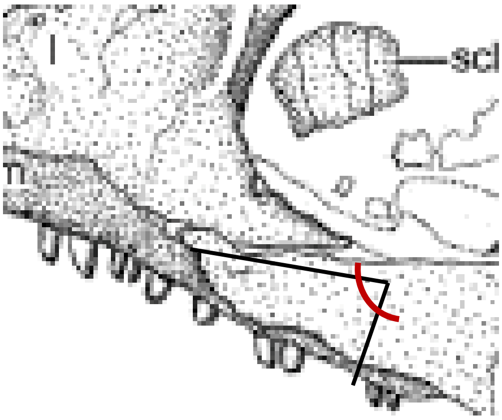


*Figure 10:* Reiszorhinus olsoni. *Graphical indication of the morphometric measurements needed for character 13a. Adapted from Sumida, Dodick et al. 2010.*

After measuring this trait in all species (character 13a), the data was plotted on an and the distribution graph was generated (Figure 11).

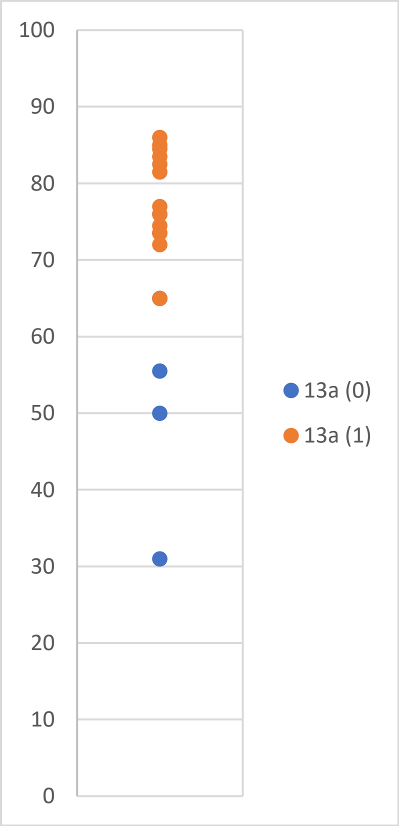
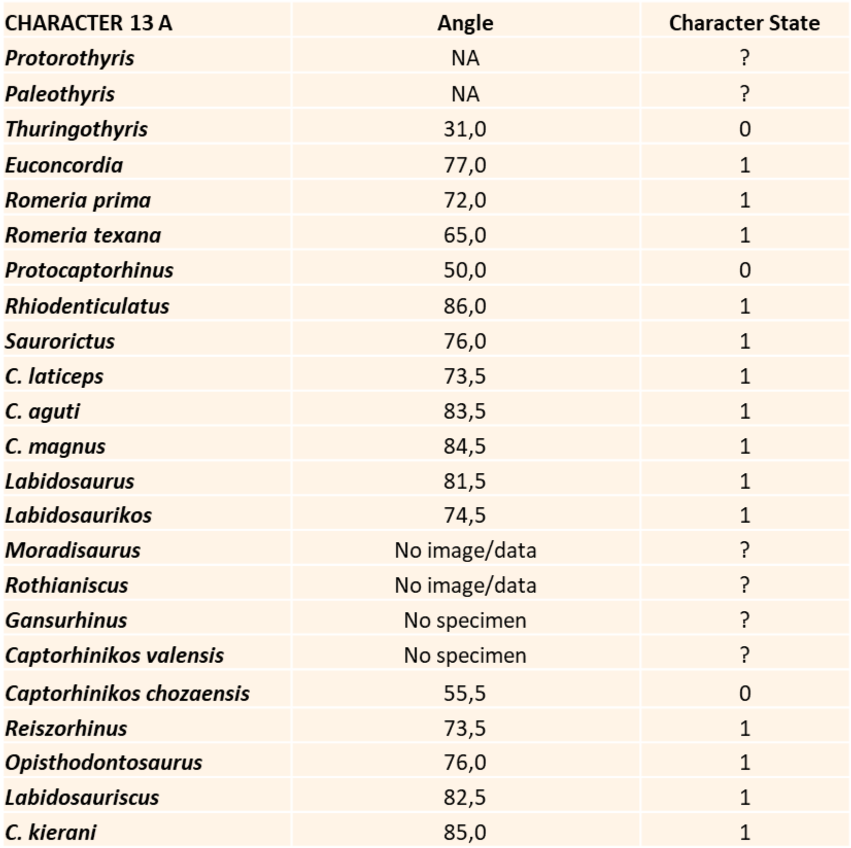


*Figure 11: Graph where morphometric data for character 13a is plotted. The widest gap (after removing outliers) sits at 60, effectively sorting the species in two distinct groups.*

We divided this data into two distinct groups (see Section 2.b.): one where the angle is below 60º and another where it is above; the species were then coded by attributing them the correspondent character status, resulting in the following table (Table 1).

*Table 1: Table summarizing morphometric data for character 13a, per species. Character state for each species is also identified.*



| CHARACTER 13 A | Angle | Character State |
|---|---|---|
| ***Protorothyris*** | NA | ? |
| ***Paleothyris*** | NA | ? |
| ***Thuringothyris*** | 31,0 | 0 |
| ***Euconcordia*** | 77,0 | 1 |
| ***Romeria prima*** | 72,0 | 1 |
| ***Romeria texana*** | 65,0 | 1 |
| ***Protocaptorhinus*** | 50,0 | 0 |
| ***Rhiodenticulatus*** | 86,0 | 1 |
| ***Saurorictus*** | 76,0 | 1 |
| ***C. laticeps*** | 73,5 | 1 |
| ***C. aguti*** | 83,5 | 1 |
| ***C. magnus*** | 84,5 | 1 |
| ***Labidosaurus*** | 81,5 | 1 |
| ***Labidosaurikos*** | 74,5 | 1 |
| ***Moradisaurus*** | No image/data | ? |
| ***Rothianiscus*** | No image/data | ? |
| ***Gansurhinus*** | No specimen | ? |
| ***Captorhinikos valensis*** | No specimen | ? |
| ***Captorhinikos chozaensis*** | 55,5 | 0 |
| ***Reiszorhinus*** | 73,5 | 1 |
| ***Opisthodontosaurus*** | 76,0 | 1 |
| ***Labidosauriscus*** | 82,5 | 1 |
| ***C. kierani*** | 85,0 | 1 |

Character 13a was then defined as follows: "**(13a) Lacrimal suture with jugal:** angle with vertical axis < 60º; angle with vertical axis > 60º".

Character 13b is another alternative to character 13 where we tried to maintain the concept of short versus well developed. As such, character status based on the ratio of two segment lengths is suggested. We considered two line segments: one formed by the lacrimal suture with jugal and another one formed by the perpendicular jugal width at orbit midpoint (Figure 12).

*Figure 12:* Reiszorhinus olsoni. *Graphical indication of the morphometric measurements needed for character 13b. The ratio is always between the segment in red and the segment in green. Adapted from Sumida, Dodick et al. 2010.*

The resulting ratio value was then plotted, where a noticeable gap is present between the values of 2,00 and 2,47 (see Appendix 6). Consequently, the species were sorted into two different groups; one with a ratio equal to or below 2,24 with character state (0), and other with a ratio superior to 2,24 with character state (1).

Character 13b is defined as:

“**(13b) Lacrimal suture with jugal:** ratio between the suture length and the jugal width at the orbital midpoint equal to or less than 2,24 (0); ratio between the suture length and the jugal width at the orbital midpoint more than 2,24 (1).”

### Character 14

**“(14) Nasolacrimal suture:** straight (0); interdigitating (1).” (Modesto et al., 2018).

We maintain this character as previously described; all character states are figured in Appendix 11.

### Character 15

“**(15) Snout:** broad, equal to or greater than 35% of skull length (0); narrow, equal to or less than 25% of skull length (1).” (Modesto et al., 2018).

Character 15 presents a new problem – i.e. even though it is defined quantitatively by the ratio of two morphometric skull measures, it is not defined how to measure both variables. Measuring a snout width subtle (or pronounced) differences along the anteroposterior axis can produce very different results. Moreover, depending on the shape of each skull, the most posterior point might be the occipital condyle, the squamosals or even the quadratojugal bones.

We propose four different alternatives to this character:

Alternative 15a maintains the definition but includes a clear statement on where the measurements should be made and the threshold values between character states were readjusted.

“**(15a) Snout:** narrow, ratio between cranium width at nostril-orbit midpoint and total cranium length smaller than 0,36 (0); broad, ratio between cranium width at nostril-orbit midpoint and total cranium length bigger than 0,36 (1).”.

New character 15b considers the ratio between posterior cranium length at nostril-orbital midpoint and total cranium length, and is defined as follows:

“**(15b) Snout:** ratio between anterior cranium length at nostril-orbital midpoint and total cranium length more than 0,28 (0); ratio between anterior cranium length at nostril-orbital midpoint and total cranium length between 0,21 and 0,28 (1); ratio between anterior cranium length at nostril-orbital midpoint and total cranium length smaller than 0,21 (2).”.

New character 15c is also a ratio, but between the premaxilla length and the total cranium length:

“**(15c) Snout:** ratio between premaxilla length in dorsal view and total cranium length superior to 0,05 (0); ratio between premaxilla length in dorsal view and total cranium length inferior to 0,05 (1).”.

Finally, we also include character 15d - comparing the cranium width at nostril-orbital midpoint with the broadest cranium width:

“**(15d) Snout:** broad, ratio between cranium width at nostril-orbital midpoint and broadest cranium width superior to 0,34 (0); narrow, ratio between cranium width at nostril-orbital midpoint and broadest cranium width inferior to 0,34 (1).”.

### Characters 16 to 17

"**(16) Antorbital/cheek region:** mainly formed by lacrimal and prefrontal (0); mostly formed by lacrimal due to dorsal expansion of the bone (1)" (Modesto et al., 2018).

**"(17) Prefrontal:** prefrontal-nasal suture shorter than lacrimal-nasal suture (0); prefrontal-nasal suture longer than lacrimal-nasal suture (1)." (Modesto et al., 2018).

We maintain these characters as previously described; all character states are figured in Appendix 11.

### Character 18

"**(18) Frontal:** anterior process short, less than 40% of the frontal sagittal length (0); anterior process long, approximately 55% of the frontal sagittal length (1)" (Modesto et al., 2018).

Character 18 is a quantitative measurement. As such, we only conducted a more precise measurement, and then updated boundary values. The updated character is now identified as 18a.

"**(18a) Frontal:** anterior process short, less than 0,59 of the frontal sagittal length; anterior process long, 0,59 or more of the frontal sagittal length".

### Character 19

"**(19) Jugal:** subtemporal process dorsoventrally low, equal to or less than 25% of skull height through orbital midpoint (0); subtemporal process dorsoventrally deep, at least 40% of skull height through orbit (1)." (Modesto et al., 2018).

Character 19 has two different issues related to how skulls in captorhinids tend to develop. There seems to exist an allometric growth that results in larger orbits present in proportionally smaller species and vice-versa. This trend may produce errors in the assessment of this character and its states. However, as in character 13, the character description does not specify where to measure the height of the subtemporal process of the jugal bone. Additionally, this process can have different shapes depending on the species considered. As such, we used several new characters as alternatives.

Character 19a keeps the original description; we further state by graphical image support (see Appendix 6) that the height of the subtemporal process of the jugal should be measured at its highest point. Consequently, the boundary values that separate state (0) from state (1) change.

“**(19a) Jugal subtemporal process height:** dorsoventrally low, equal to or less than 0,52 of skull height through orbital midpoint (0); dorsoventrally deep, at least 0,52 of skull height through orbital midpoint (1).”

Character 19b is the same as character 19a, with the distinction of considering the length of the subtemporal process of the jugal instead of its height. It should be measured along the suture, starting on the node where the postorbital, jugal and squamosal bones meet, all the way to the lower limit of the skull in lateral view.

“**(19b) Jugal subtemporal process length:** dorsoventrally low, equal to or less than 0,52 of skull height through orbital midpoint (0); dorsoventrally deep, at least 0,52 of skull height through orbital midpoint (1)”.

Character 19c compares the length of the jugal-postorbital suture with the skull height through orbital midpoint:

“**(19c) Jugal-postorbital suture length:** short, equal to or less than 0,68 of skull height through orbital midpoint (0); long, at least 0,68 of skull height through orbital midpoint (1).”.

Character 19d compares this same suture with the length of the jugal subtemporal process, as shown in Appendix 6:

“**(19d) Jugal-postorbital suture length:** short, less than 0,84 of jugal subtemporal process length (0); long, equal to or more than 0,84 of jugal subtemporal process length (1).”.

Character 19e on the angle that the jugal-postorbital suture makes with the lower limit of orbit midpoint:

“**(19e) Jugal-postorbital suture:** angle with lower limit of orbit midpoint smaller than 30º (0); angle with lower limit of orbit midpoint equal to or bigger than 30º (1).”.

Character 19f is defined by a different angle: the angle between the jugal-postorbital suture and the dorsal plan:

“**(19f) Jugal-postorbital suture:** angle with dorsal plan bigger than 33º (0); angle with dorsal plan between 19º and 33º (1); angle with dorsal plan smaller than 19º (2).”.

Finally, character 19g attempts to classify the shape of the subtemporal process of the jugal.

“**(19g) Jugal subtemporal process shape:** fanning out (0); descending (1).”.

### Character 20

“**(20) Jugal:** anterior extent ends posterior to anterior orbital margin (0); anterior extent reaches beyond anterior orbital margin (1).” (Modesto et al., 2018).

We maintain this character as previously described; all character states are figured in Appendix 11.

It is, however, important to note that this character is not independent of character 13; “long contacts between jugal and lacrimal exist because the anterior extent end of the jugal is posterior to the orbital margin; if one is present the other is also present” (Modesto, pers. comm.).

### Characters 21 and 22

“**(21) Jugal:** postorbital extent shorter than remaining anterior extent (0); postorbital extent equal or longer (1)” (Modesto et al., 2018).

**“(22) Quadratojugal:** anteroposteriorly elongate (0); short, not extending anteriorly beyond midpoint of postorbital margin (1).” (Modesto et al., 2018).

We redefined these two characters as follows:

“**(21) Postorbital-Jugal suture:** shorter than the squamosal-postorbital suture (0); equal or longer (1).

**(22) Quadratojugal:** anteroposteriorly elongate (0); short, not extending anteriorly beyond midpoint of postorbital region (1).”.

All character states are figured in Appendix 11.

### Characters 23 and 24

“**(23) Quadratojugal:** acuminate anteriorly (0); square-tipped anteriorly (1)” (Modesto et al., 2018).

**“(24) Quadratojugal:** expanded dorsally (0); posteriorly straight or decreasing in height (1).” (Modesto et al., 2018).

We maintain these characters as previously described; all character states are figured in Appendix 11. We propose a tentative of redescription of characters 23 and 24 amongst the alternative new characters suggested for replacing character 25 (character 25c and 25d, respectively).

### Character 25

“**(25) Quadratojugal:** maximum height approximately equal to one-third or less that of squamosal (0); nearly equal to half of squamosal height (1).” (Modesto et al., 2018).

Character 25 presents the same issue as characters 13 and 19. Although the heights of two bones are compared, there is no indication of where exactly those measurements should be done.

We propose a new character (25a) that keeps the same definition as character 25, only establishing the measurements in more clearly – see Appendix 6 and Appendix 11.

“**(25a) Quadratojugal maximum height versus squamosal height measured in the same vertical line:** approximately equal to or less than 0,36 (0); more than 0,36 (1).”.

Character 25b compares the length of the jugal to the posterior length of the cranium, measured from the posteriormost limit of the orbit.

“**(25b) Quadratojugal maximum length versus posterior cranium length from posteriormost orbital limit:** more than 0,66 (0); equal to or less than 0,66 (1).”.

Character 25c defines qualitatively the shape of the anterior process of the quadratojugal:

“**(25c) Quadratojugal anterior process shape:** acuminate (0); square (1).”.

As previously mentioned, character 25d defines the longitudinal shape of the quadratojugal in lateral view:

“**(25d): Quadratojugal longitudinal shape:** elevated (0); straight (1).”.

Finally, character 25e compares the maximum length of the quadratojugal with the total cranium length in lateral view:

“**(25e) Quadratojugal maximum length versus total cranium length:** more than 0,2 (0); equal to or less than 0,2 (1).”.

### Character 26

“**(26) Postorbital cheek:** relatively straight (0); moderately expanded laterally (1); greatly expanded laterally (2).” (Modesto et al., 2018).

Like character 13, character 26 is defined qualitatively. Unless the postorbital cheek shape is strongly expanded (see most Protorothyrididae or *Rothisaniscus* and *Labidosaurus* for extreme examples), it is hard to assign each skull into a particular state. In addition, not only two but three different character states are required to be easily identifiable. We opted to split this character into two clear states: 26a, a quantitative character, and 26b, a qualitative character.

“**(26a) Postorbital cheek:** not expanded laterally, ratio between width of cranium at midorbital point and largest cranium width superior to 0,58 (0); expanded laterally, ratio between width of cranium at midorbital point and largest cranium width equal to or inferior to 0,58 (1).

**(26b) Postorbital cheek:** relatively straight (0); with sigmoidal shape (1).”.

### Characters 27 and 28

“**(27) Parietal:** distinct anterolateral process present that partially separates postfrontal and postorbital (0); does not strongly project between postfrontal and postorbital (1)” (Modesto et al., 2018).

**“(28) Pineal foramen:** positioned at midpoint of interparietal suture (0); anterior to midpoint of interparietal suture (1); posterior to midpoint of interparietal suture (2).” (Modesto et al., 2018).

We maintain these characters as previously described; all character states are figured in Appendix 11.

### Character 29

“**(29) Sculpturing:** skull surface relatively smooth, with only small honeycombing pits or grooves (0); with pits and grooves with notably larger, randomly positioned pits on posterior skull table (1); low ridge-and-pit system with tiny pits and furrows (2).” (Modesto et al., 2018).

Character 29 concerns the skull sculpturing and as such will have its own separate section further on this chapter and on the Discussion chapter. The original character 29 was removed.

### Character 30

“**(30) Supratemporal:** obliquely oriented into anteromedial direction, thereby lying within a facet of the parietal (0); positioned mediolaterally at the posterior edge of the parietal (1).” (Modesto et al., 2018).

We redefined character 30 as follows:

“**(30) Supratemporal:** obliquely oriented into anteromedial direction, thereby lying within a facet of the parietal (0); positioned posterolaterally at the posterior edge of the parietal (1).”.

All these characters and character states were figured using visual representations (see Appendix 11).

### Characters 31 to 37

“**(31) Supratemporal:** small, slender element (0); large, contributing to skull table (1)” (Modesto et al., 2018).

**“(32) Supratemporal-postparietal contact:** tenuous or absent (0); well developed (1)” (Modesto et al., 2018).

**“(33) Postparietal:** contacts mate dorsally only, postparietals separated slightly ventrally by supraoccipital (0); contacts mate fully along height (1)” (Modesto et al., 2018).

**“(34) Postparietal:** transversely short with tabular present (0); transversely elongate with tabular absent (1)” (Modesto et al., 2018).

**“(35) Postparietal:** contribution to skull table absent or forms only narrow edge (0); contribution to skull table large, forming sculptured posterior portion of skull table (1)” (Modesto et al., 2018).

**“(36) Skull table occipital margin:** embayed bilaterally (0); straight (1); with single median embayment (2)” (Modesto et al., 2018).

**“(37) Vomer:** denticulated (0); edentulous (1).” (Modesto et al., 2018).

We maintain this character as previously described; all character states are figured in Appendix 11.

### Character 38

“**(38) Vomer-pterygoid contact:** extensive, at least 50% median border of vomer (0); short, no more than 33% median border of vomer (1).” (Modesto et al., 2018).

Character 38, like character 18, is a quantitative measure in which the morphometric elements are clearly identified. Hence, we used a more precise measurement. All species values were updated and character 38 is now identified as 38a.

“**(38a) Vomer-pterygoid contact:** extensive, at least 0,66 times median border of vomer (0); short, no more than 0,66 times median border of vomer (1).”.

### Character 39

“**(39) Palatine:** denticulated (0); edentulous (1)” (Modesto et al., 2018).

We maintain this character as previously described; all character states are figured in Appendix 11.

### Character 40

**“(40) Jugal/ectopterygoid:** ectopterygoid present and alary process absent (0); ectopterygoid absent and alary process present, but no higher than the midpoint of the suborbital process of the jugal and distinct from the orbital margin (1); ectopterygoid absent and alary process present and positioned dorsally on the medial surface of the jugal, flush with orbital margin (2)” (Modesto et al., 2018).

Due to its complexity, this character was divided in two: 40a, regarding the presence or absence of the ectopterygoid bone, and 40b, regarding the presence or absence of the alary process of the jugal and its position on the medial surface of the jugal.

“**(40a) Ectopterygoid:** present (0); absent (1).

**(40b) Alary process of the jugal:** inexistent (0); present and no higher than the midpoint of the suborbital process of the jugal, distinct from orbital margin (1); present and positioned dorsally on the medial surface of the jugal, flush with orbital margin (2).”.

### Characters 41 to 43

**“(41) Dentition on palatal ramus of pterygoid:** present (0); greatly reduced or absent (1)” (Modesto et al., 2018).

**“(42) Pterygoid:** transverse flange dentition consists of shagreen (i.e. cluster) of denticles (0); transverse flange dentition consists of at least one row of functional teeth (1); transverse flange dentition absent (2)” (Modesto et al., 2018).

**“(43) Pterygoid:** transverse flange broad-based and distinctly angular in ventral view (0); transverse flange narrow and tongue-like in ventral view (1).” (Modesto et al., 2018).

We maintain these characters as previously described; all character states are figured in Appendix 11.

### Character 44

“**(44) Suborbital foramen:** absent (0); present (1); anteroposteriorly elongate (2).” (Modesto et al., 2018).

This character was removed. Character 44 is defined based on a morphological character difficult to identify (in agreement with Modesto, pers. comm. 2018).

### Characters 45 to 46

“**(45) Parasphenoid:** cultriform process extends anteriorly (0); cultriform process extends slightly dorsally at roughly 15º to the basal plane (1); cultriform process extends anterodorsally at more than 45º to the basal plane (2)” (Modesto et al., 2018).

**“(46) Parasphenoid:** edentulous (0); denticulated (1).” (Modesto et al., 2018).

We maintain these characters as previously described; all character states are figured in Appendix 11.

### Character 47

“**(47) Parasphenoid:** deep ventral groove between cristae ventrolateralis absent (0); deep ventral groove between cristae ventrolateralis present (1).” (Modesto et al., 2018).

Like characters 21 and 22, we redefined character 47 as follows in the next paragraph.

“**(47) Parasphenoid:** deep ventral groove formed by cristae ventrolateralis absent (0); deep ventral groove formed by cristae ventrolateralis present (1).”

All character states are figured in Appendix 11.

### Characters 48 to 50

**“(48) Parasphenoid:** posterolateral wing narrow, meets narrow head of stapes (0); wing broad, meets large head of stapes, in an elongate, nearly parasagittal suture (1)” (Modesto et al., 2018).

**“(49) Opisthotic:** paroccipital process long, extending near to medial edge of squamosal (0); process short, extending only slightly beyond body of opisthotic (1)” (Modesto et al., 2018).

**“(50) Paroccipital process:** broad (0); narrow (1).” (Modesto et al., 2018).

We maintain these characters as previously described; all character states are figured in Appendix 11.

### Character 51

“**(51) Stapes:** distal process short (0); distal process elongate (1).” (Modesto et al., 2018).

We removed this character because it is extremely hard to identify.

### Character 52

“**(52) Supraoccipital:** slopes anterodorsally (0); aligned vertically or slopes posterodorsally (1).” (Modesto et al., 2018).

We maintain this character as previously described; all character states are figured in Appendix 11.

### Character 53

“**(53) Supraoccipital:** lateral ascending processes account for half or less height of bone (0); lateral ascending processes account two-thirds or more height of the bone (1).” (Modesto et al., 2018).

Despite being clearly defined, this trait presents a problem different from the ones listed so far. This character requires to observe a braincase element (the supraoccipital) and its ascending processes that are very rarely exposed. This can be done with access to isolated supraoccipitals, but these are extremely rare and high-resolution CT scans are even more scarce. As such, no changes were made, and we used the codings by Modesto et al. 2018 for it. All these characters and character states were figured using visual representations (see Appendix 11).

### Character 54

“**(54) Occipital condyle:** at level of quadrate condyles (0); immediately anterior to condyles (1).” (Modesto et al., 2018).

We maintain this character as previously described; all character states are figured in Appendix 11.

### Character 55

“**(55) Exoccipital:** lateral process on dorsal ramus absent (0); lateral process present (1).” (Modesto et al., 2018).

We removed this uninformative character because there is only one species classified as character state (1).

### Characters 56 to 58

**“(56) Dentary:** Anterior dentary teeth: teeth uniformly small (0), multiple enlarged teeth present anteriorly (1) (i.e. caniniform region sensu Modesto); single enlarged tooth present anteriorly (2)” (Modesto et al., 2018).

**“(57) Dentary:** first tooth oriented mainly vertically (0); first tooth leans strongly anteriorly (1)” (Modesto et al., 2018).

**“(58) Mandibular ramus:** relatively straight in ventral view (0); sigmoidal in ventral view (1).” (Modesto et al., 2018).

We maintain these characters as previously described; all character states are figured in Appendix 11.

### Character 59

“**(59) Mandibular ramus:** narrow, 8% or less of total jaw length (0); broad, no less than 14% of total jaw length (1).” (Modesto et al., 2018).

Character 59, similarly to characters 38 and 18, requires a quantitative measure in which the definition of morphometric elements is made clearer. Hence the boundary values were redefined, and the character is now identified as 59a.

“**(59a) Mandibular ramus:** narrow, 0,13 or less of total jaw length in dorsal view (0); broad, more than 0,13 of total jaw length in dorsal view (1).”.

### Characters 60 to 61

“**(60) Mandibular ramus:** posterior end rectilinear in lateral view (0) or acuminate in lateral view (1)” (Modesto et al., 2018).

**“(61) Mandibular ramus:** lateral shelf absent (0); lateral shelf present below coronoid process (1).” (Modesto et al., 2018).

We maintain these characters as previously described; all character states are figured in Appendix 11.

### Character 62

“**(62) Coronoid**: anterior process short (0); elongate (1).” (Modesto et al., 2018).

Like character 13 and 26, character 62 is defined qualitatively. The words “short” and “elongate” are used in order to try to translate a concept of length. However, without a proper frame of reference, this character is susceptible to personal interpretation. Hence, two alternative characters are here proposed.

Character 62a compares the length of the posterior process of the coronoid, measured posteriorly from the anteriormost limit of the surangular bone, with the total coronoid length.

“**(62a) Posterior process of the coronoid:** equal to or longer than 0,42 of total coronoid length (0); shorter than 0,42 of total coronoid length (1).”

Character 62b compares the length of the anterior process of the coronoid with the total coronoid length.

“**(62b) Anterior process of the coronoid:** equal to or longer than 0,32 of total coronoid length (0); shorter than 0,32 of total coronoid length (1).”.

### Character 63

“**(63) Meckelian foramen (i.e. foramen intermandibularis caudalis):** small, anteroposterior length roughly 9% or less of total jaw length (0); large, anteroposterior length greater than or equal to 14% of total jaw length (1).” (Modesto et al., 2018).

Like characters 59, 38 and 18, character 63 is a quantitative measurement in which the definition of morphometric elements is very clear. Hence, we performed precise measurements considering clear lengths and boundaries. The updated character is now identified as 63a.

“**(63a) Meckelian foramen:** small, anteroposterior length roughly 0,08 or less of total jaw length (0); large, anteroposterior length equal or greater than 0,08 of total jaw length (1).”

### Character 64

“**(64) Coronoid:** posterodorsal process slender, forms dorsal-most quarter of lateral wall of adductor fossa (0); posterodorsal process deep, forms dorsal-most third of lateral wall of adductor fossa (1).” (Modesto et al., 2018).

Like characters 63, 59, 38 and 18, character 64 is a quantitative measure in which the definition of morphometric elements is not very clear. As such, we performed precise measurements considering the elements listed and updated values and character state thresholds. The updated character is now identified as:

“**(64a) Posterodorsal process of the coronoid:** slender, less than 0,25 of lateral wall of adductor fossa (0); deep, more than 0,25 of lateral wall of adductor fossa (1).”.

### Characters 65 to 77

“**(65) Retroarticular process:** absent (0); present and broader transversely than long (1); present and longer anteroposteriorly than broad (2)” (Modesto et al., 2018).

**“(66) Dorsal neural arches:** narrow (0), lateral expansion present (1), or exaggerated lateral expansion swelling present (2)” (Modesto et al., 2018).

**“(67) Neural spines of dorsal vertebrae:** height or shape alternation absent (0); height or shape alternation present (1)” (Modesto et al., 2018).

**“(68) Anterior dorsal centra:** strongly ventrolaterally constricted (0); not strongly ventrolaterally constricted (1)” (Modesto et al., 2018).

**“(69) Sacral ribs:** first and second sacral rib roughly equal in size (0); first sacral rib larger than second rib (1)” (Modesto et al., 2018).

**“(70) Ilium:** iliac blade expanded dorsally (0); iliac blade narrow dorsally (1)” (Modesto et al., 2018).

**“(71) Stylo- and zeugopodium:** shaft slender and heads only moderately expanded (0); shaft massive and with proximal and distal heads significantly expanded, resulting in an overall stout impression (1)” (Modesto et al., 2018).

**“(72) Humerus:** supinator process parallel to shaft (0); supinator process absent (1). Modified slightly from Modesto et al. (2014)” (Modesto et al., 2018).

**“(73) Manus and pes:** elements long and slender (0); elements short and broad (1)” (Modesto et al., 2018).

**“(74) Fourth metatarsal:** less than half the length of tibia (0); more than half the length of tibia (1)” (Modesto et al., 2018).

**“(75) First metacarpal:** more than half the length of fourth metacarpal (0); less than half the length of fourth metacarpal (1).” (Modesto et al., 2018).

“**(76) Dentary:** lingual shelf absent (0) or present (1)” (Modesto, Richards, Ide & Sidor, 2019).

**“(77) anterior maxillary foramen:** absent (0) or present (1).” (Castanhinha and Modesto, pers. comm.).

We maintain these characters as previously described; all character states of cranial characters are figured in Appendix 11.

Characters 76 and 77 are new. Character 76 appears for the first time in Modesto et al., 2019. Character 77 was proposed by Castanhinha and Modesto (pers. comm).

### Characters 78 and 79

Character 78 is a new character based on one of the morphological characteristics that authors deBraga, Bevitt and Reisz used to distinguish the *Captorhinus kierani* holotype from the species *Captorhinus magnus* (deBraga et al., 2019). The authors state that the angle of the suture between nasal and frontals for *C. magnus* is of 45º, wherein for *C. kierani* is 70º. As such, we propose a character based on this skull feature.

After the process of measuring, plotting the data in a graph and analysing it, the character definition and character states are established as follows:

"**(78) Suture between nasal and frontals:** angle smaller than 70º (0); angle between 70º and 90º (1); angle superior to 90º (2)."

Character 79 is also a new character but based on characters previously defined. It is established by comparing the length of the postorbital-jugal suture with the total cranium length in lateral view.

"**(79) Postorbital-jugal suture:** ratio with cranium length smaller than 0,15 (0); ratio with cranium length equal to or bigger than 0,15 (1).".

## c. Updating captorhinid character matrix

The new characters described in the previous section can be seen in Appendix 6.

### d. Captorhinid phylogeny (without problematic characters)

First, using PAUP* we ran a matrix based on Modesto et al. 2018 without all problematic characters (See Appendix 3 and 4). We followed a parsimony analysis based on a branch-and-bound algorithm and started by generating the phylogeny according to a strict consensus rule (Figure 13).

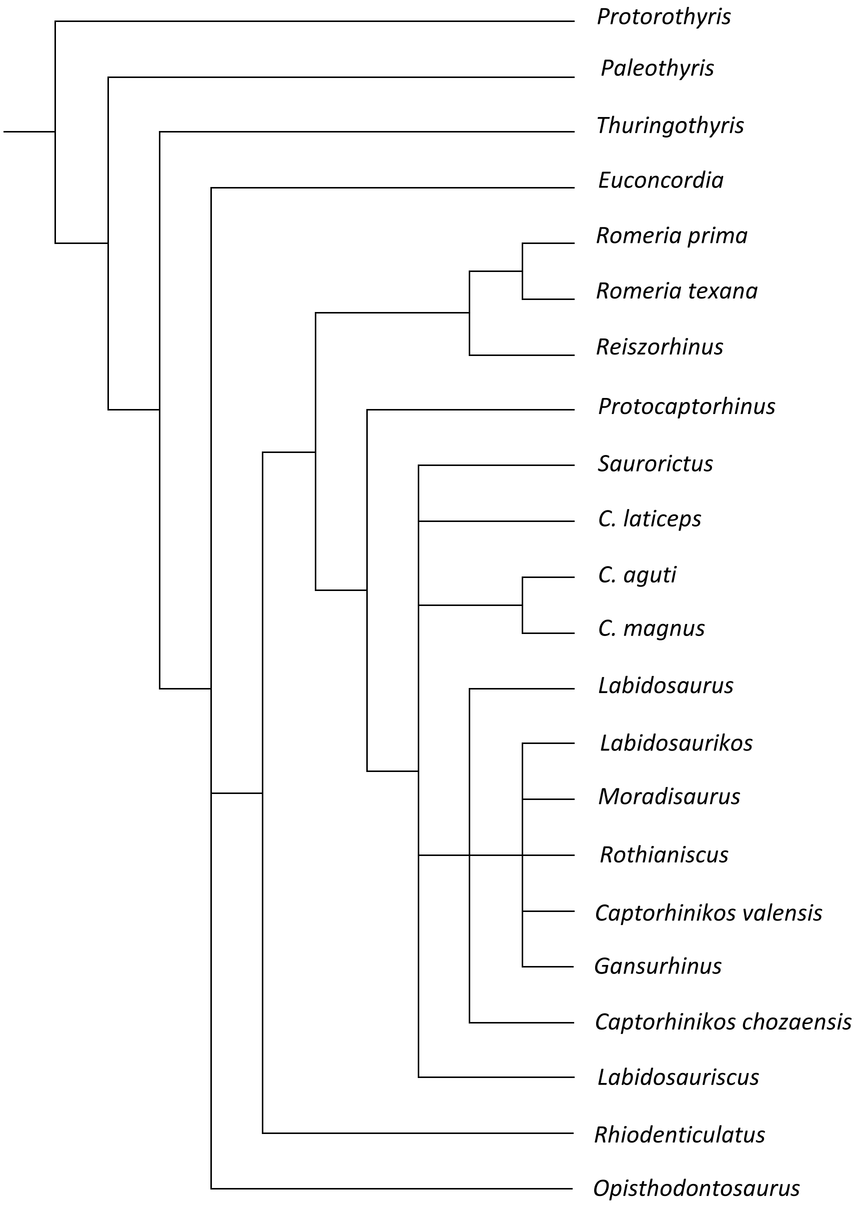


*Figure 13: Strict consensus phylogenetic tree of captorhinomorphs, excluding problematic characters (60 characters used).. Based on Modesto et al., 2018. (Appendix 3 and 4)*

This phylogenetic tree is badly resolved, with multiple polytomies. In order to analyse the phylogeny in a more coherent way and to have a more well-resolved tree, we switched from a strict consensus rule to a 50% majority consensus rule. The result is the tree present below (Figure 14).

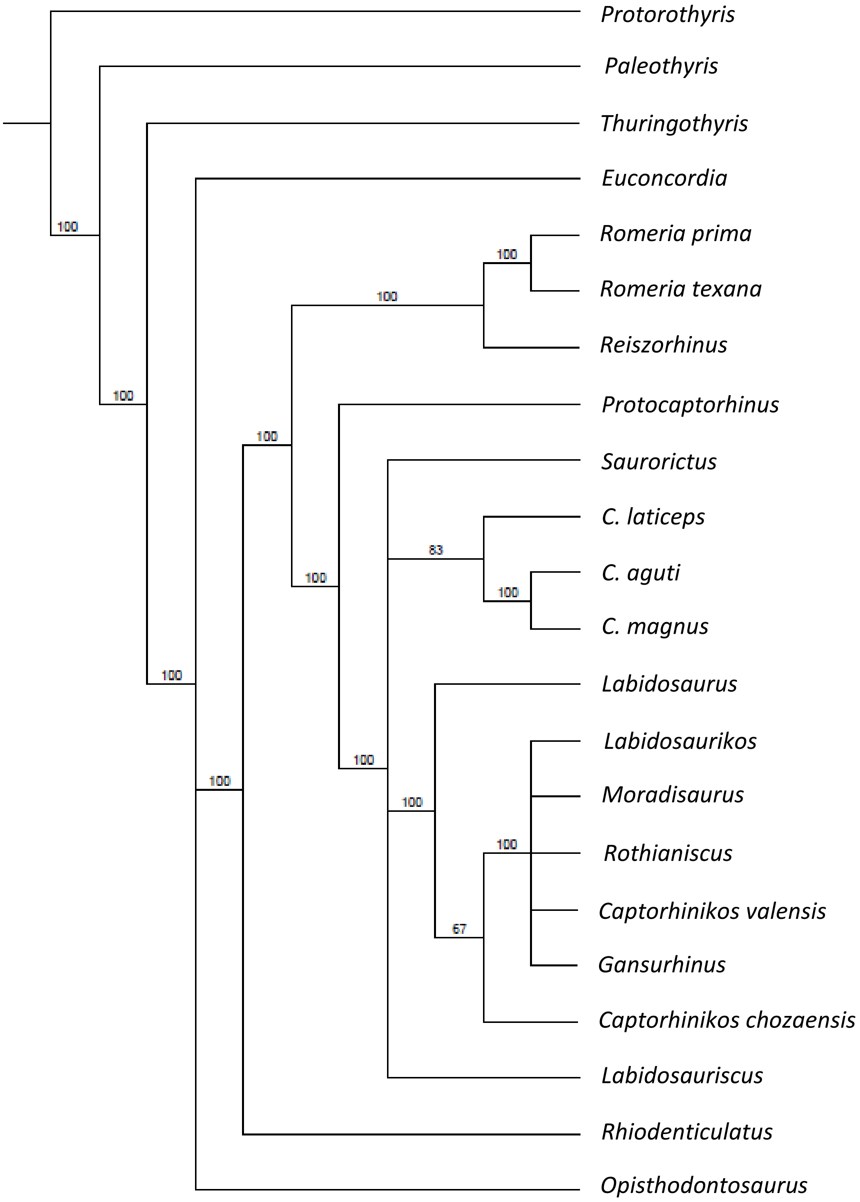


*Figure 14: Majority rule (50%) consensus phylogenetic tree of captorhinomorphs, excluding problematic characters (60 characters used). Values above branches represent the percentage of best-ranked trees used to generate the consensus tree that corroborates those phylogenetic proximities. Based on Modesto et al., 2018. (Appendix 3 and 4)*

Most branches are well-resolved, but there are three polytomies present. One of them is in the group Moradisaurinae: *Labidosaurikos* + *Moradisaurus* + *Rothianiscus* + *Captorhinikos valensis* + *Gansurhinus*. The second polytomy is formed by the following species: *Saurorictus*, *Captorhinus aguti* + *Captorhinus laticeps* + *Captorhinus magnus*, *Labidosaurikos* + *Moradisaurus* + *Rothianiscus* + *Captorhinikos valensis* + *Gansurhinus* + *Captorhinikos chozaensis*, and *Labidosauriscus*. Finally, these groups plus *Euconcordia*, *Romeria prima* + *Romeria texana* + *Reiszorhinus*, *Protocaptorhinus*, *Rhiodenticulatus* and *Opisthodontosaurus* form the third polytomy. Most branches have over 83% of concordance between the best-ranked trees that compose the consensus tree, except for the branch that separates *Captorhinikos chozaensis* from *Labidosaurikos*, *Moradisaurus*, *Rothianiscus*, *Captorhinikos valensis* and *Gansurhinus*.

### e. Captorhinid phylogeny (without problematic characters + *Captorhinus kierani*)

*Captorhinus kierani* was described this year by deBraga, Bevitt and Reisz (deBraga, Bevitt & Reisz, 2019). As such, it is not present in the phylogenetic analysis by Modesto et al., 2018. We coded this species according to the character list in Appendix 3 and ran the resulting matrix (Appendix 5), following the same process. The correspondent 50% majority-rule consensus tree is represented in Figure 15.

This phylogeny is not as well resolved as the previous one (Figure 14), having now four polytomies. The group Moradisaurinae now has two polytomies. One is between species *Labidosaurikos* + *Moradisaurus* + *Rothianiscus* + *Captorhinikos valensis* + *Gansurhinus*, that already existed. The other is made of this group + *Labidosaurus* + *Captorhinikos chozaensis*. The branch *Captorhinus laticeps* + *Captorhinus aguti* + *Captorhinus magnus* is well-resolved but makes a polytomy with *Saurorictus*, *Labidosaurikos* + *Moradisaurus* + *Rothianiscus* + *Captorhinikos valensis* + *Gansurhinus* + *Labidosaurus* + *Captorhinikos chozaensis, Labidosauriscus* and *Captorhinus kierani.* Finally, *Saurorictus*, *Captorhinus aguti* + *Captorhinus laticeps* + *Captorhinus magnus*, *Labidosaurikos* + *Moradisaurus* + *Rothianiscus* + *Captorhinikos valensis* + *Gansurhinus* + *Captorhinikos chozaensis*, *Labidosauriscus*, *Euconcordia*, *Romeria prima* + *Romeria texana* + *Reiszorhinus*, *Protocaptorhinus*, *Rhiodenticulatus* and *Opisthodontosaurus* form the fourth polytomy. All solved branches are present in 100% of the best-ranked trees used to generate the consensus tree. Non-solved branches have a value below 50%.

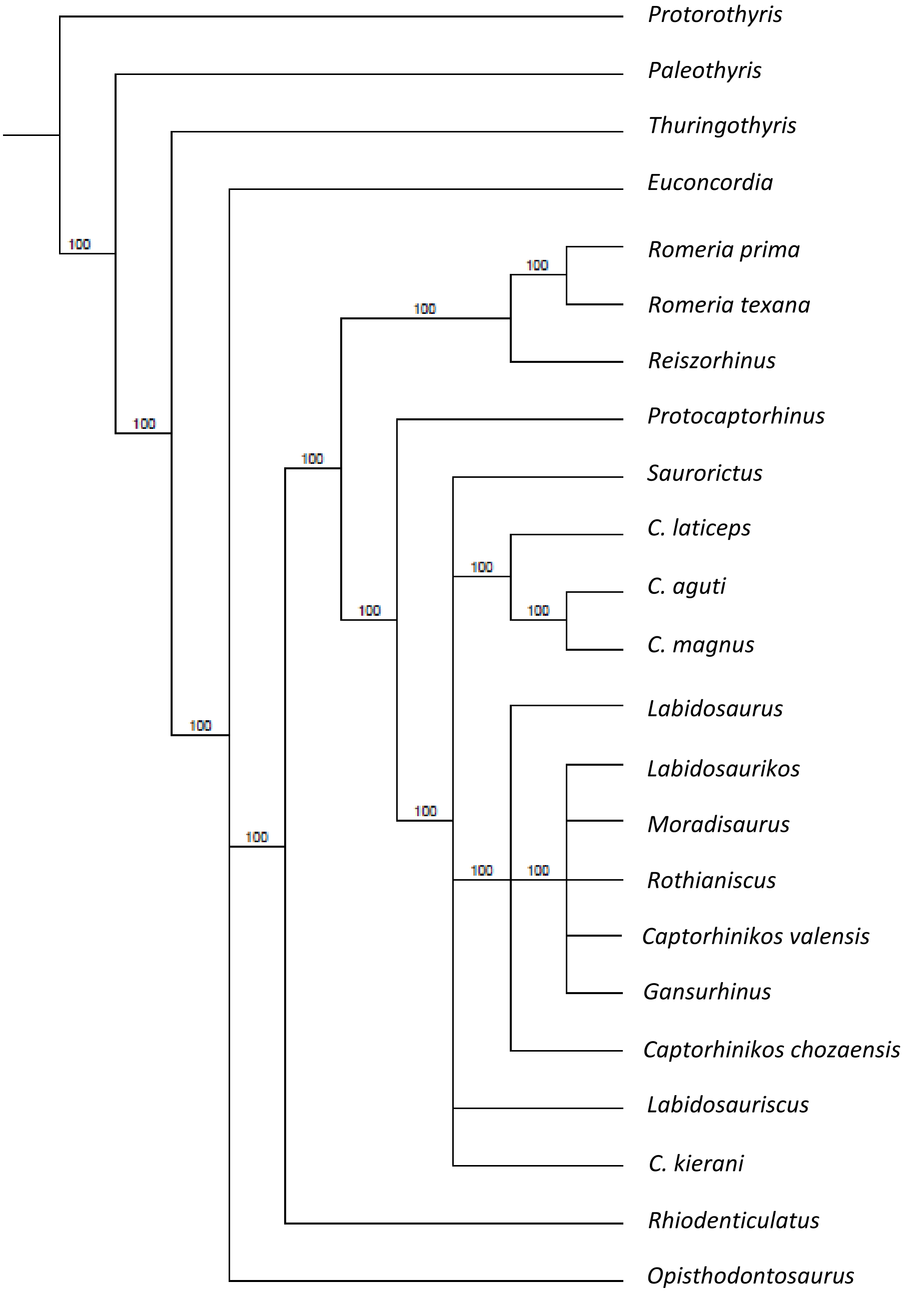


*Figure 15: Majority rule (50%) consensus phylogenetic tree of captorhinomorphs; based on Modesto et al. 2018. Problematic characters removed (60 characters used). Species* Captorhinus kierani *added (see Appendix 3 and 5). Values above branches represent the percentage of best-ranked trees used to generate the consensus tree that corroborates those phylogenetic proximities.*

### f. Captorhinid phylogeny (without skull sculpturing)

A new matrix (updated character list but with no skull sculpturing characters; see Section 3. c., Appendix 7 and Appendix 8) was run on PAUP*, following a parsimony analysis based on a branch-and-bound algorithm and using a 50% majority rule consensus (Figure 16). Almost all polytomies are solved, only two remained. One is formed by the species that compose the Moradisaurinae group: *Moradisaurus* + *Rothianiscus* + *Gansurhinus*. The other is comprised of the following species: the group *Romeria prima* + *Romeria texana* + *Protocaptorhinus* + *Reiszorhinus*, the group *Captorhinus laticeps* + *Captorhinus kierani* + *Captorhinus aguti* + *Labidosauriscus* + *Captorhinus magnus*, the group *Labidosaurus* + *Labidosaurikos* + *Moradisaurus* + *Rothianiscus* + *Gansurhinus* + *Captorhinikos valensis* + *Captorhinikos chozaensis*, *Rhiodenticulatus*, and *Saurorictus*. All solved branches have a percentage of agreement of 100%, except for the branches inside the *Captorhinus* sp. + *Labidosauriscus* group (60%) and the branches that separate *Captorhinikos valensis*, *Labidosaurikos* and *Moradisaurus* + *Rothianiscus* + *Gansurhinus* (60%). Moradisaurinae form a monophyletic group.

*Figure 16: Majority rule (50%) consensus phylogenetic tree of captorhinomorphs, based on the new matrix in Section 3.c. (excludes skull sculpturing characters; 89 characters used) (See Appendix 7 and 8). Values above branches represent the percentage of best-ranked trees used to generate the consensus tree that corroborates those phylogenetic proximities.*

### g. Skull sculpturing – definition of new characters

In captorhinid phylogenetic studies, the only skull sculpturing character and its correspondent states used so far is (Modesto et al., 2018):

"(29) Sculpturing: skull surface

- relatively smooth, with only small honeycombing pits or grooves (0);
- with pits and grooves with notably larger, randomly positioned pits on posterior skull table (1);
- low ridge-and-pit system with tiny pits and furrows (2);"

There are several problems with this character. First, there is only one species with character state (2), rendering it uninformative. Secondly, the wording itself is confusing. State (0) mentions pits or grooves, but state (1) refers to the presence of both, omitting its shape, while they are stated as being honeycombing for state (0). State (2) refers to pits and furrows. However, is difficult to distinguish furrows from grooves and the use of the words "small", "larger" and "tiny" are not quantifiable. Moreover, there is no visual representation of what each type of sculpturing and character status looks like.

In 2010, Witzmann, Scholz, Müller and Kardjilov published a paper on the sculpture and vascularization of dermal bones in basal tetrapods, including three captorhinid specimens (Witzmann, Scholz, Müller & Kardjilov, 2010). In that paper, following a morphological and morphogenetic approach, the authors investigate the outer sculptural morphology of the cranium in several groups of basal tetrapods, distinguishing sculptured patterns and describing their evolution and development, and ascertaining the phylogenetic signal of these patterns (Witzmann et al., 2010). The authors start by defining the anatomic terms used to describe dermal bone sculpture, providing an excellent anatomical framework to build upon and in which this research is partially based on (Witzmann et al., 2010).

As Witzmann et al. state, there are two basic dermal sculptural patterns - a polygonal sculpture and a radial sculpture – with a transitional pattern between these two also being possible. The polygonal structure consists of hexagonal or rounded polygons, and each polygon is comprised of a pit surrounded by sculptural ridges (Witzmann et al., 2010). The points of intersection of sculptural ridges are called nodal points (Witzmann et al., 2010). The authors state these as being homologous points present in the sculpturing patterns, using them for comparison between patterns (Witzmann et al., 2010). The radial structure is made of furrows and sculptured ridges, radiating from the ossification centres out (Witzmann et al., 2010). Bystrow demonstrated in 1935 that the polygonal sculpturing develops from the radial sculpturing pattern during ontogeny by the formation of walls within the ridges, and as such is considered a juvenile character, even if it can be retained in some adult specimens (Bystrow, 1935).

When the bone grows peripherically, radiating sculpting ridges appear between the ones already formed (Witzmann et al., 2010) (Figure 17).

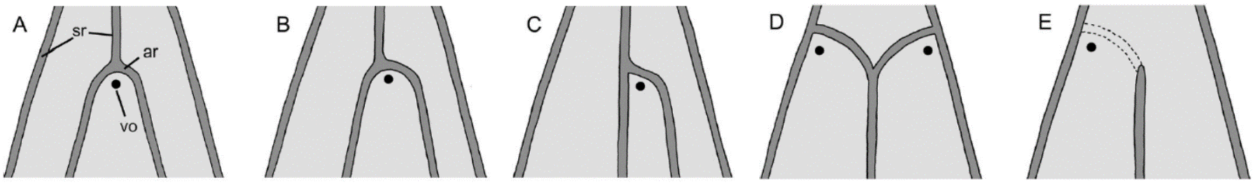


*Figure 17: Formation of new sculptural ridges at the bone periphery during growth. In Witzmann et al. 2010.*

A sculptural ridge can bifurcate symmetrically, right in front of a vascular opening (Figure 17 A), or the vascular opening can be located laterally to the ridge, making the bifurcation asymmetric (Figure 17 B and C) (Witzmann et al., 2010). Two ridges from opposite sides may also fuse and close a furrow (Figure 17 D). (Witzmann et al., 2010). Finally, a sculptural ridge can also be suppressed to the point where it gives the impression of an abrupt origin (Figure 17 E) (Witzmann et al., 2010).

The transition from radial structure to a polygonal structure can be divided into three distinct steps (Figure 18): first, there is a development of a radial sculpture with low ridges, which may broaden at discrete points; then, dividing walls form inside the furrows between those points, and form square-shaped sculptural cells (Witzmann et al., 2010). Lastly, these square-shaped cells attain a more polygonal outline during further bone development by means of a shift of nodal points sideways, ideally obtaining a hexagonal shape (Witzmann et al., 2010).

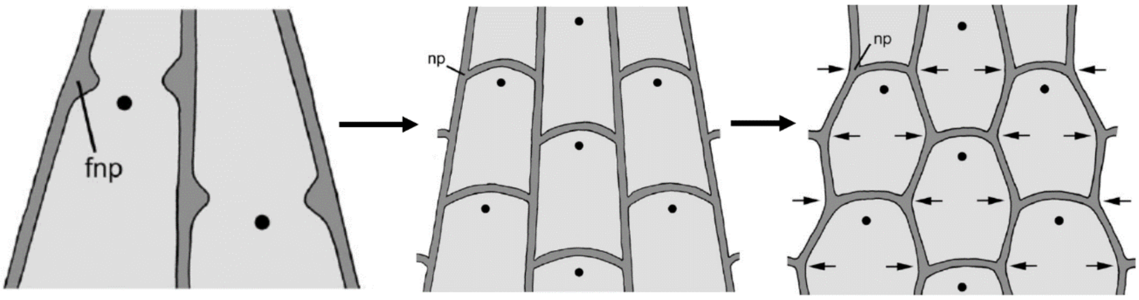


*Figure 18: Development of polygonal structure from radial structure. Adapted from Witzmann et al. 2010.*

Some taxa present a sculpturing intermediate described as tubercular sculpture (Witzman et al. 2010). In this case, the sculptural ridges are less pronounced, and the nodal points are quite prominent, giving the overall structure a tubercular appearance (Witzmann et al. 2010). If several nodal points are connected through prominent ridges, a vermiculate sculpture can be observed (Witzmann et al., 2010). It should be noted that even if the sculpturing present has “aberrant” knobs and spines, those characteristics can be traced to one of the forms that have been described previously (Witzmann et al., 2010).

In order to evaluate the phylogenetic signal of sculptural patterns, Witzmann et al. ran a principal component analysis (PCA) based on 12 discrete characters of dermal sculpturing (Witzmann et al. 2010). We used these 12 characters as a starting point for the definition of characters to be used in phylogenetic analyses here presented. This also allows for the comparison of results with the results published by Witzmann et al.

A few years later in 2018, authors Antczak and Bodzioch publish a paper based on Witzmann et al., applying the same methodology to the fossil amphibian *Metoposaurus krasiejowensis*. To analyse the characteristics of the polygonal and radial structure of both clavicle and skull bones, the authors used over 20 characters, including some of the 12 used by Witzmann et al. 2010 (Antczak & Bodzioch, 2018).

By cross-referencing and comparing all characters used by Antczak and Bodzioch with characters proposed by Witzmann et al., we compiled a list of characters to be included in a thorough phylogenetic analysis of captorhinid skull (Witzmann et al., 2010; Antczak & Bodzioch, 2018). The characters and their corresponding possible traits are listed below:

29a. Sculptural ridges on each bone

(0) differ in width

(1) width is constant

29b. Sculptural ridges

(0) mostly rounded

(1) some rounded, some edged/narrow

(2) mostly edged/narrow

29c. Sculptural ridges

(0) undulated

(1) straight

29d. Nodal points

(0) some same width as ridges around it, others distinctively bigger than ridges around it

(1) same width as ridges around it

29e. Nodal points

(0) form tubercules

(1) do not form tubercules

29f. Sculpture

(0) regions without sculpture or with subdued sculpture present

(1) sculpture present on all cranial dermal bones

29g. Sculpture

(0) mostly cells

(1) cells and radial ridges

(2) mostly radial ridges

29h. Sculpture on each bone

(0) more than one type

(1) only one type

29i. Cell shape

(0) mostly oval

(1) mostly polygonal

29j. Cell size

(0) small

(1) large

29k. Cell density

(0) dense

(1) sparse

The resulting character matrix pertaining to skull sculpturing is reproduced below (Table 2); use of 0&1 or 1&2 represents the existence of both character states.

*Table 2: Character matrix pertaining to skull sculpturing characters.*

| **Species/Characters** | **29a** | **29b** | **29c** | **29d** | **29e** | **29f** | **29g** | **29h** | **29i** | **29j** | **29k** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Protorothyris* | ? | 0 | 0 | ? | ? | 0 | 0 | 0 | 0 | 0 | 0 |
| *Paleothyris* | ? | 1 | 1 | ? | ? | 0 | 1 | 0 | 0 | 0 | 1 |
| *Thuringothyris* | 0 | 1 | 0 | ? | ? | 0 | 2 | 0 | 1 | 1 | 1 |
| *Euconcordia* | 1 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 |
| *Romeria prima* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Romeria texana* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Protocaptorhinus* | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| *Rhiodenticulatus* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Saurorictus* | ? | 0 | 0 | ? | ? | 0 | 1 | 0 | 0 | 0 | 1 |
| *Captorhinus laticeps* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0&1 | 0 | 0 | 0 |
| *Captorhinus aguti* | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 |
| *Captorhinus magnus* | 1 | 0 | 1 | 1 | ? | 0 | 1 | ? | 1 | 0 | 0 |
| *Labidosaurus* | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| *Labidosaurikos* | 0 | 1 | 0 | 1 | ? | 1 | 1 | 0 | 0 | 0 | 0 |

| **Species/Characters** | **29a** | **29b** | **29c** | **29d** | **29e** | **29f** | **29g** | **29h** | **29i** | **29j** | **29k** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Moradisaurus* | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 |
| *Rothianiscus* | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Gansurhinus* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Captorhinikos valensis* | ? | 0 | ? | ? | ? | ? | 2 | ? | 0 | 1 | ? |
| *Captorhinikos chozaensis* | ? | ? | ? | ? | ? | ? | 0 | ? | 0 | 0 | ? |
| *Reiszorhinus* | ? | ? | ? | ? | ? | ? | 2 | ? | 1 | 0 | 0 |
| *Opisthodontosaurus* | 1 | 2 | 1 | ? | ? | ? | 2 | 0 | 0 | 0 | 1 |
| *Labidosauriscus* | 1 | 2 | 1 | ? | ? | ? | 1&2 | 0 | 0 | 0 | 1 |
| *Captorhinus kierani* | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 |

### h. Skull sculpturing phylogeny

After running the previously presented skull sculpturing character matrix (Table 2) on PAUP*, the following phylogenetic tree was obtained, following a parsimony analysis based on a branch-and-bound algorithm and using a 50% majority rule consensus (Figure 19). There is one big polytomy comprised of the following species: *Paleothyris*, group *Thuringothyris* + *Reiszorhinus* + *Rothianiscus* + *Moradisaurus* + *Labidosaurikos* + *Labidosaurus*, the group *Protocaptorhinus* + *Captorhinikos valensis*, *Saurorictus*, *Captorhinus laticeps*, the group *Captorhinus aguti* + *Captorhinus kierani* + *Captorhinus magnus*, *Captorhinikos chozaensis*, the group *Opisthodontosaurus* + *Labidosauriscus*, and *Euconcordia*. However, inside of the mentioned groups, the branches are well-resolved without polytomies. In the group *Thuringothyris* + *Reiszorhinus* + *Rothianiscus* + *Moradisaurus* + *Labidosaurikos* + *Labidosaurus*, the percentage of agreement between best-ranked trees is above 83%. In the group *Protocaptorhinus* + *Captorhinikos valensis*, it has a value of 52%. In the group *Captorhinus aguti* + *Captorhinus kierani* + *Captorhinus magnus*, the percentages start at 76%. Finally, for *Opisthodontosaurus* + *Labidosauriscus*, the percentage of agreement between best-ranked trees is of 82%.

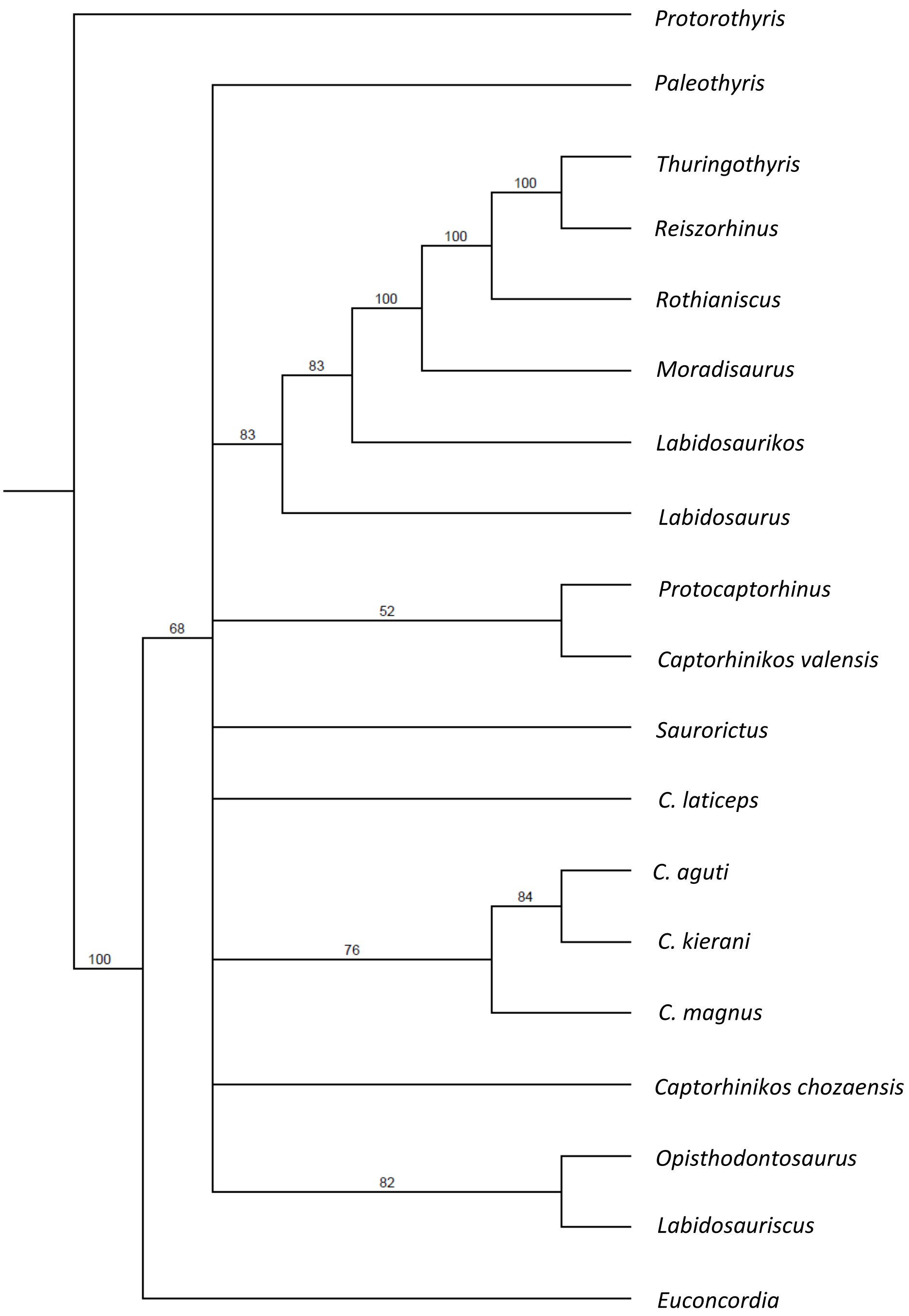


*Figure 19: Majority rule (50%) consensus phylogenetic tree of captorhinomorphs, based on the matrix presented on Section 3.g. (11 characters, referring to skull sculpturing only) (See Table 2). Values above branches represent the percentage of best-ranked trees used to generate the consensus tree that corroborate those phylogenetic proximities.*

### i. Captorhinid Phylogeny (all characters)

A new character matrix was generated. It is comprised of all 89 characters present in Section 3. a., and the 11 skull sculpturing characters listed on Section 3. d., summing 100 different morphological characters (see Appendixes 9 and 10). This new matrix was then run through PAUP*, following a parsimony analysis based on a branch-and-bound algorithm and using a 50% majority rule consensus resulting in the following phylogeny (Figure 20).

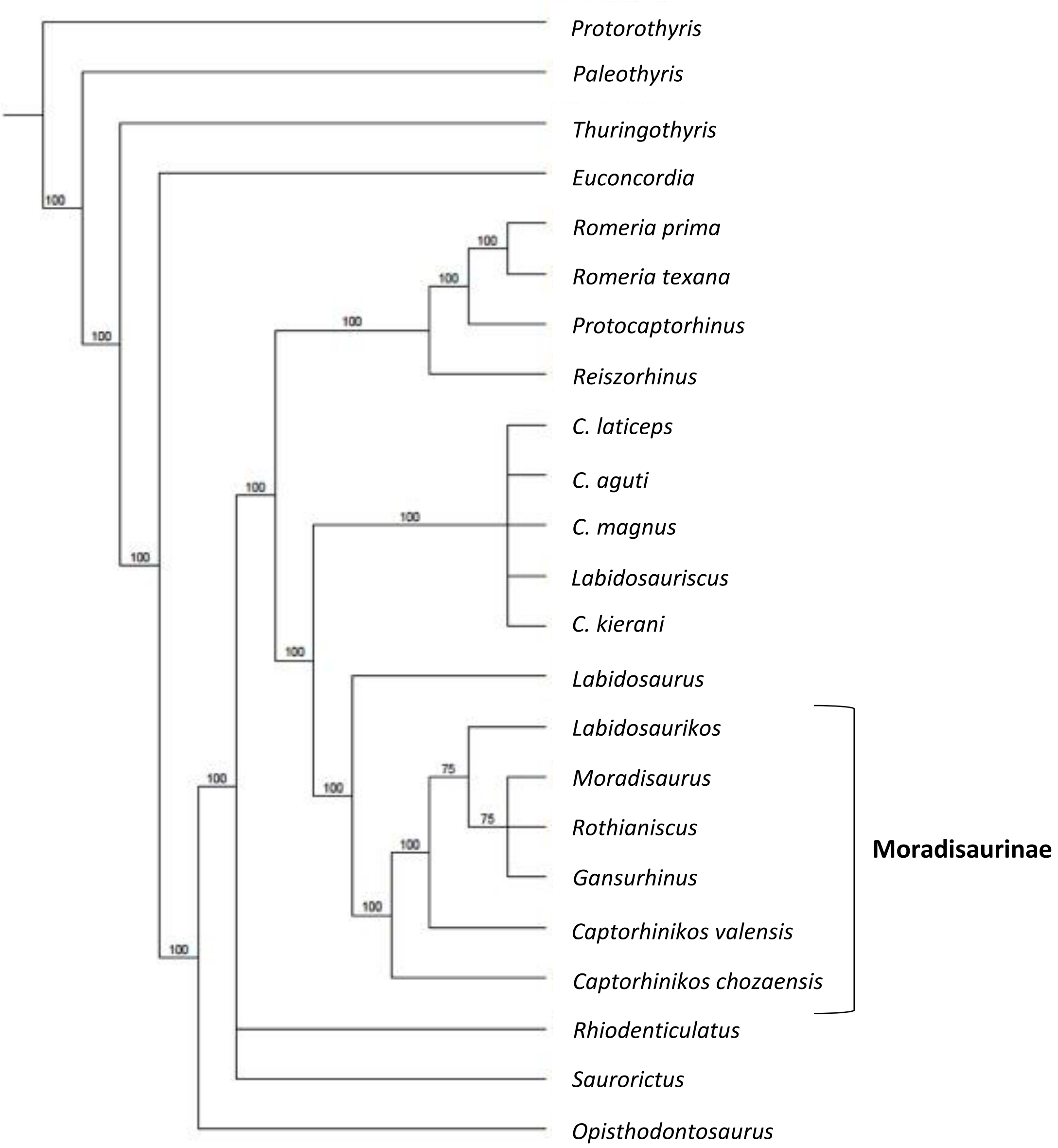


*Figure 20: Majority rule (50%) consensus phylogenetic tree of captorhinomorphs, based on the new matrix presented in Appendix 10. (100 characters). (See Appendixes 9 and 10). Values above branches represent the percentage of best-ranked trees used to generate the consensus tree that corroborate those phylogenetic proximities.*

Strict consensus rule tree for this matrix is present in Appendix 12 of this work.

This tree has three polytomies but is otherwise sufficiently well-resolved. There are three polytomies present. First, the polytomy inside the Moradisaurine group that was present in previous trees was not resolved and is still comprised of the same species: *Moradisaurus*, *Rothianiscus* and *Gansurhinus*. Species *Captorhinus* sp. and *Labidosauriscus* are all in a polytomy now, opposed to previously being in a well-resolved branch. The group *Romeria prima* + *Romeria texana* + *Protocaptorhinus* + *Reiszorhinus*, the group *Captorhinus laticeps* + *Captorhinus kierani* + *Captorhinus aguti* + *Labidosauriscus* + *Captorhinus magnus*, the group *Labidosaurus* + *Labidosaurikos* + *Moradisaurus* + *Rothianiscus* + *Gansurhinus* + *Captorhinikos valensis* + *Captorhinikos chozaensis*, *Rhiodenticulatus*, and *Saurorictus* make up the third polytomy, that we reported before. All branches have a percentage of concordance between the best-ranked trees used to generate the consensus tree of 100%, except for the branches that separate *Captorhinikos valensis*, *Labidosaurikos* and *Moradisaurus* + *Rothianiscus* + *Gansurhinus* (75%). Moradisaurinae still form a monophyletic group.

### j. Skull sculpturing – statistical analysis

In this section, we employ statistical analysis in order to test the presence or absence of symmetry between several areas of the skull: left/right, anterior/posterior, and a mix of these two categories. The species we analysed are *Xenosaurus newmanorum, Captorhinus aguti, Captorhinus kierani, Captorhinus laticeps, Protocaptorhinus. Xenosaurus newmanorum* is an extant reptile with skull sculpturing and serves the purpose of control. Captorhinomorphs were selected considering the quality of images we had access to.

The presence or absence of symmetry is evaluated in terms of the distribution of cells in each part of the skull and their respective areas.

### *Xenosaurus newmanorum*

In the case of the cells present in the cranium of *Xenosaurus newmanorum*, the following values were obtained for the Shapiro-Wilk normality test:

- W = 0,93058
- p = $1{,}345^{-10} < 0{,}05$

This means that the data distribution is not normal. As such, we ran a Wilcox test to compare the cell distribution data present on the left and right sides. The values yielded were:

- W = 10313
- p = 0,2571 > 0,05

As p > 0,05, there is no significant difference between the left and right sides of the skull.

The histograms comparing the cell distribution (in terms of area) in the left and right side of the cranium follow below (Figure 21):

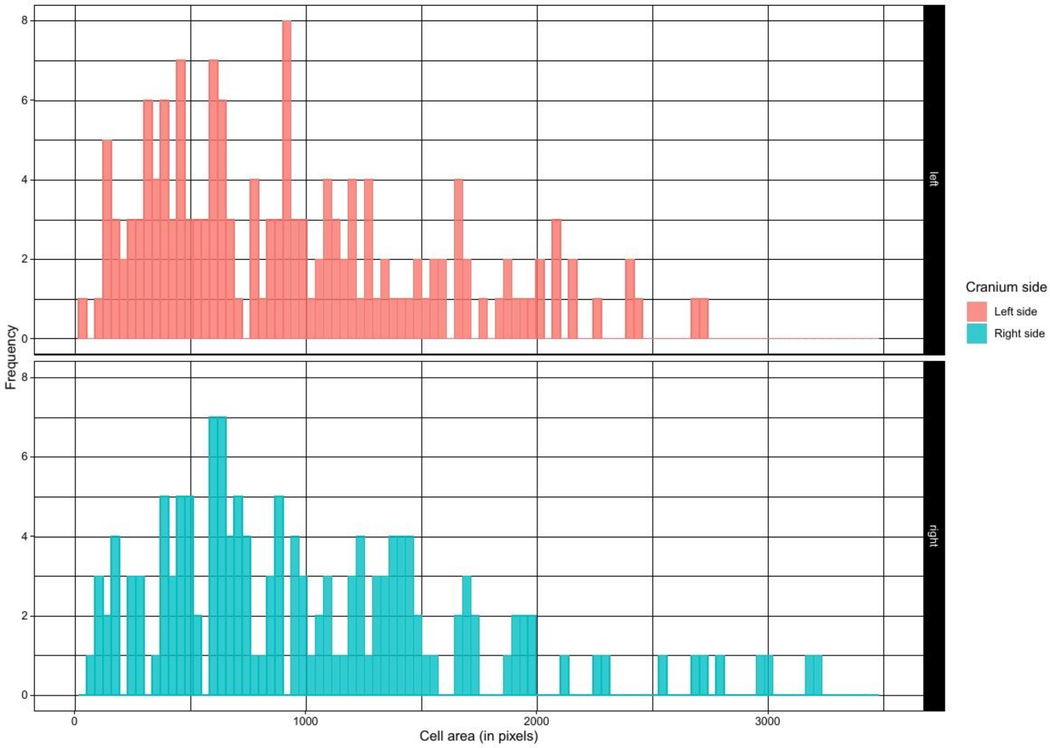


*Figure 21: Frequency histograms of cell distribution for left and right sides of* Xenosaurus *skull.*

Then, we ran a Wilcox test to compare the cell distribution data present on the anterior and posterior areas of the skull. The Wilcox test results were:

- W = 7959
- p = 0,00266 < 0,05

As p < 0,05, there is a significant difference between anterior and posterior areas of the skull.

The histograms comparing the cell distributions (in terms of area) in the anterior and posterior areas of the cranium follow below (Figure 22):

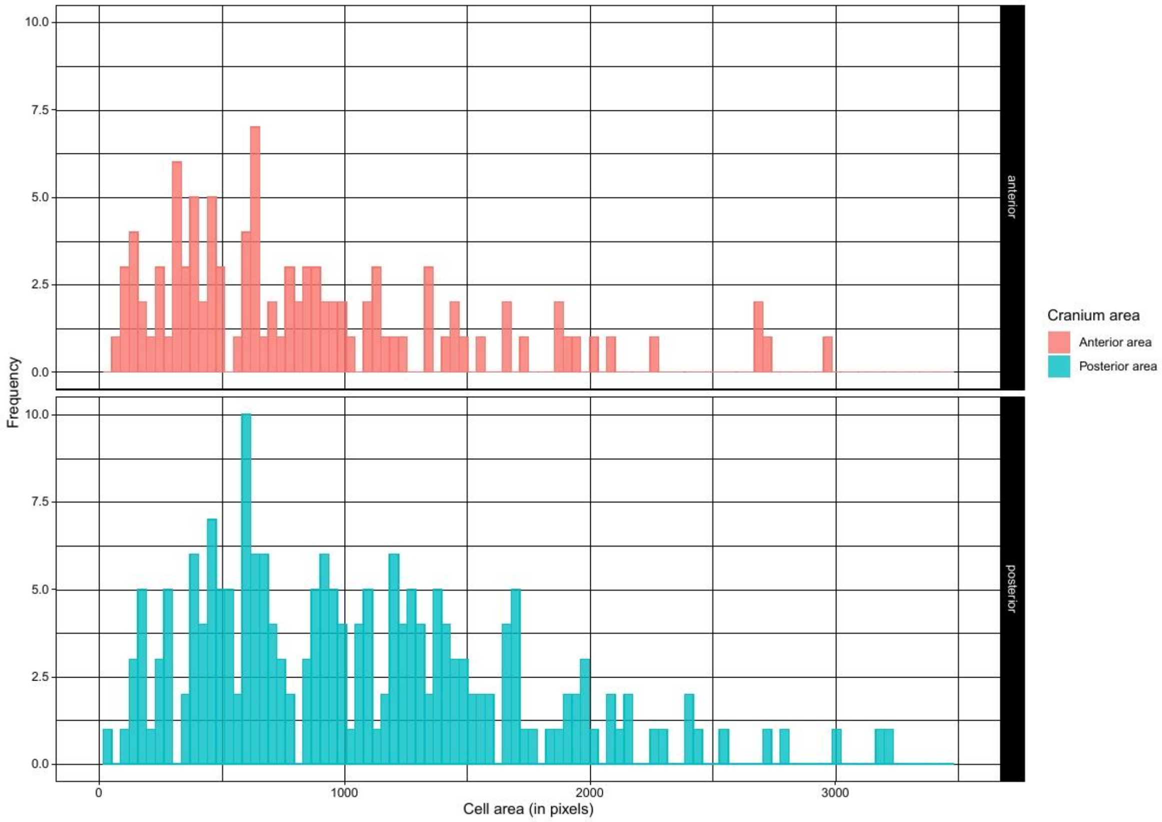


*Figure 22: Frequency histograms of cell distribution for anterior and posterior areas of* Xenosaurus *skull.*

Finally, we ran a Kruskall-Wallis test in order to compare the cell distribution data in all four quadrants of the skull table, which resulted in the following values:

- chi-squared = 10,936
- p = 0,01208 < 0,05

The value obtained for p is < 0,05. Hence, there is a significant difference between cell distribution data in the four quadrants of the skull.

The histograms comparing the cell distributions (in terms of area) in the four quadrants of the cranium follow below (Figure 23):

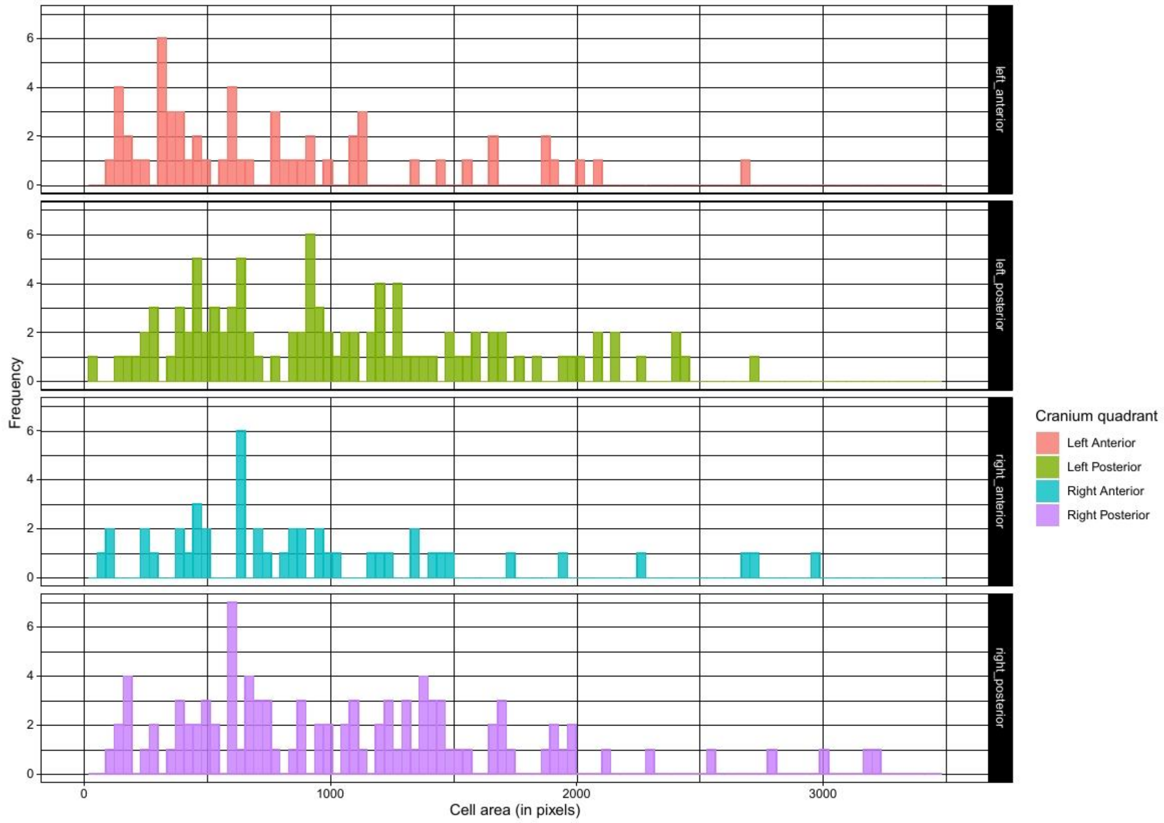


*Figure 23: Frequency histograms of cell distribution for all quadrants of* Xenosaurus *skull.*

Knowing that there was a difference between the quadrants of the skull, we performed a Dunn test to verify pairs were significantly different, yielding the results present in the next table (Table 3):

*Table 3: Results of Dunn test considering all table skull quadrants for* Xenosaurus*. LA = left anterior, LP = left posterior, RA = right anterior, RP = right posterior.*

| | **LA** | **LP** | **RA** |
|---|---|---|---|
| **LP** | -2,819746<br>p=0,0024 * | | |
| **RA** | -1,360550<br>p=0,0868 | 1,119279<br>p=0,1315 | |
| **RP** | -3,017424<br>p=0,0013 * | -0,230500<br>p=0,4089 | -1,303519<br>p=0,0962 |

### Captorhinus aguti

In the case of the cells present in the cranium of *Captorhinus aguti*, the following values were obtained for the Shapiro-Wilk normality test:

- W = 0,41171
- p < $2,2^{-16}$ < 0,05

This means that the data distribution is not normal. As such, we ran a Wilcox test to compare the cell distribution data present on the left and right sides. The values yielded were:

- W = 58831
- p = 0,0003789 < 0,05

As p < 0,05, there is a significant difference between the left and right sides of the skull.

The histograms comparing the cell distribution (in terms of area) in the left and right side of the cranium follow below (Figure 24):

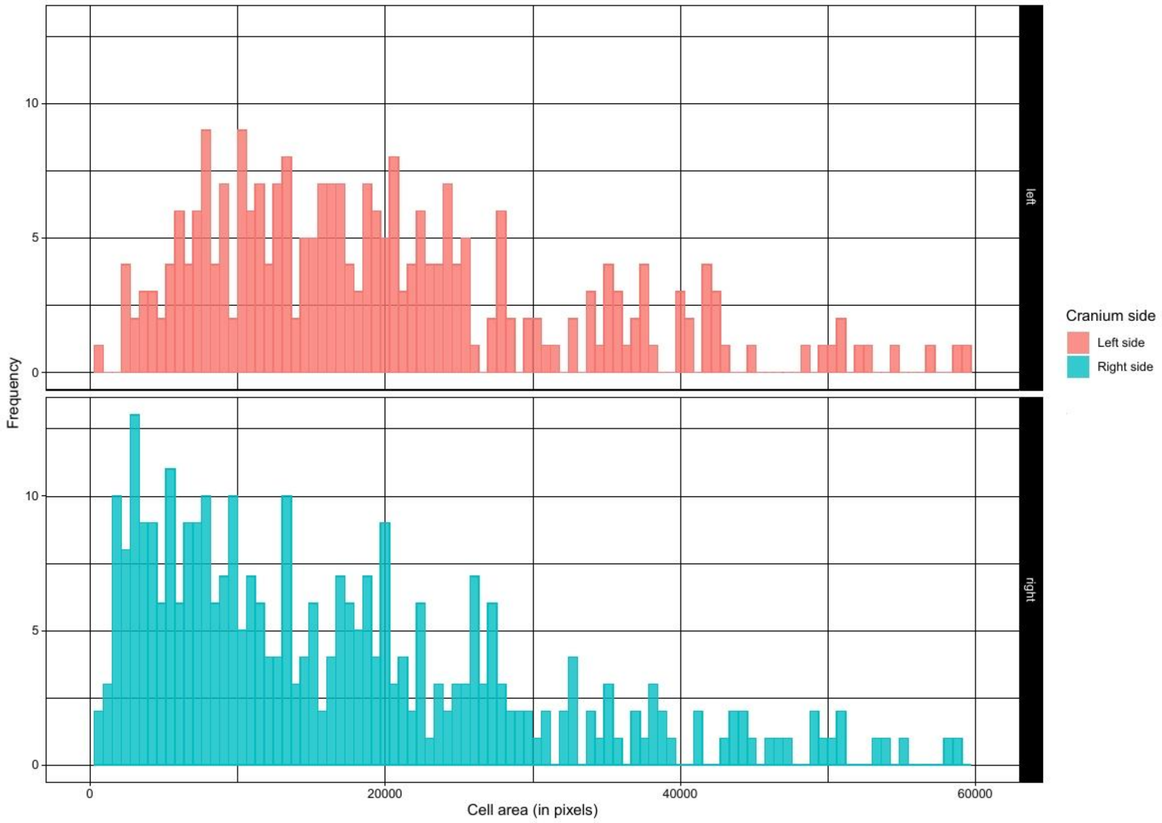


*Figure 24: Frequency histograms of cell distribution in the left and right sides of* Captorhinus aguti *skull.*

Then, we ran a Wilcox test to compare the cell distribution data (in terms of area) present on the anterior and posterior areas of the skull. The Wilcox test results were:

- W = 64468
- $p = 4{,}223^{-14} < 0{,}05$

As $p < 0{,}05$, there is a significant difference between anterior and posterior areas of the skull.

The histograms comparing the cell distribution (in terms of area) in the anterior and posterior areas of the cranium follow below (Figure 25):

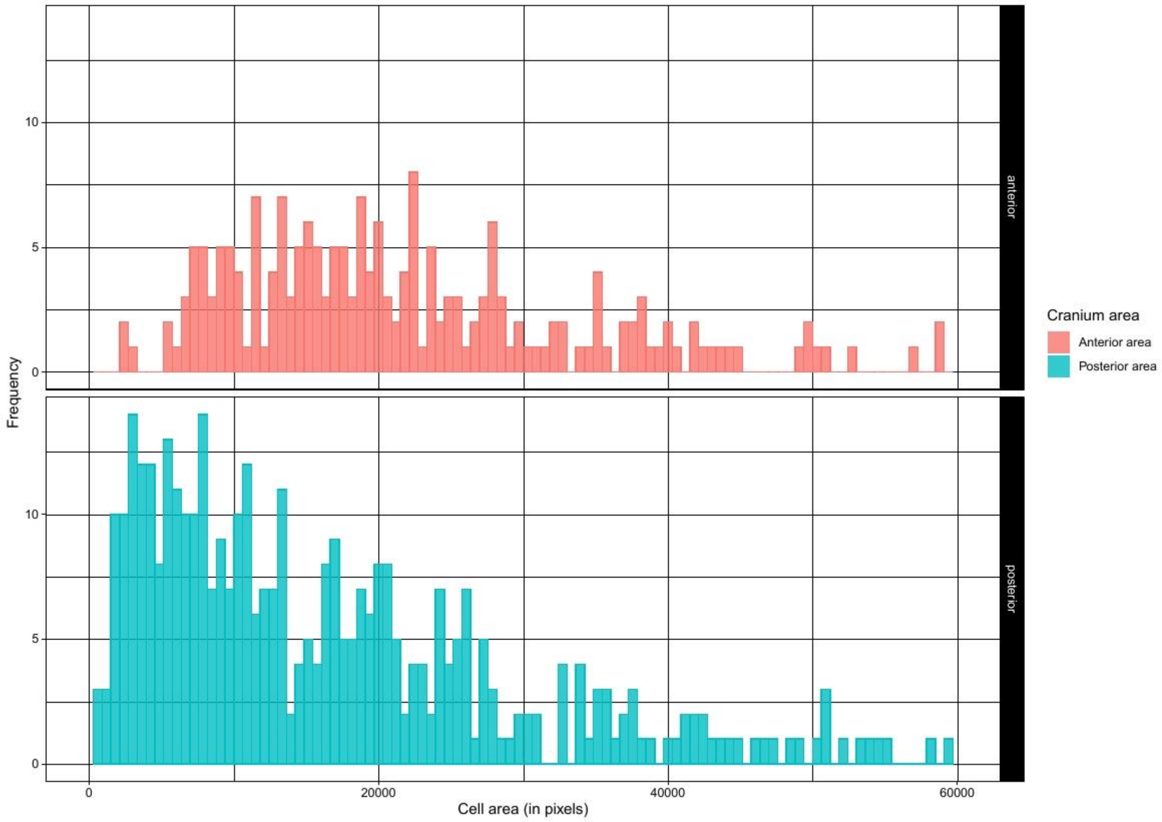


*Figure 25: Frequency histograms of cell distribution for anterior and posterior areas of* Captorhinus aguti *skull.*

Finally, we ran a Kruskall-Wallis test in order to compare the cell distribution data in all four quadrants of the skull table, which resulted in the following values:

- chi-squared = 66,835
- p = $2,031^{-14}$ < 0,05

The value obtained for p is < 0,05. Hence, there is a significant difference between cell distribution in the four quadrants of the skull.

The histograms comparing the cell distributions (in terms of area) in the four quadrants of the cranium follow below (Figure 26):

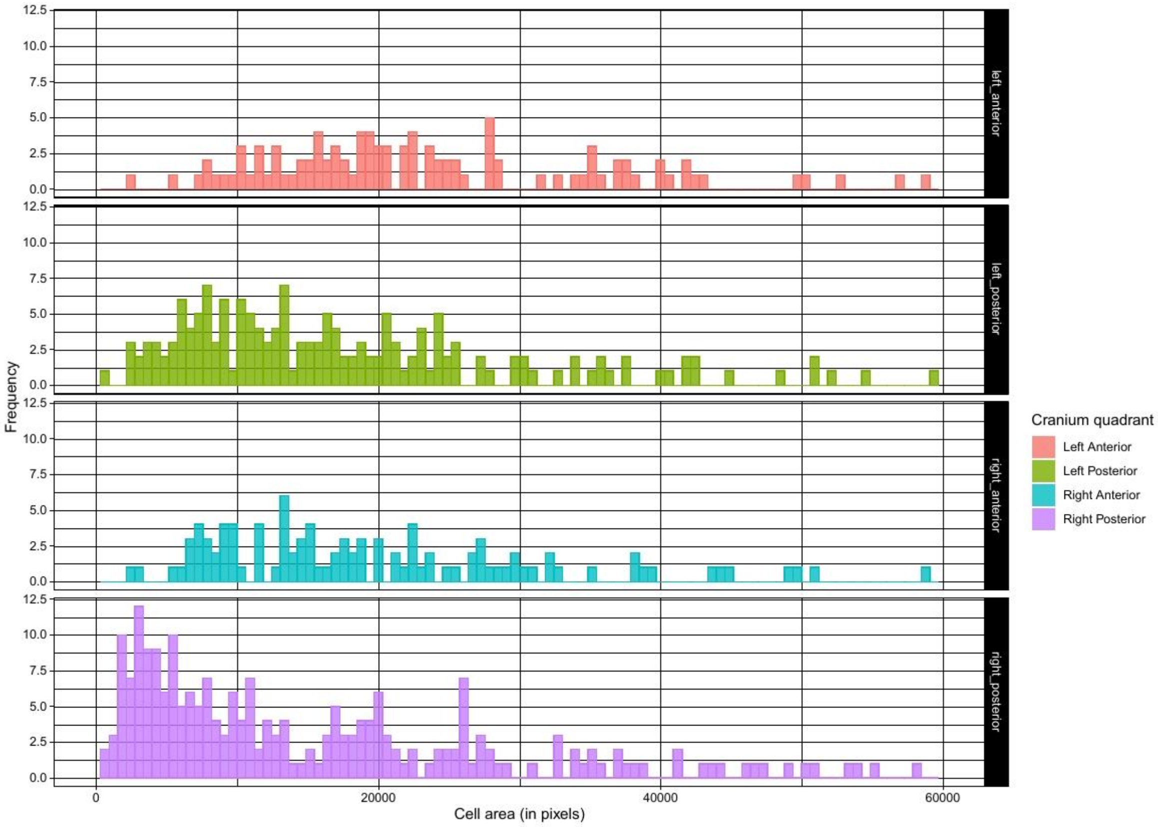


*Figure 26: Frequency histograms of cell distribution for all quadrants of* Captorhinus aguti *skull.*

Knowing that there was a difference between the quadrants of the skull, we performed a Dunn test to verify pairs were significantly different, yielding the results present in the next table (Table 4):

*Table 4: Results of Dunn test considering all table skull quadrants for* Captorhinus aguti*. LA = left anterior, LP = left posterior, RA = right anterior, RP = right posterior.*

| | **LA** | **LP** | **RA** |
|---|---|---|---|
| **LP** | 4,6521<br>p=0,0000 * | | |
| **RA** | 1,469917<br>p=0,0708 | -3,077320<br>p=0,0010 * | |
| **RP** | 7,343144<br>p=0,0000 * | 2,758377<br>p=0,0029 * | 5,705858<br>p=0,0000 * |

### *Captorhinus kierani*

In the case of *Captorhinus kierani*, the following values were obtained for the Shapiro-Wilk normality test:

- $W = 0,17178$
- $p < 2,2^{-16} < 0,05$

$p < 0,05$ means that the data distribution is not normal. As such, we ran a Wilcox test to compare the cell distribution data present on the left and right sides. The values yielded were:

- $W = 14514$
- $p = 0,04319 < 0,05$

As $p < 0,05$, there is a significant difference between left and right sides of the skull.

The histograms comparing the cell distribution (in terms of area) in the left and right side of the cranium follow below (Figure 27):

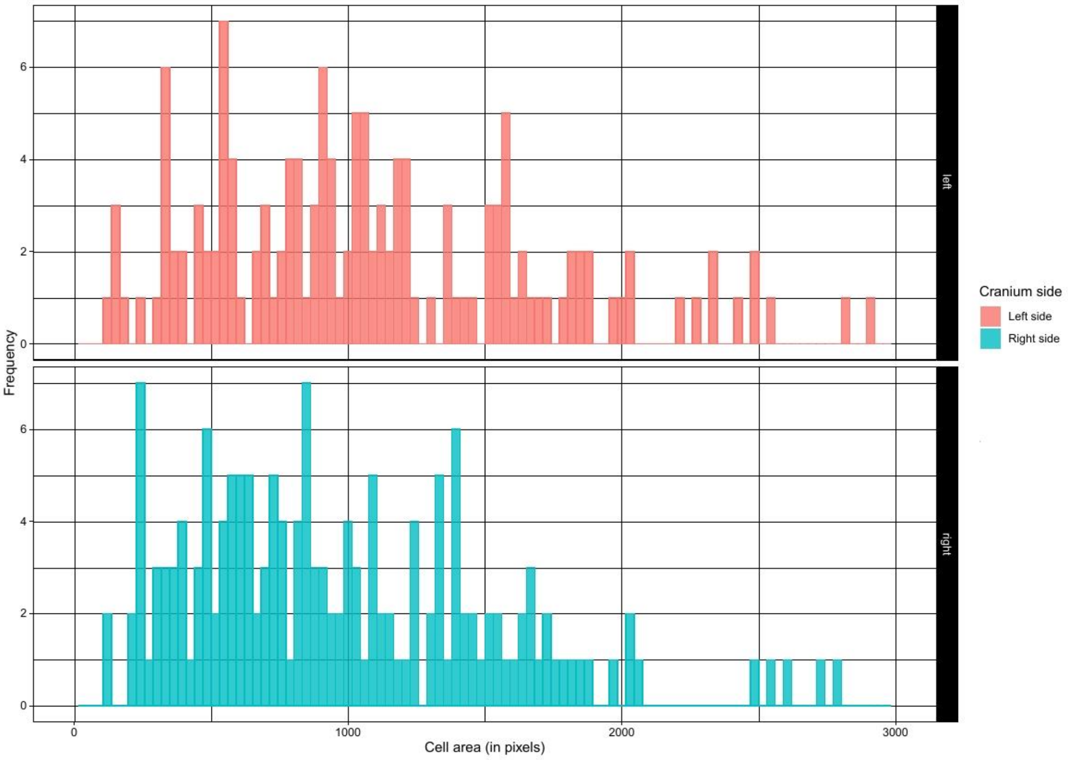


*Figure 27: Frequency histograms of cell distributions for the left and right sides of* Captorhinus kierani *skull.*

Then, we ran a Wilcox test to compare the cell distribution data present on the anterior and posterior areas of the skull. The Wilcox test results were:

- W = 12910
- p = 0,3401 > 0,05

As p > 0,05, there is no significant difference between anterior and posterior areas of the skull.

The histograms comparing the cell distribution (in terms of area) in the anterior and posterior areas of the cranium follow below (Figure 28):

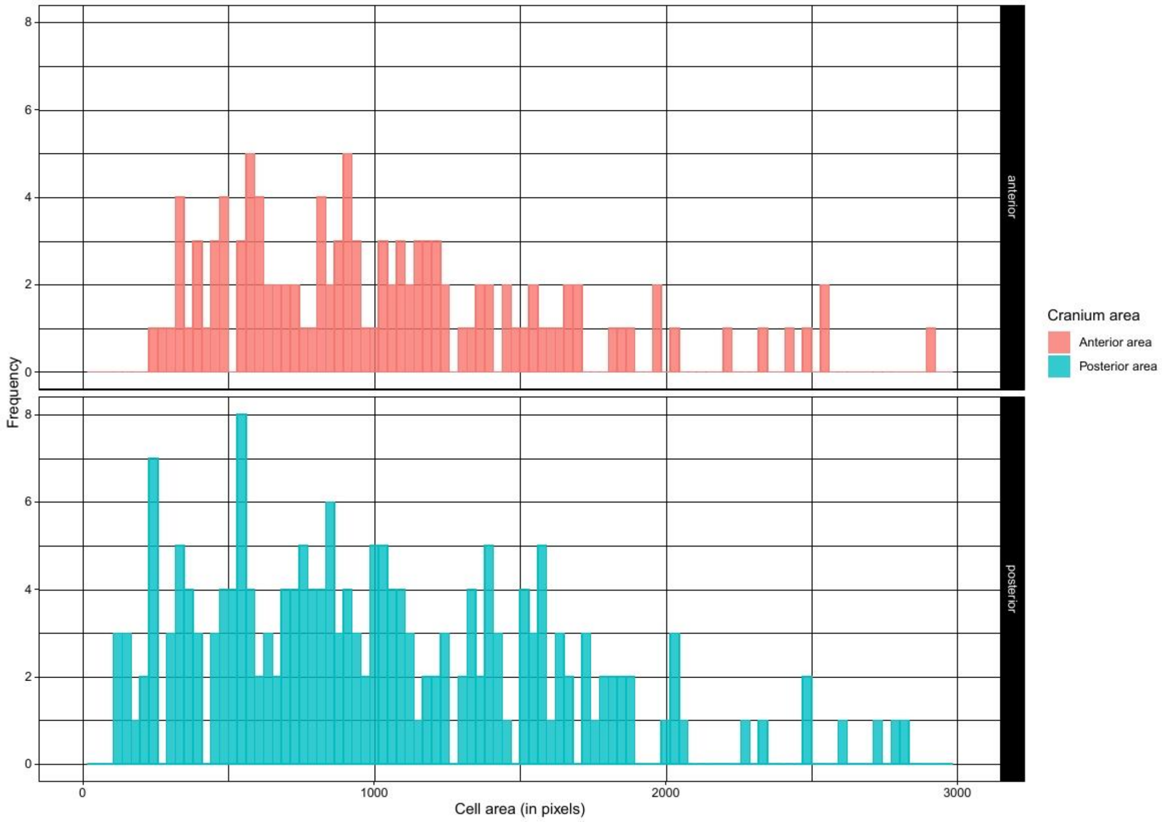


*Figure 28: Frequency histograms of cell distributions if anterior and posterior areas of* Captorhinus kierani *skull.*

Finally, we ran a Kruskall-Wallis test in order to compare the cell distribution data in all four quadrants of the skull table, which resulted in the following values:

- chi-squared = 10,228
- p = 0,01672 < 0,05

The value obtained for p is < 0,05. Hence, there is a significant difference between cell distribution data in the four quadrants of the skull.

The histograms comparing the cell distributions (in terms of area) in the four quadrants of the cranium follow below (Figure 29):

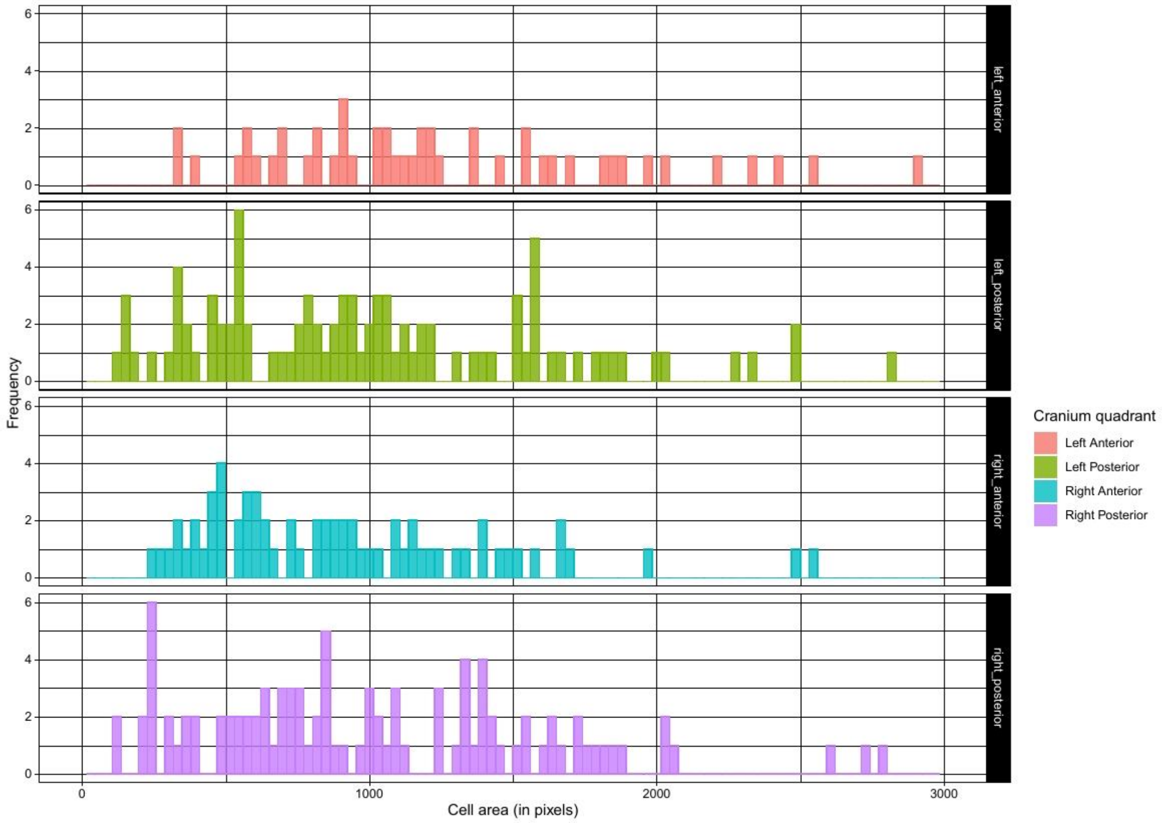


*Figure 29: Frequency histograms of cell distributions in all quadrants of* Captorhinus kierani *skull.*

Knowing that there was a difference between the quadrants of the skull, we performed a Dunn test to verify pairs were significantly different, yielding the results present in the next table (Table 5):

*Table 5: Results of Dunn test considering all table skull quadrants for* Captorhinus kierani*. LA = left anterior, LP = left posterior, RA = right anterior, RP = right posterior.*

| | **LA** | **LP** | **RA** |
|---|---|---|---|
| **LP** | 2,370602<br>p=0,0089 * | | |
| **RA** | 3,040141<br>p=0,0012 * | 0,961353<br>p=0,1682 | |
| **RP** | 2,610962<br>p=0,0045 * | 0,272622<br>p=0,3926 | -0,719807<br>p=0,2358 |

### *Captorhinus laticeps*

In the case of *Captorhinus laticeps*, the following values were obtained for the Shapiro-Wilk normality test:

- W = 0,83569
- $p < 2,2^{-16} < 0,05$

This means that the data distribution is not normal. As such, we ran a Wilcox test to compare the cell distribution data present on the left and right sides. The values yielded were:

- W = 79732
- $p = 0,223 > 0,05$

As $p > 0,05$, there is no significant difference between the left and right sides of the skull.

The histograms comparing the cell distribution (in terms of area) in the left and right side of the cranium follow below (Figure 30):

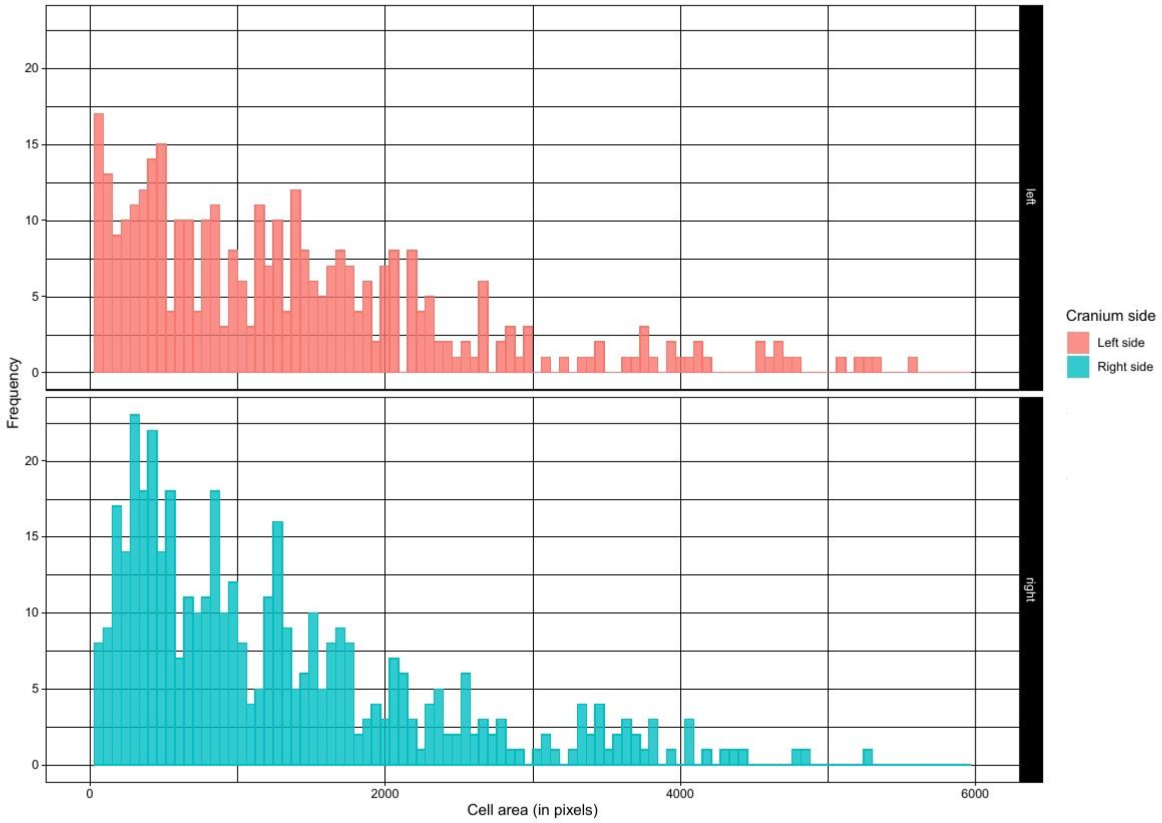


*Figure 30: Frequency histograms of cell distributions in the left and right sides of* Captorhinus laticeps *skull.*

Then, we ran a Wilcox test to compare the cell distribution data present on the anterior and posterior areas of the skull. The Wilcox test results were:

- W = 71658
- p = 0,5445 > 0,05

As p > 0,05, there is no significant difference between anterior and posterior areas of the skull.

The histograms comparing the cell distribution (in terms of area) in the anterior and posterior areas of the cranium follow below (Figure 31):

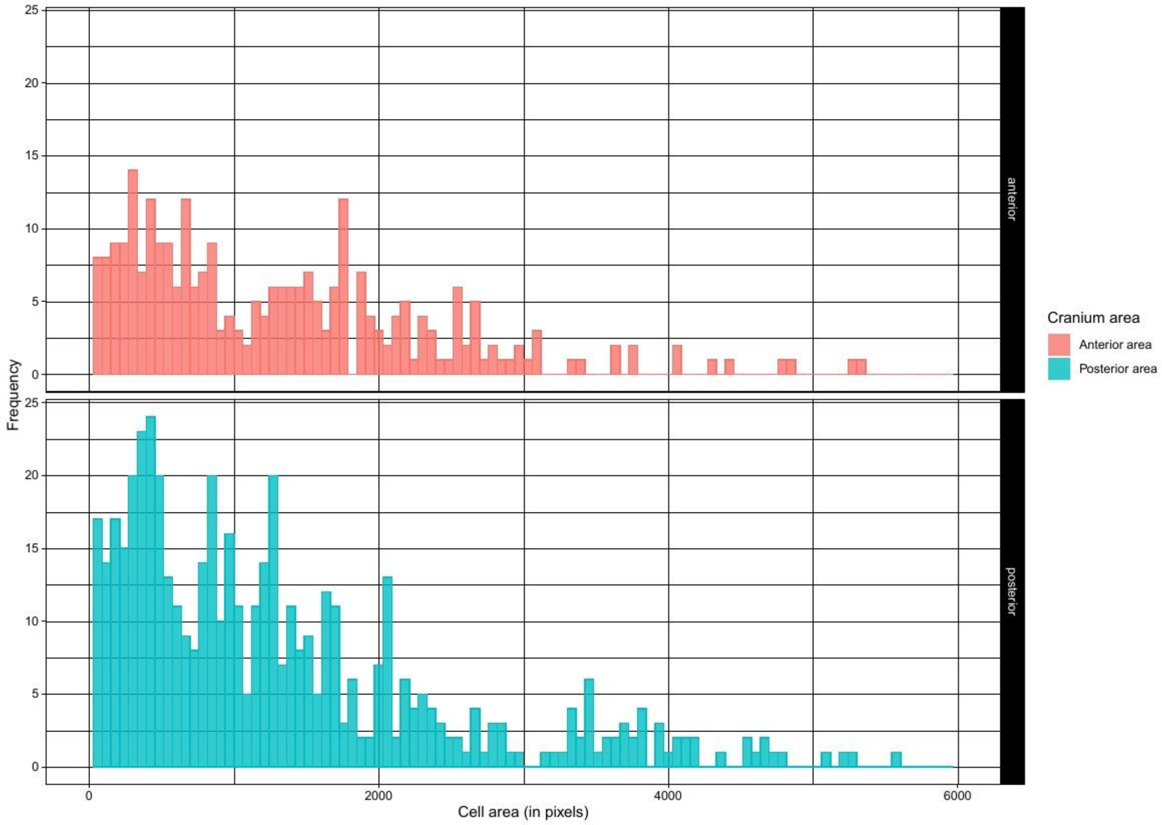


*Figure 31: Frequency histograms of cell distributions for anterior and posterior areas of* Captorhinus laticeps *skull.*

Finally, we ran a Kruskall-Wallis test in order to compare the cell distribution data in all four quadrants of the skull table, which resulted in the following values:

- chi-squared = 5,0034
- p = 0,1715 > 0,05

The value obtained for p is > 0,05. Hence, there is no significant difference between cell distribution data in the four quadrants of the skull.

A Dunn test was not performed given the Kruskall-Wallis test results.

### *Protocaptorhinus pricei*

In the case of *Protocaptorhinus pricei*, the following values were obtained for the Shapiro-Wilk normality test:

- W = 0,90189
- $p < 2,2^{-16} < 0,05$

This means that the data distribution is not normal. As such, we ran a Wilcox test to compare the cell distribution data present on the left and right sides. The values yielded were:

- W = 65090
- $p = 0,5261 > 0,05$

The value obtained for p is > 0,05. Hence, there is no significant difference between cell distribution in the left and right sides of the skull.

The histograms comparing the cell distribution (in terms of area) in the left and right side of the cranium follow below (Figure 32):

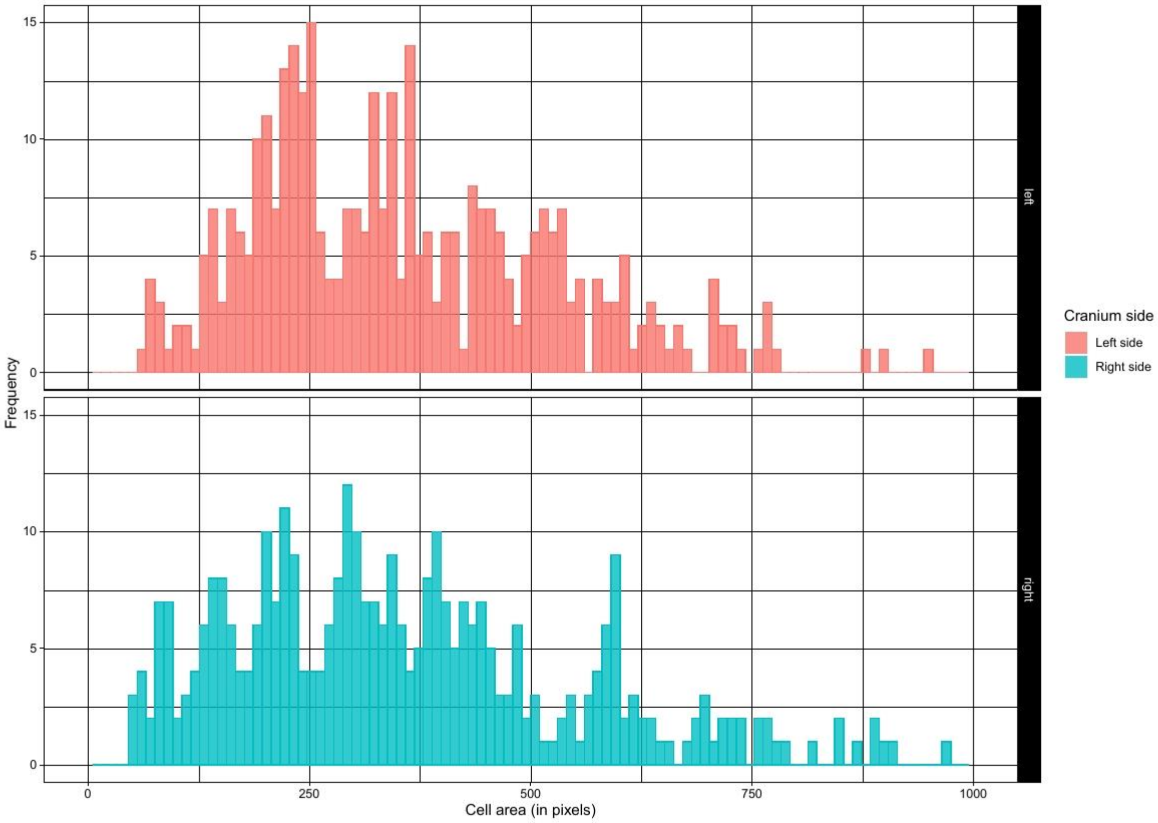


*Figure 32: Frequency histograms of cell distributions for the left and right sides of* Protocaptorhinus *skull.*

When comparing the cell distribution data (in terms of area) present on anterior and posterior areas of the skull table, the Wilcox test results were:

- W = 57972
- p = 0,1316 > 0,05

The value obtained for p is > 0,05. Hence, there is no significant difference between cell distribution in anterior and posterior areas of the skull.

The histograms comparing the cell distribution (in terms of area) in the anterior and posterior areas of the cranium follow below (Figure 33):

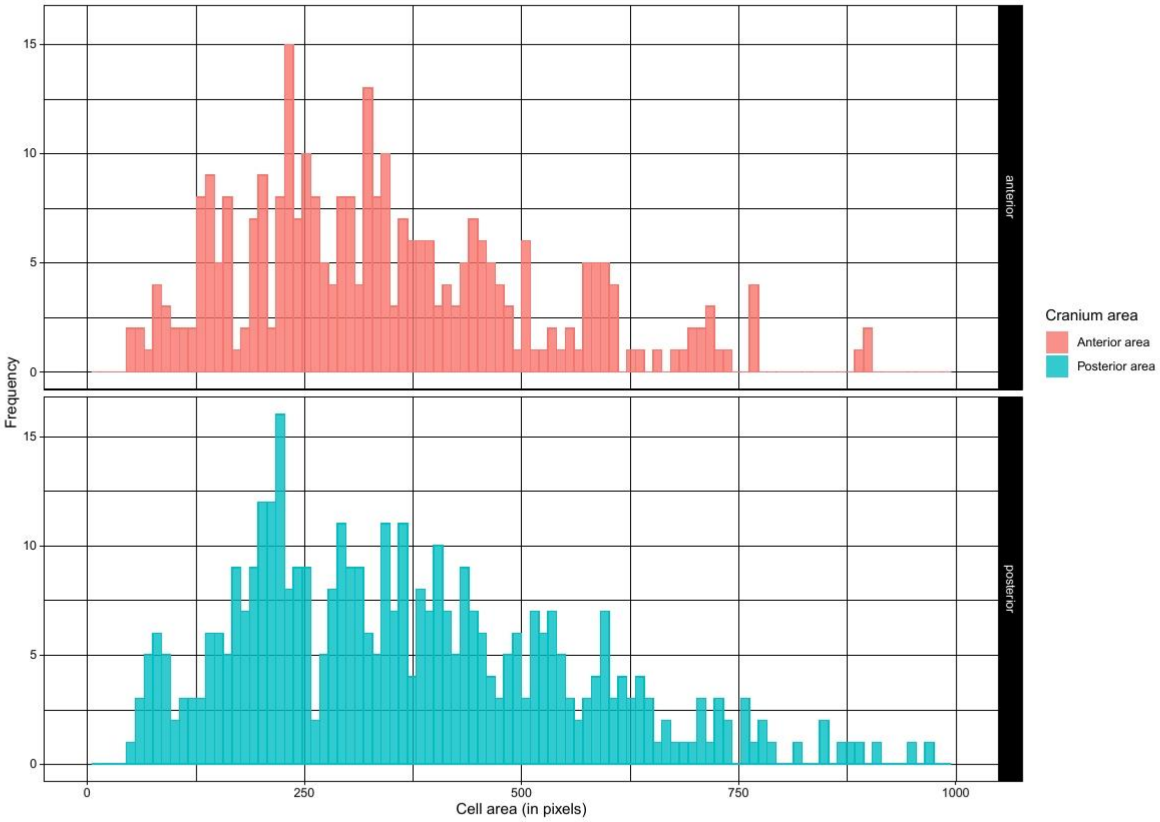


*Figure 33: Frequency histograms of cell distributions in anterior and posterior areas of* Protocaptorhinus *skull.*

Finally, we ran a Kruskall-Wallis test in order to compare the cell distribution data in all four quadrants of the skull table, which resulted in the following values:

- chi-squared = 2,7625
- p = 0,4297 > 0,05

The value obtained for p is > 0,05. Hence, there is no significant difference between cell distribution data in the four quadrants of the skull.

A Dunn test was not performed given the Kruskall-Wallis test results.

A table summarizing statistic results obtained follows (Table 6):

*Table 6: Summary of results obtained from skull sculpturing statistical analysis*

| | ***Xenosaurus newmanorum*** | ***C. aguti*** | ***C. kierani*** | ***C. laticeps*** | ***Protocaptorhinus pricei*** |
|---|---|---|---|---|---|
| Left vs Right | 0,2571 | 0,0003 * | 0,04319 * | 0,223 | 0,5261 |
| Anterior vs Posterior | 0,00266 * | 4,223^-14 * | 0,3401 | 0,5445 | 0,1316 |

# 4. Discussion

This chapter is divided into two sections.

One is dedicated to the morphological characters used in phylogenetic analyses of captorhinids and the discussion of the results obtained in sections 3. b-f. and 3. i.

The second part focuses on skull sculpturing, and consequently, the discussion of results obtained in sections 3. a., 3. g-h., and 3. j.

## a. Phylogenetic trees generated with new characters

The latest captorhinid phylogeny published in the literature (Appendix 1) includes a character matrix in which the phylogeny was based (Appendix 2). This phylogenetic tree is reproduced below (Figure 34) (Modesto et al 2018). It is mostly a well-resolved tree, in which the Moradisaurinae clade includes *Labidosaurus* and forms with the *Captorhinus genera* a monophyletic group. However, these species are included in a polytomy with *Labidosauriscus*. Species like *Paleothyris*, *Thuringothyris*, *Euconcordia*, *Opisthodontosaurus* and *Rhiodenticulatus* are retrieved as basal. Both *Romeria* species make a monophyletic group and are closely linked to *Reiszorhinus*. Moradisaurinae is paraphyletic.

As described in the Methods section, we removed the problematic characters (Appendix 3) and obtained a smaller matrix with 60 characters (Appendix 4) that generated the phylogeny represented in Section 3. d, Figure 14.

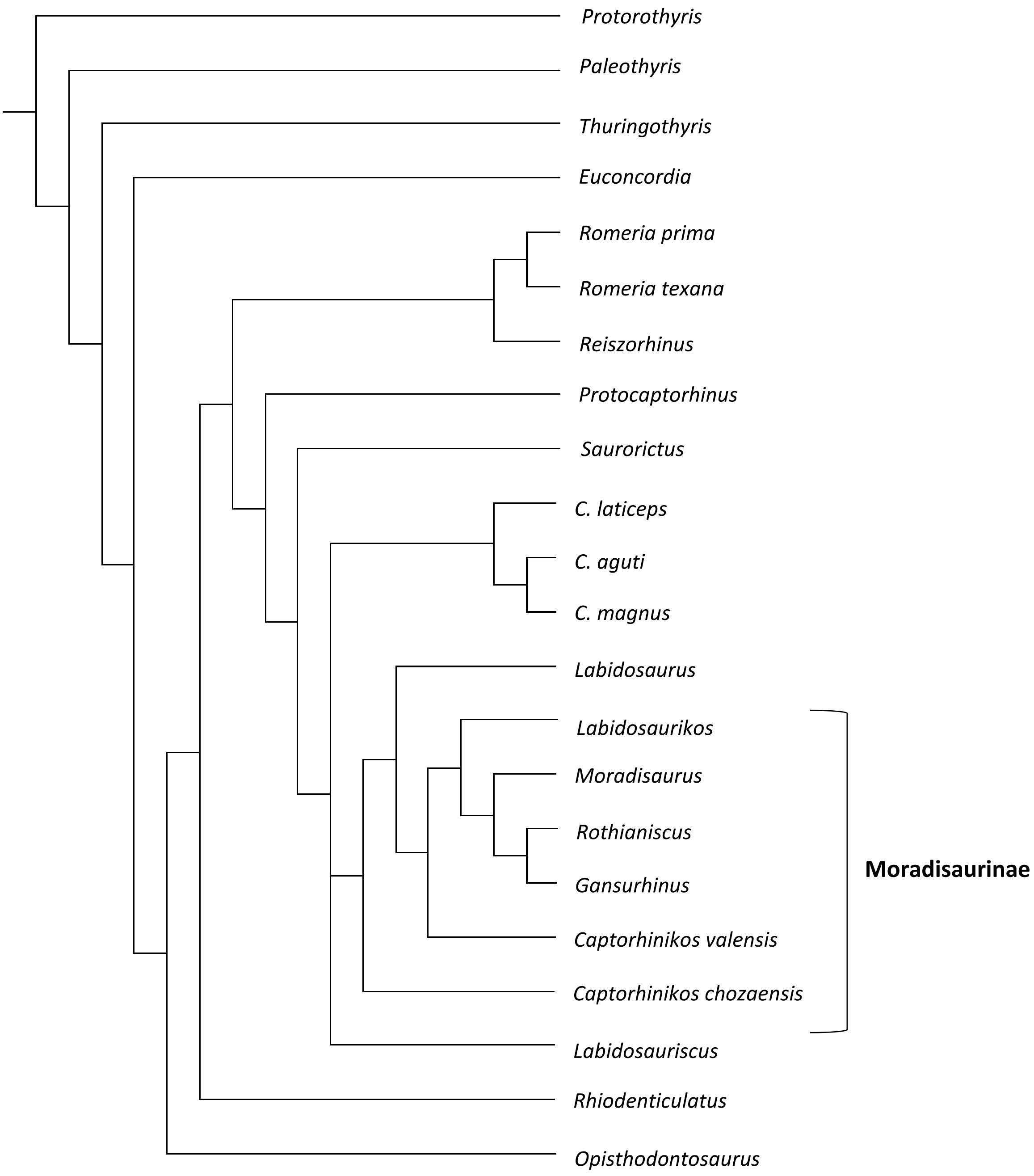


*Figure 34: Strict consensus phylogenetic tree of captorhinomorphs. In Modesto et al., 2008.*

Some clades are monophyletic in both trees (Fig. 34 and Fig. 14) namely: *Romeria prima + Romeria texana + Reiszorhinus*; the Moradisaurinae + *Labidosaurus*; and the three *Captorhinus* species. However, Moradisaurinae is no longer resolved. Moradisaurinae, *Labidosaurus*, the three *Captorhinus* species*, Labidosauriscus* + *Saurorictus* form a polytomy. *Protorothyris*, *Paleothyris*, *Thuringothyris*, *Euconcordia*, *Opisthodontosaurus* and

*Rhiodenticulatus* are still the most basal species and appear in the same correspondent branch order. However, *Euconcordia* and *Opisthodontosaurus* make a polytomy with the more derived species (in Fig 14).

A new species of *Captorhinus*, *Captorhinus kierani*, was first described in 2019 and consequently was not included in the matrix of Modesto et al. 2018 (deBraga et al. 2019). As such, we decided to code it based on the previously mentioned 60 characters (Appendix 5) and include it in our phylogenetic analysis. We obtained the phylogeny represented in Section 3. e (Figure 15).

Adding *Captorhinus kierani* creates more polytomies (See Figures 14, 15 and 34). *C. kierani* forms a polytomy with Moradisaurinae + *Labidosaurus*, the other three species of *Captorhinus*, *Labidosauriscus,* and *Saurorictus*. In addition, *Labidosaurus* now forms a polytomy with *Captorhinikos chozaensis* (see Fig. 15).

We then created a new matrix by adding the 29 new characters described in Section 3. b. (total of 89 characters; see Appendix 7 and 8). The resulting phylogenetic tree is presented in Section 3. f as Figure 16.

This tree is better resolved (compare with Figure 15), however, there is a polytomy that includes *Saurorictus*, *Rhiodenticulatus*, and a clade composed of the following species: *Romeria prima* + *Romeria texana* + P*rotocaptorhinus* + *Reiszorhinus*, the group *Captorhinus laticeps* + *Captorhinus kierani* + *Captorhinus aguti* + *Labidosauriscus* + *Captorhinus magnus*, and the group Moradisaurinae + *Labidosaurus*. The other polytomy is present inside the Moradisaurinae and includes *Moradisaurus* + *Rothianiscus* + *Gansurhinus*. The Moradisaurinae clade appears monophyletic, unlike in Modesto et al. 2018, where it is paraphyletic.

*Labidosauriscus* is retrieved inside the resolved clade that includes all *Captorhinus* species, suggesting that the polytomy initially presented by Modesto et al. is now solved (Modesto et al., 2018). However, the consistency indexes of these branches seem low for a robust conclusion. *Protocaptorhinus* is now present as a more derived species, clustered with *Romeria* and *Reiszorhinus*.

In order to further test the consistency of all these results, we added the 11 new skull sculpturing characters (See Section 3. g., namely Table 2) and generated new trees based on a total of 100 characters (see Appendix 9 and 10). The resulting phylogenetic tree is represented in Section 3. i., Figure 20.

Starting with the most basal species, the general topology corresponds to the one published by Modesto et al. in 2018, up until *Opisthodontosaurus* (See Fig. 34 and 20). The Moradisaurinae clade is still monophyletic and well-resolved, except for the polytomy previously mentioned (*Moradisaurus* + *Rothianiscus* + *Gansurhinus*). A possible explanation may be related to the fact that *Gansurhinus* is based on very fragmentary material from two specimens: the holotype (partial left premaxilla, dental plate of right maxilla, partial braincase, right pterygoid) and a referred specimen (partial dental plate). As a result, very few characters can be coded, in addition, the ones that are scored are similar to *Rothianiscus* and *Moradisaurus*.

*Romeria prima* and *Romeria texana* are still a monophyletic group along with *Reiszorhinus.* This proximity between the two *Romeria* species has been proved very robust during all analyses here presented. *Protocaptorhinus* is still grouped with these three species but is now in a polytomy with *Reiszorhinus* instead of appearing as more derived (and closer to both *Romeria*). This indicates that the addition of skull sculpturing characters may reveal a more derived position of the species, but not enough to place it in a monophyletic clade with *Saurorictus, Labidosaurus*, the other *Captorhinus* species, and the Moradisaurinae group. Additionally, *Saurorictus* is retrieved as being more basal than *Rhiodenticulatus*, while Modesto et al. 2018 retrieved *Rhiodenticulatus* as being more basal than *Saurorictus* (Figure 34). This suggests that the characters we added accentuate how basal *Saurorictus* is and how derived *Rhiodenticulatus* is.

It is important to note that when we replace some of the characters used in Modesto et al. 2018 we defined new characters and increased the number of characters that access similar traits (i.e. a proportion between measurable dimensions of a structure). Thus, we may have created a bias in some traits. We strongly suggest that further work should be done to test this hypothesis.

Finally, the clade *Captorhinus* is now a polytomy (that includes *Labidosauriscus*). This seems to suggest that the skull sculpturing characters do reinforce the close phylogenetic relationship between these species (*C. aguti*, *C. magnus*, *C. laticeps*, *C. kierani* and *Labidosauriscus*), but is not enough to distinguish them and resolve the polytomy. Additionally, it shows that the phylogenetic relationship between all those species may not be as well resolved as initially thought (i.e. hard polytomy). This hypothesis was somehow previously mentioned (deBraga et al. 2019). In fact, all these species share the same locality (Richards Spur, Oklahoma, U.S.A.) except for *C. laticeps* (McCann Quarry, Oklahoma, U.S.A. and Mitchell Creek, Texas, U.S.A.) (deBraga et al., 2019). There is the indication of possible resource partitioning among these captorhinids, based on the existence of heteromorphic dentition across them (Modesto et al. 2018). *Labidosauriscus* is almost indistinguishable from other *Captorhinus* species in regard to skull morphology, except for the postcaniniform teeth, which are most similar to those of *C. laticeps* (Modesto et al. 2018). Additionally, the only notable difference on the skull table between *C. kierani*, *C. aguti* and *C. magnus* pertains to the angle formed by the frontals, and their relative skull size, which makes the dental morphology very informative (deBraga et al. 2019). Recently, however, authors deBraga, Bevitt and Reisz in 2019 attempted to re-examine the dental variation within the *Captorhinus* genus and raised some concerns. Regarding the assignment of disarticulated dental fragments to particular species, they consider them as "remain[ing] problematic at this time" (deBraga et al., 2019). They also criticise the currently accepted assumption that every multiple-rowed member of this genus is assignable to *C. aguti*, as they question the inexistence of other captorhinid species with multiple tooth rows (deBraga et al., 2019). There are other morphological traits pertaining to *Captorhinus* teeth (such as the presence or absence of a slight kink in the mandible around the 9th tooth or the presence or absence of ridges on tooth crowns) that are not usually coded, or that were not able to be identified without CT-scans. As such, it comes as no surprise that in this particular group of species we retrieve a polytomy. All this strongly suggests that more precise diagnostic features are needed, at least for this clade.

### b. Skull sculpturing nomenclature

Authors started describing captorhinomorphs in the late 19th century (Cope 1878). Since then, they refer to the skull sculpturing present in captorhinomorph craniums with three distinct expressions: “skull sculpturing”; “skull texturing” and “skull ornamentation”. This can easily lead to confusion and mistakes. Sometimes an author uses the words “texturing” or “sculpturing” to describe small pits, fenestrae and evidence of muscular attachment, or of blood vessels instead of the sulcus, ridges and comb-like structures that are so characteristic of captorhinid skulls. Any scar or modification in the bone surface can be considered “sculpturing”. The use of the expression "skull ornamentation" is not an alternative to distinguishing between those two terms because protuberances like horns or frills can also be considered as ornamentations.

The word "ornament" and its derivate verbs and adjective suggest something that is additional and somewhat decorative. The Merriam-Webster thesaurus lists as synonyms of ornament the following nouns: adornment, beautifier, caparison, decoration, doodah, embellisher, embellishment, frill, garnish, garnishment, garniture, ornamentation, setoff, trim (Merriam-Webster thesaurus). All these expressions entail the idea of something that is essentially aesthetic.

It is also important to add that the word "ornament" already has a specific definition in the field of Biology: a characteristic of an animal that appears to serve a decorative function rather than a utilitarian function (Enbody, Lantz and Karubian, 2017). Many are secondary sexual characteristics (Enbody et al., 2017). As an example, we can look at birds like *Pavo cristatus* and *Pavo muticus* (Indian and green peafowl, respectively), where the males exhibit their exuberantly coloured, long feathers in order to attract a female mate (Alcock, 1997).

Finally, "skull ornamentation" is not as commonly used as "skull sculpturing" or "skull texturing" throughout the captorhinomorph literature we reviewed (over 80 works).

All things considered, it is clear that "skull ornamentation" should not be used in this context. As so, the expressions "skull sculpturing" or "skull texturing" are obvious alternatives.

Searching the words "texture", "textured" and "texturing" yields the next results: the visual or tactile surface characteristics and appearance of something, essential part: substance, identifying quality: character, basic scheme or structure, overall structure (noun); to give a particular texture to (verb) (Merriam-Webster dictionary).

"Texture" is presented to us as an essential part and an identifying quality of something. However, considering the verb "texturing", it refers to active changing motion, just like for "sculpturing" - "to give a particular texture to". The thesaurus does not offer any synonym for "texture" neither related words (Merriam-Webster thesaurus).

The Merriam-Webster dictionary defines "sculpture", "sculptured" and "sculpturing" as impressed or raised markings or a pattern of such especially on a plant or animal part (noun); to form an image or representation of from solid material (such as wood or stone), to shape by or as if by carving or moulding (verb) (Merriam-Webster dictionary). The dictionary points to a definition of "sculpture" that somewhat fits the anatomical shape of the captorhinid skull bones. The thesaurus has listed "carve" and "sculpt" as synonyms for "sculpture" and the following as related words: chisel, engrave, etch, grave, incise, inscribe, knap, cast, form, model, mould, shape, which all reinforce the idea of something that is actively enforced upon (Merriam-Webster thesaurus).

Throughout the literature here reviewed, "skull sculpture/sculpturing" is by far more frequently used by authors than "skull texture/texturing" (182 times and 39 times, respectively. This means that adopting this expression as the *de facto* definition would be easier than forcing a less used term. Additionally, one of the definitions of "sculpture" is "imprints on part of an animal" (Merriam-Webster dictionary), which is precisely what is being considered in this research.

Taking all this into consideration, we propose the usage of skull sculpture[ing] as the best denomination for the feature here defined as: “shape or pattern of the cranial bone surface”.

### c. (Only) Skull sculpturing

The phylogenetic tree generated with only skull sculpturing characters is present on Section 3.h. as Figure 19.

Below, a table representing a summary of all skull sculpturing character states for 19 species (excluding *Romeria* sp., *Rhiodenticulatus* and *Gansurhinus,* see explanation in Section 3. h.).

*Table 7: Summary of skull sculpturing character states for all considered species.*

| | Ridges | | | Nodes | | Sculpture | | | Cell | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Width** | **Shape** | **Path** | **Width** | **Tubercules** | **ST bones** | **Type** | **Bone** | **Shape** | **Size** | **Density** |
| ***Protorothyris*** | ? | Round | Undulated | ? | ? | Some | Cells | Diff. | Oval | Small | Dense |
| ***Paleothyris*** | ? | Mix | Straight | ? | ? | Some | Mix | Diff. | Oval | Small | Sparse |
| ***Thuringothyris*** | Diff. | Mix | Undulated | ? | ? | Some | Ridges | Diff. | Polygon | Big | Sparse |
| ***Reiszorhinus*** | ? | ? | ? | ? | ? | ? | Ridges | ? | Polygon | Small | Dense |
| ***Rothianiscus*** | Diff. | Mix | Undulated | Diff. | Yes | Some | Cells | Diff. | Polygon | Small | Dense |
| ***Moradisaurus*** | Diff. | Mix | Undulated | Const. | Yes | All | Cells | Same | Polygon | Small | Dense |
| ***Labidosaurikos*** | Diff. | Mix | Undulated | Const. | ? | All | Mix | Diff. | Oval | Small | Dense |
| ***Labidosaurus*** | Const. | Round | Undulated | Const. | No | All | Mix | Diff. | Oval | Small | Dense |
| ***Protocaptorhinus*** | Const. | Round | Straight | Diff. | No | All | Cells | Same | Oval | Big | Dense |
| ***Captorhinikos valensis*** | ? | Round | ? | ? | ? | ? | Mix | ? | Oval | Big | ? |
| ***Saurorictus*** | ? | Round | Undulated | ? | ? | Some | Mix | Diff. | Oval | Small | Sparse |
| ***Captorhinus laticeps*** | Const. | Round | Straight | Const. | No | Some | Mix | Mix | Oval | Small | Dense |
| ***Captorhinus aguti*** | Const. | Round | Straight | Const. | No | Some | Mix | Diff | Polygon | Small | Dense |
| ***Captorhinus kierani*** | Const. | Round | Straight | Const. | No | All | Mix | Same | Polygon | Small | Dense |
| ***Captorhinus magnus*** | Const. | Round | Straight | Const. | ? | All | Mix | ? | Polygon | Small | Dense |
| ***Captorhinikos chozaensis*** | ? | ? | ? | ? | ? | ? | Cells | ? | Oval | Small | ? |
| ***Opisthodontosaurus*** | Const. | Straight | Straight | ? | ? | ? | Ridges | Diff. | Oval | Small | Sparse |
| ***Labidosauriscus*** | Const. | Straight | Straight | ? | ? | ? | Mix + Ridges | Diff. | Oval | Small | Sparse |
| ***Euconcordia*** | Const. | Round | Undulated | Diff. | Yes | ? | Cells | Diff | Oval | Small | Dense |

*Protorothyris* (the outgroup) and *Euconcordia* present the following morphologies: undulated ridges with rounded edges, sculpturing pattern mostly composed of oval, small, and dense cells. They may have different types of sculpturing on the same bone.

As seen in Figure 19, *Thuringothyris*, *Reiszorhinus*, *Rothianiscus*, *Moradisaurus*, *Labidosaurikos* and *Labidosaurus* make a monophyletic group with *Thuringothyris* and *Reiszorhinus* standing as the most derived species. This suggests that the sculpturing characters present in *Thuringothyris* and *Reiszorhinus* may have evolved independently, as these species are quite far apart from the others in all other phylogenies (See Fig 14, 15, 16 and 20). All these species except for *Labidosaurus* have ridges with a mix of both round and straight edges, and different widths in the same bone. Additionally, the sculpturing cells of these species are small and dense (except *Thuringothyris)*. This group of species has polygonal cells (except for *Labidosaurus* and *Labidosaurikos*, which have oval cells). All this suggests that the most derived skull sculpturing characteristics (at least inside this clade) include: ridges with different width along bones, with a mix of straight and round corners; skull sculpturing not present in all skull table; sculpturing comprised mostly of ridges in detriment of cell-reticulate sculpturing; presence of different types of sculpturing on the same bone.

*Protocaptorhinus* and *Captorhinikos valensis* are retrieved as sister taxa, characterized by the existence of ridges with round-shaped edges, and big oval cells, sharing almost all character status.

Interestingly, *Captorhinus laticeps* does not form a monophyletic group with the other *Captorhinus* species, despite sharing many similarities with them, and is the only *Captorhinus* with round-shaped cells. The other three *Captorhinus* make a monophyletic group with the following characteristics: ridges with a constant width, round edges and a straight path, constant-width nodes, a mix of both types of sculpturing (ridges and cells), where all cells are polygonal, small and dense.

The skull sculpturing is not well known in *Captorhinikos chozaensis*. All that could be used is that its sculpturing was mainly comprised of small, oval cells. For this reason, it stands in a single branch, forming a polytomy with most other species.

Finally, *Opisthodontosaurus* and *Labidosauriscus* appear as sister taxa. Even though *Labidosauriscus* is known to be a more derived species, both share almost all skull sculpturing character traits, namely: ridges with constant width, straight edges and straight paths, small, oval and sparse sculpturing cells, and a prominence of the ridged type of sculpturing in detriment of cell reticulate sculpturing.

There are other skull sculpturing characters that can prove themselves useful in future analysis. However, we decided not to use them here as they require either direct observation and measurement of the specimens or at least high definition images.

The skull anatomy of the *Captorhinus* genus is extremely conserved but the skull sculpturing differs. As so, it would be important to define additional skull sculpturing characters and include them in a revised diagnosis of those species.

### d. A statistical approach to measuring skull sculpturing

If all qualitative morphological characters could be measured with precision, the resulting phylogeny would probably be more accurate and reproducible. As such, we decided to statistically analyse one specific characteristic of the skull sculpturing in captorhinids: the distribution of cells and their respective area, namely the presence or absence of similarity for different areas along the skull table. Similarities detected in the fossilized specimens are only useful if also present in life. However, in order to exclude characteristics acquired post-death (during or after the fossilization process) we opted to start to analyse an extant species (as control). The control species should share the presence of skull sculpturing and should be as similar as possible to the captorhinid size, habitat and classification. As such, we used *Xenosaurus newmanorum*, also known as Newman's knob-scaled lizard as a control. This species is part of the family Xenosauridae, they can be found in Mexico and Central America (Bhullar, 2011) (Figure 35).

*Figure 35: Juveniles of* Xenosaurus newmanorum *in captivity. Copyright of Great Basin Serpentarium. 2015.*

The *Xenosaurus* cranium examined (Figure 36), showed no significant differences between the cell distribution on the left and right sides (p-value=0,2571).

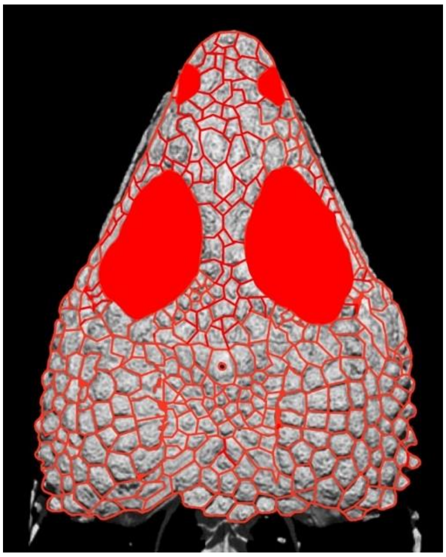


*Figure 36:* Xenosaurus newmanorum*; tracing of skull sculpturing features. Specimen UMMZ 126056. Adapted from Bhullar 2011.*

This shows that the cranial pattern in *Xenosaurus* is bilaterally symmetrical.

However, there is a statistically significant difference between the anterior and posterior part of the skull (p-value=0,00266).

In the case of *Captorhinus laticeps* (Figure 38) and *Protocaptorhinus pricei* (Figure 37), there are no significant differences between the cell distributions in the left and right side of the skull (p-value=0,223; p-value=0,5251, respectively).

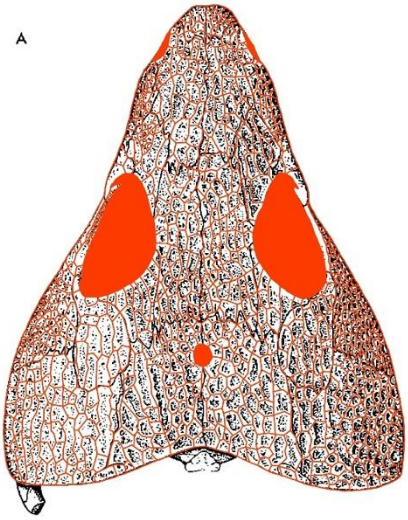


*Figure 38:* Captorhinus laticeps*; tracing of skull sculpturing features. Adapted from Heaton 1979.*

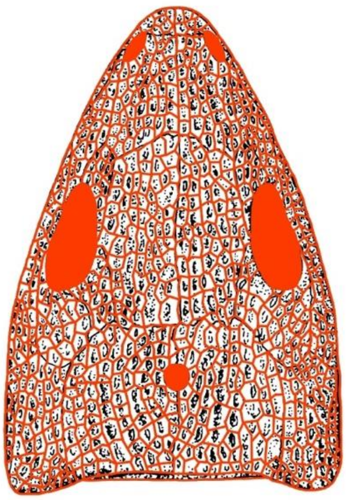


*Figure 37:* Protocaptorhinus pricei*; tracing of skull sculpturing features. Adapted from Olson 1964.*

Among other factors, it is important to notice that the analysis of these two skulls was based on skull reconstructions drawn by the authors (Olson, 1964; Heaton, 1979). This might be a problem because they were drawn by humans trying to reconstruct a complete skull based on multiple skull fragments. These biases can impact on the analysis here performed.

*Captorhinus aguti* (Figure 39), presents differences in cell distribution between left and right sides of the skull and between anterior and posterior regions. However, the p-value for the left/side difference is of 0,03 and for the anterior/posterior areas is of $4{,}223^{-14}$, many magnitude orders smaller. This suggests that the anterior/posterior cell distribution difference is more pronounced than the left/right side distribution. In fact, the p-value shown for cell distribution differences between pairs left anterior/left posterior, right anterior/right posterior and left anterior/right posterior is 0. P-value for pairs left posterior/right anterior and left posterior/right posterior are still below 0,05 – 0,0010 and 0,0029, respectively. The only pair where we did not detect differences was between right anterior/left anterior, indicating that at least for the anterior part of the skull, the cell distribution is uniform. Considering that we extracted the data from a skull illustration (Modesto, 1998) and that the skull is slightly deformed on the posterior-left side, we should also account for the possible contribution of this distortion that might produce differences between posterior left and right sides. We solved this as described in Section 2. b.

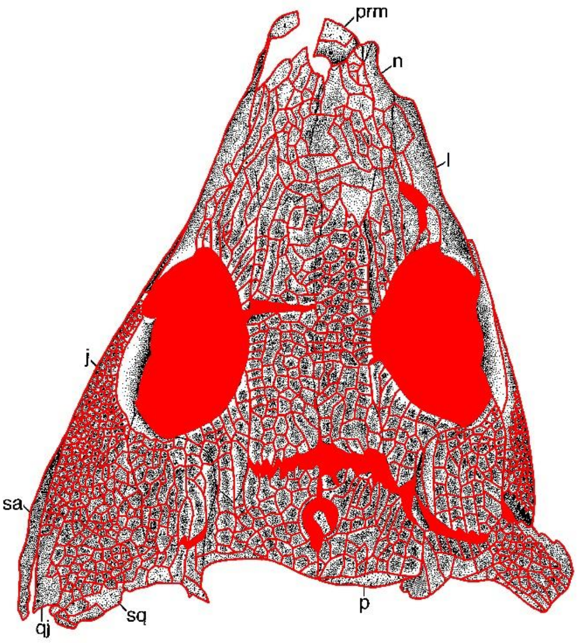


*Figure* 39*:* Captorhinus aguti*; tracing of skull sculpturing features. Adapted from Modesto 1998.*

In *Captorhinus kierani* (Figure 40) there is no significant difference between cell distributions of anterior and posterior areas of the cranium (p-value=0,3401). However, there are differences between the left and right sides (p-value=0,04319). Although close to the threshold of 0,05, the pairs left anterior/left posterior, left anterior/right anterior and left anterior/right posterior show significant differences – with p-values of 0,0089, 0,0012 and 0,0045 respectively Interestingly, there is no cranial deformation, and the sculpturing is present in roughly the same proportion on the right anterior area. One possible explanation is the presence of longer, more polygonal and bigger cells, compared to the other areas.

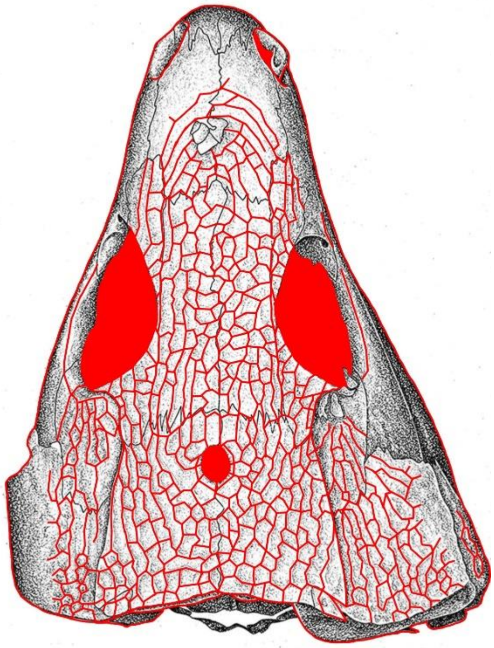


*Figure 40:* Captorhinus kierani*; tracing of skull sculpturing features. Adapted from deBraga et al. 2019.*

Taking all this in consideration, this statistical analysis reveals the presence of differences between the skull sculpturing patterns present on several captorhinid species, three of them part of the *Captorhinus* genus, corroborating the hypothesis that this characteristic could be a good method to distinguish them and improve future phylogenetic and taxonomical studies.

# Conclusions and future work

We produced a new captorhinid morphological character matrix – restructured, optimized and reviewed. This increases the reproducibility and eases the construction of more robust captorhinid cladograms. The phylogenetic analyses here presented shows that branches that were previously thought of as well-resolved need deeper study and updating – like the *Captorhinus* clade. Additionally, it is also clear that more captorhinid specimens need to be discovered and analysed, especially in continents where their presence has been reported but in very small numbers. As examples, *Gansurhinus* (Asia) and *Saurorictus* (Africa) are either one of the few or the only species known from their respective continent, and only one or two incomplete specimens of each species have been discovered so far.

The second contribution of this dissertation pertains to skull sculpturing as a morphological character. We conducted not only a complete review of current literature about the trait for captorhinomorphs but also redefined the trait itself and its character states in these species, with improved detail and precision. Furthermore, this trait has also shown potential to be a criterion to help to distinguish captorhinomorph species, while also shedding some light on its own evolutionary history.

The methodology here developed can also be used as a basis to conduct similar research in other animal groups, extant or extinct, making it very valuable from a research perspective.

This thesis produced an extremely useful portfolio (see Appendix 11) to illustrate all morphological skull characters used in phylogenetic studies in captorhinomorphs, solving possible interpretation issues, ambiguities and questions that could arise from reading the character list alone. It is then an additional tool and valuable help for new and upcoming researchers in this area when conducting their own analysis and future projects.

Despite all that has been mentioned, it is imperative to point out that the results here presented need to be validated by direct observation of specimens. Quality and resolution of the images here used varied, depending on how old the material was. Images (pictures, illustrations and CT scans) do not replace the direct observation of specimens and this should be the next approach to further test all hypothesis here presented. As such, this is the primary goal for the future development of this project.

In order to better understand the Present, we have to look back and see how things happened in the Past: that is why palaeontology research is so helpful, especially from an Evo-Devo perspective. Understudied groups like Captorhinidae and Protorothyrididae not only hold a privileged position on the evolutionary history of Amniota but are also crucial groups when it comes to understand basal reptilian structure, relationships and even ecology. The keys to these overarching themes hide (partially) inside captorhinomorph skulls, surely along with many other wonders. It is up to us, researchers, to unearth them and bring them to light, once more.

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# Appendix 1

**List and definition of characters used in the phylogenetic analysis; in Modesto, Scott and Reisz 2018.**

Characters from Modesto *et al*. (2014). Character states for characters 20, 24, 27, 33, 46, 67–69, 72, and 73 have been reversed so that the outgroup *Protorothyris* exhibits the primitive state.

*Skull roof*

(1) Premaxilla: ventral margin aligned anteroposteriorly in lateral view (0); ventral margin aligned anteroventrally in lateral view (1).

(2) Premaxilla: alary process absent (0); alary process present on posterodorsal process (1).

(3) Premaxillary dentition: first tooth relatively small relative to maxillary caniniform (0); subequal to maxillary caniniform (1). In taxa lacking maxillary caniniforms, state 1 applies when the first premaxillary tooth is the largest marginal tooth present.

(4) Maxilla: relatively straight (0); posterior end flexed laterally (1).

(5) Maxilla: posterior-most tooth positioned at level of posterior margin of orbit (0) or positioned more anteriorly (1).

(6) Maxillary dentition: tooth stations number 30 teeth or more (0); teeth number 18–26 (1); teeth number 14–17 (2); teeth number 13 or less (3). For multiple-rowed taxa, only those teeth with unobstructed profiles when viewed laterally are considered.

(7) Teeth on maxillary dental field: none (0); less than 40 (1); 40 or more (2). Definition modified from Reisz *et al*. (2011) for clarity.

(8) Maxillary caniniform teeth: present (0); absent (1).

(9) Number of tooth rows in the upper jaw: one (0); two to four (1); five (2); six or more (3).

(10) Marginal dentition: ‘cheek’ teeth recurved (0); chisel-shaped (1); bulbous and ogival (2); bulbous at base and conical above (3).

(11) Maxilla: double row of teeth extend far anteriorly on tooth row absent (0); double row of teeth extend far anteriorly on tooth row present (1).

(12) Dental tooth wear: absent (0); present, modest (1); present, saddle shaped (2).

(13) Lacrimal: suture with jugal small (0); well developed (1).

(14) Nasolacrimal suture: straight (0); interdigitating (1).

(15) Snout: broad, equal to or greater than 35% of skull length (0); narrow, equal to or less than 25% of skull length (1).

(16) Antorbital/cheek region: mainly formed by lacrimal and prefrontal (0); mostly formed by lacrimal due to dorsal expansion of the bone (1).

(17) Prefrontal: prefrontal-nasal suture shorter than lacrimal-nasal suture (0); prefrontal-nasal suture longer than lacrimal-nasal suture (1).

(18) Frontal: anterior process short, less than 40% of the frontal sagittal length (0); anterior process long, approximately 55% of the frontal sagittal length (1).

(19) Jugal: subtemporal process dorsoventrally low, equal to or less than 25% of skull height through orbital midpoint (0); subtemporal process dorsoventrally deep, at least 40% of skull height through orbit (1).

(20) Jugal: anterior extent ends posterior to anterior orbital margin (0); anterior extent reaches beyond anterior orbital margin (1).

(21) Jugal: postorbital extent shorter than remaining anterior extent (0); postorbital extent equal or longer (1).

(22) Quadratojugal: anteroposteriorly elongate (0); short, not extending anteriorly beyond midpoint of postorbital margin (1).

(23) Quadratojugal: acuminate anteriorly (0); square-tipped anteriorly (1).

(24) Quadratojugal: expanded dorsally (0); posteriorly straight or decreasing in height (1).

(25) Quadratojugal: maximum height approximately equal to one-third or less that of squamosal (0); nearly equal to half of squamosal height (1).

(26) Postorbital cheek: relatively straight (0); moderately expanded laterally (1); greatly expanded laterally (2).

(27) Parietal: distinct anterolateral process present that partially separates postfrontal and postorbital (0); does not strongly project between postfrontal and postorbital (1).

(28) Pineal foramen: positioned at midpoint of interparietal suture (0); anterior to midpoint of interparietal suture (1); posterior to midpoint of interparietal suture (2).

(29) Sculpturing: skull surface relatively smooth, with only small honeycombing pits or grooves (0); with pits and grooves with notably larger, randomly positioned pits on posterior skull table (1); low ridge-and-pit system with tiny pits and furrows (2).

(30) Supratemporal: obliquely oriented into anteromedial direction, thereby lying within a facet of the parietal (0); positioned mediolaterally at the posterior edge of the parietal (1).

(31) Supratemporal: small, slender element (0); large, contributing to skull table (1).

(32) Supratemporal-postparietal contact: tenuous or absent (0); well developed (1).

(33) Postparietal: contacts mate dorsally only, postparietals separated slightly ventrally by supraoccipital (0); contacts mate fully along height (1).

(34) Postparietal: transversely short with tabular present (0); transversely elongate with tabular absent (1).

(35) Postparietal: contribution to skull table absent or forms only narrow edge (0); contribution to skull table large, forming sculptured posterior portion of skull table (1).

(36) Skull table occipital margin: embayed bilaterally (0); straight (1); with single median embayment (2).

*Palate*

(37) Vomer: denticulated (0); edentulous (1).

(38) Vomer-pterygoid contact: extensive, at least 50% median border of vomer (0); short, no more than 33% median border of vomer (1).

(39) Palatine: denticulated (0); edentulous (1).

(40) Jugal/ectopterygoid: ectopterygoid present and alary process absent (0); ectopterygoid absent and alary process present, but no higher than the midpoint of the suborbital process of the jugal and distinct from the orbital margin (1); ectopterygoid absent and alary process present and positioned dorsally on the medial surface of the jugal, flush with orbital margin (2).

(41) Dentition on palatal ramus of pterygoid: present (0); greatly reduced or absent (1).

(42) Pterygoid: transverse flange dentition consists of shagreen of denticles (0); transverse flange dentition consists of at least one row of functional teeth (1); transverse flange dentition absent (2).

(43) Pterygoid: transverse flange broad-based and distinctly angular in ventral view (0); transverse flange narrow and tongue-like in ventral view (1).

(44) Suborbital foramen: absent (0); present (1); anteroposteriorly elongate (2).

*Braincase*

(45) Parasphenoid: cultriform process extends anteriorly (0); cultriform process extends slightly dorsally at roughly 15º to the basal plane (1); cultriform process extends anterodorsally at more than 45º to the basal plane (2).

(46) Parasphenoid: edentulous (0); denticulated (1).

(47) Parasphenoid: deep ventral groove between cristae ventrolateralis absent (0); deep ventral

groove between cristae ventrolateralis present (1).

(48) Parasphenoid: posterolateral wing narrow, meets narrow head of stapes (0); wing broad, meets large head of stapes, in an elongate, nearly parasagittal suture (1).

(49) Opisthotic: paroccipital process long, extending near to medial edge of squamosal (0); process short, extending only slightly beyond body of opisthotic (1).

(50) Paroccipital process: broad (0); narrow (1).

(51) Stapes: distal process short (0); distal process elongate (1).

(52) Supraoccipital: slopes anterodorsally (0); aligned vertically or slopes posterodorsally (1).

(53) Supraoccipital: lateral ascending processes account for half or less height of bone (0); lateral ascending processes account two-thirds or more height of the bone (1).

(54) Occipital condyle: at level of quadrate condyles (0); immediately anterior to condyles (1).

(55) Exoccipital: lateral process on dorsal ramus absent (0); lateral process present (1).

### *Mandible*

(56) Dentary: Anterior dentary teeth: teeth uniformly small (0), multiple enlarged teeth present anteriorly (1); single enlarged tooth present anteriorly (2).

(57) Dentary: first tooth oriented mainly vertically (0); first tooth leans strongly anteriorly (1).

(58) Mandibular ramus: relatively straight in ventral view (0); sigmoidal in ventral view (1).

(59) Mandibular ramus: narrow, 8% or less of total jaw length (0); broad, no less than 14% of total jaw length (1).

(60) Mandibular ramus: posterior end rectilinear in lateral view (0) or acuminate in lateral view (1).

(61) Mandibular ramus: lateral shelf absent (0); lateral shelf present below coronoid process (1).

(62) Coronoid: anterior process short (0); elongate (1).

(63) Meckelian foramen: small, anteroposterior length roughly 9% or less of total jaw length (0); large, anteroposterior length greater than or equal to 14% of total jaw length (1).

(64) Coronoid: posterodorsal process slender, forms dorsal-most quarter of lateral wall of adductor fossa (0); posterodorsal process deep, forms dorsal-most third of lateral wall of adductor fossa (1).

(65) Retroarticular process: absent (0); present and broader transversely than long (1); present and longer anteroposteriorly than broad (2).

*Postcrania*

(66) Dorsal neural arches: narrow (0), lateral expansion present (1), or exaggerated lateral expansion swelling present (2).

(67) Neural spines of dorsal vertebrae: height or shape alternation absent (0); height or shape alternation present (1).

(68) Anterior dorsal centra: strongly ventrolaterally constricted (0); not strongly ventrolaterally constricted (1).

(69) Sacral ribs: first and second sacral rib roughly equal in size (0); first sacral rib larger than second rib (1).

(70) Ilium: iliac blade expanded dorsally (0); iliac blade narrow dorsally (1).

(71) Stylo- and zeugopodium: shaft slender and heads only moderately expanded (0); shaft massive and with proximal and distal heads significantly expanded, resulting in an overall stout impression (1).

(72) Humerus: supinator process parallel to shaft (0); supinator process absent (1). Modified slightly from Modesto *et al*. (2014).

(73) Manus and pes: elements long and slender (0); elements short and broad (1).

(74) Fourth metatarsal: less than half the length of tibia (0); more than half the length of tibia (1).

(75) First metacarpal: more than half the length of fourth metacarpal (0); less than half the length of fourth metacarpal (1).

# Appendix 2

**Data matrix; in Modesto, Scott and Reisz 2018.**

Modified from Reisz *et al*. (2015). *Abbreviation*: A, polymorphism for 0&1.

*Protorothyris* 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0

0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 ? 0 0 0 ? ?

*Paleothyris* 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 0 0 1 2 0 0 0 0 1 0 0 0 0 0 0 0 0

0 0 0 0 1 0 ? 0 0 0 0 0 0 0 0 0 0 0 0 0 ? ? ? 0 0 0 0 0 1 0 0 0 1 1

*Thuringothyris* 0 0 0 0 0 1 0 1 0 0 0 0 1 0 0 1 1 0 0 1 0 1 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0

0 0 0 0 0 0 0 0 0 0 ? ? 0 0 0 ? ? ? ? 0 0 0 0 ? ? 1 0 1 1 1

*Euconcordia* 0 1 0 0 1 1 0 0 0 0 0 0 1 1 0 1 1 0 0 1 1 0 ? ? 0 0 0 1 0 0 0 0 1 1 0 0 0 ? 0 0 0

0 0 1 0 1 0 ? 0 0 0 0 0 0 ? 0 0 0 0 0 0 ? ? ? 0 ? ? ? ? ? ? ? ? ? ?

*Romeria prima* 1 1 1 1 0 1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 1 0 0 0 0 1 0 ? 0 0 0 1 1 0 0 1 ? 0 ? ? 0 ? 1 0

0 0 0 0 0 1 0 ? 0 ? 1 0 0 0 0 0 ? ? ? 0 ? 1 ? 1 ? 1 ? 1 ? ?

*Romeria texana* 1 1 1 1 0 1 0 0 0 0 0 0 ? ? 0 0 1 0 0 0 1 1 0 0 0 0 0 1 ? 0 0 0 1 1 0 0 1 0 0 ? 0 0 0 1 0

? 0 ? 0 ? 1 0 ? 0 0 1 0 0 0 0 0 ? ? ? 0 ? ? ? ? ? ? ? ? ? ?

*Protocaptorhinus* 1 1 1 1 0 1 0 0 0 0 0 0 1 1 0 0 0 0 0 1 1 1 0 ? 0 0 1 1 0 1 0 0 0 1 0 1 ? ? ? 1 ?

0 0 1 0 ? 0 ? ? 0 1 0 0 0 ? ? 0 0 0 0 0 ? ? ? 1 1 1 ? ? 1 1 1 1 ? ?

*Rhiodenticulatus* 1 1 0 1 0 1 0 0 0 0 0 0 1 1 0 1 1 0 0 1 1 0 1 1 0 0 0 1 ? ? ? 0 0 1 0 1 ? 1 0 1 0

0 0 1 0 0 0 0 0 ? 1 ? 0 0 0 1 0 0 0 0 0 1 ? ? ? 1 ? 1 0 ? 1 1 1 ? ?

*Saurorictus* ? 1 1 1 1 1 0 0 0 0 0 0 1 ? 0 0 1 0 0 1 0 0 1 1 0 0 1 0 0 ? ? ? 0 1 0 ? ? ? ? ? ? ?

? 1 ? ? ? ? ? ? ? 0 ? ? ? 1 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?

*Captorhinus laticeps* 1 1 1 1 1 1 0 0 0 1 0 0 1 1 0 0 0 0 0 0 1 0 1 1 0 1 0 1 0 1 0 0 0 1 0 2 1 1 0 2 0

0 1 1 1 0 1 0 0 0 1 0 0 0 0 1 1 0 0 1 0 1 0 0 2 1 1 1 1 0 1 1 1 0 0

*Captorhinus aguti* 1 1 1 1 1 1 1 0 1 2 0 1 1 1 0 0 0 0 0 1 1 0 1 1 0 1 0 1 0 1 0 0 0 1 0 2 1 1 0 2 0
0 1 1 1 A 1 0 0 0 1 0 0 0 0 1 1 0 0 1 0 1 0 0 2 1 1 1 1 0 1 1 1 0 0

*Captorhinus magnus* 1 1 1 1 1 1 0 0 0 2 0 0 1 1 0 0 0 0 0 1 1 0 1 1 0 1 0 1 0 1 0 0 0 1 0 2 1 1 0 2 0
0 1 ? 1 0 1 0 0 0 1 0 0 0 0 1 1 0 0 1 0 1 0 ? 2 1 1 1 ? ? 1 1 1 ? ?

*Labidosaurus* 1 1 1 1 1 1 0 1 0 1 0 0 1 0 1 0 0 1 1 1 1 0 1 1 0 1 0 1 1 1 0 1 0 1 0 2 1 1 0 1 0
0 1 1 2 0 1 0 0 1 1 1 1 1 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0 1 1 1 0 1

*Labidosaurikos* 1 1 1 1 1 2 2 1 3 3 1 2 1 0 1 0 0 1 1 1 1 0 1 1 1 1 1 1 1 1 1 1 0 1 1 2 1 1 1 1 1 1 1 1 2
0 1 1 0 1 1 1 1 1 0 2 ? 1 1 1 1 0 1 1 1 ? ? ? ? ? ? ? ? ? ?

*Moradisaurus* 1 ? 1 1 0 2 2 0 3 3 0 1 1 ? 0 1 ? ? 1 ? ? ? ? ? ? 2 ? 1 1 ? 1 ? ? ? 1 1 1 1 1 1 1 1
1 2 2 0 1 1 1 1 ? 1 1 0 1 2 1 1 1 1 1 0 1 1 1 2 1 ? ? ? 1 ? 1 0 ?

*Rothianiscus* 1 ? 1 1 0 3 1 1 2 3 1 2 ? ? 1 ? ? ? ? 1 ? ? ? ? 1 2 ? 1 1 ? 1 ? ? ? ? 1 1 1 1 ? 1 2
1 2 ? 0 1 ? ? ? ? ? ? ? ? 2 ? 1 1 1 ? ? ? ? 1 2 1 1 ? ? ? ? 1 ? ?

*Captorhinikos valensis* ? ? ? ? ? 1 2 1 2 3 0 2 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 0 0
? ? ? ? ? ? ? ? ? ? ? ? 2 ? ? ? ? ? ? ? ? ? 2 1 ? ? ? ? ? ? ? ?

*Gansurhinus* 1 ? ? 1 ? 3 2 1 2 3 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
? ? ? 1 ? ? ? ? ? ? ? 1 ? ? ? ? ? ? ? ? ? ? 2 1 1 ? ? ? 1 ? ? ?

*Captorhinikos chozaensis* 1 1 1 1 1 1 1 1 1 1 0 1 1 ? 0 0 ? 0 ? 0 ? ? ? ? ? 1 ? 1 0 ? ? ? ? ? ? ? ?
? 0 1 0 0 1 ? ? 0 ? ? ? ? 1 ? ? 1 ? 2 0 1 0 1 1 ? ? ? 1 1 ? 1 1 0 1 0 1 ? 0

*Reiszorhinus* 1 1 1 1 0 1 0 0 0 0 0 0 1 0 0 0 0 0 0 1 1 0 0 1 0 0 0 1 0 0 0 0 1 1 0 1 ? ? ? ? ?
? ? ? ? ? ? ? ? ? 1 0 0 0 ? 1 0 0 1 0 ? 1 1 ? 0 ? ? ? ? ? ? ? ? ? ?

*Opisthodontosaurus* ? ? 0 1 1 3 0 0 0 3 0 0 1 ? ? ? ? ? 0 0 1 1 0 ? 0 1 0 1 0 ? ? ? ? ? ? ? 0 ? 0 2 0 0
0 1 0 0 1 0 ? ? 1 ? ? ? ? 0 1 0 0 0 1 1 0 1 0 1 ? 0 ? ? 1 1 0 ? ?

*Labidosauriscus* 1 1 1 1 1 2 0 0 0 1 0 0 1 1 0 0 0 0 0 1 0 ? ? ? ? 1 ? 1 2 ? ? ? ? ? ? 2 1 1 0 2 0 0 1 2 1 1
1 0 ? ? 1 ? ? ? ? 1 0 0 0 1 1 1 0 0 ? ? ? ? ? ? ? ? ? ? ?

# Appendix 3

**List of non-problematic characters used to generate Figures 13 and 14; 60 characters total. Based on Modesto et al., 2018.**

*Skull roof*

(1) Premaxilla: ventral margin aligned anteroposteriorly in lateral view (0); ventral margin aligned anteroventrally in lateral view (1).

(2) Premaxilla: alary process absent (0); alary process present on posterodorsal process (1).

(3) Premaxillary dentition: first tooth relatively small relative to maxillary caniniform (0); subequal to maxillary caniniform (1). In taxa lacking maxillary caniniforms, state 1 applies when the first premaxillary tooth is the largest marginal tooth present.

(4) Maxilla: relatively straight (0); posterior end flexed laterally (1).

(5) Maxilla: posterior-most tooth positioned at level of posterior margin of orbit (0) or positioned more anteriorly (1).

(6) Maxillary dentition: tooth stations number 30 teeth or more (0); teeth number 18–26 (1); teeth number 14–17 (2); teeth number 13 or less (3). For multiple-rowed taxa, only those teeth with unobstructed profiles when viewed laterally are considered.

(8) Maxillary caniniform teeth: present (0); absent (1).

(9) Number of tooth rows in the upper jaw: one (0); two to four (1); five (2); six or more (3).

(10) Marginal dentition: ‘cheek’ teeth recurved (0); chisel-shaped (1); bulbous and ogival (2); bulbous at base and conical above (3).

(11) Maxilla: double row of teeth extend far anteriorly on tooth row absent (0); double row of teeth extend far anteriorly on tooth row present (1).

(12) Dental tooth wear: absent (0); present, modest (1); present, saddle shaped (2).

(14) Nasolacrimal suture: straight (0); interdigitating (1).

(16) Antorbital/cheek region: mainly formed by lacrimal and prefrontal (0); mostly formed by lacrimal due to dorsal expansion of the bone (1).

(17) Prefrontal: prefrontal-nasal suture shorter than lacrimal-nasal suture (0); prefrontal-nasal suture longer than lacrimal-nasal suture (1).

(20) Jugal: anterior extent ends posterior to anterior orbital margin (0); anterior extent reaches beyond anterior orbital margin (1).

(21) Jugal: postorbital extent shorter than remaining anterior extent (0); postorbital extent equal or longer (1).

(22) Quadratojugal: anteroposteriorly elongate (0); short, not extending anteriorly beyond midpoint of postorbital margin (1).

(23) Quadratojugal: acuminate anteriorly (0); square-tipped anteriorly (1).

(24) Quadratojugal: expanded dorsally (0); posteriorly straight or decreasing in height (1).

(27) Parietal: distinct anterolateral process present that partially separates postfrontal and postorbital (0); does not strongly project between postfrontal and postorbital (1).

(28) Pineal foramen: positioned at midpoint of interparietal suture (0); anterior to midpoint of interparietal suture (1); posterior to midpoint of interparietal suture (2).

(30) Supratemporal: obliquely oriented into anteromedial direction, thereby lying within a facet of the parietal (0); positioned mediolaterally at the posterior edge of the parietal (1).

(31) Supratemporal: small, slender element (0); large, contributing to skull table (1).

(32) Supratemporal-postparietal contact: tenuous or absent (0); well developed (1).

(33) Postparietal: contacts mate dorsally only, postparietals separated slightly ventrally by supraoccipital (0); contacts mate fully along height (1).

(34) Postparietal: transversely short with tabular present (0); transversely elongate with tabular absent (1).

(35) Postparietal: contribution to skull table absent or forms only narrow edge (0); contribution to skull table large, forming sculptured posterior portion of skull table (1).

(36) Skull table occipital margin: embayed bilaterally (0); straight (1); with single median embayment (2).

*Palate*

(37) Vomer: denticulated (0); edentulous (1).

(39) Palatine: denticulated (0); edentulous (1).

(40) Jugal/ectopterygoid: ectopterygoid present and alary process absent (0); ectopterygoid absent and alary process present, but no higher than the midpoint of the suborbital process of the jugal and distinct from the orbital margin (1); ectopterygoid absent and alary process present and positioned dorsally on the medial surface of the jugal, flush with orbital margin (2).

(41) Dentition on palatal ramus of pterygoid: present (0); greatly reduced or absent (1).

(42) Pterygoid: transverse flange dentition consists of shagreen of denticles (0); transverse flange dentition consists of at least one row of functional teeth (1); transverse flange dentition absent (2).

(43) Pterygoid: transverse flange broad-based and distinctly angular in ventral view (0); transverse flange narrow and tongue-like in ventral view (1).

*Braincase*

(45) Parasphenoid: cultriform process extends anteriorly (0); cultriform process extends slightly dorsally at roughly 15º to the basal plane (1); cultriform process extends anterodorsally at more than 45º to the basal plane (2).

(46) Parasphenoid: edentulous (0); denticulated (1).

(47) Parasphenoid: deep ventral groove between cristae ventrolateralis absent (0); deep ventral groove between cristae ventrolateralis present (1).

(48) Parasphenoid: posterolateral wing narrow, meets narrow head of stapes (0); wing broad, meets large head of stapes, in an elongate, nearly parasagittal suture (1).

(49) Opisthotic: paroccipital process long, extending near to medial edge of squamosal (0); process short, extending only slightly beyond body of opisthotic (1).

(50) Paroccipital process: broad (0); narrow (1).

(52) Supraoccipital: slopes anterodorsally (0); aligned vertically or slopes posterodorsally (1).

(54) Occipital condyle: at level of quadrate condyles (0); immediately anterior to condyles (1).

*Mandible*

(56) Dentary: Anterior dentary teeth: teeth uniformly small (0), multiple enlarged teeth present anteriorly (1); single enlarged tooth present anteriorly (2).

(57) Dentary: first tooth oriented mainly vertically (0); first tooth leans strongly anteriorly (1).

(58) Mandibular ramus: relatively straight in ventral view (0); sigmoidal in ventral view (1).

(60) Mandibular ramus: posterior end rectilinear in lateral view (0) or acuminate in lateral view (1).

(61) Mandibular ramus: lateral shelf absent (0); lateral shelf present below coronoid process (1).

(65) Retroarticular process: absent (0); present and broader transversely than long (1); present and longer anteroposteriorly than broad (2).

*Postcrania*

(66) Dorsal neural arches: narrow (0), lateral expansion present (1), or exaggerated lateral expansion swelling present (2).

(67) Neural spines of dorsal vertebrae: height or shape alternation absent (0); height or shape alternation present (1).

(68) Anterior dorsal centra: strongly ventrolaterally constricted (0); not strongly ventrolaterally constricted (1).

(69) Sacral ribs: first and second sacral rib roughly equal in size (0); first sacral rib larger than second rib (1).

(70) Ilium: iliac blade expanded dorsally (0); iliac blade narrow dorsally (1).

(71) Stylo- and zeugopodium: shaft slender and heads only moderately expanded (0); shaft massive and with proximal and distal heads significantly expanded, resulting in an overall stout impression (1).

(72) Humerus: supinator process parallel to shaft (0); supinator process absent (1). Modified slightly from Modesto *et al*. (2014).

(73) Manus and pes: elements long and slender (0); elements short and broad (1).

(74) Fourth metatarsal: less than half the length of tibia (0); more than half the length of tibia (1).

(75) First metacarpal: more than half the length of fourth metacarpal (0); less than half the length of fourth metacarpal (1).

(76) Dentary: lingual shelf absent (0); lingual shelf present (1).

(77) Anterior maxillary foramen: absent (0); present (1).

# Appendix 4

**Data matrix based on the character list present in Appendix 3. Used to generate the phylogeny present in Figures 13 e 14. 60 characters. Based on Modesto et al. 2018.**

*Abbreviation:* polymorphism for {0 1}, {1 2}

*Protorothyris* 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0. 0 0 0 0 0
0 0 0 0 0 0 0 0 0 ? 0 0 0 ? ? 0 ?

*Paleothyris* 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 1 2 0 0 1 0 0 0 0 0 ? 0 0 0 0 1 0 ? 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 0 0

*Thuringothyris* 0 0 0 0 0 1 1 0 0 0 0 0 1 1 0 1 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 ?
? 0 0 ? 0 0 0 0 ? ? 1 0 1 1 1 0 0

*Euconcordia* 0 1 0 0 1 1 0 0 0 0 0 1 1 1 0 1 1 1 ? ? 0 1 0 0 1 1 0 0 0 0 0 0 0 0 0 1 0 ? 0 0 0 0 0
0 0 0 0 0 ? ? ? ? ? ? ? ? ? ? ? 0

*Romeria prima* 1 1 1 1 0 1 0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 0 0 0 1 1 0 0 1 0 ? ? 0 ? 0 0 0 0 0 0 0 0
1 0 0 0 0 0 ? 1 ? 1 ? 1 ? 1 ? ? 0 0

*Romeria texana* 1 1 1 1 0 1 0 0 0 0 0 ? 0 1 0 0 1 1 0 0 0 1 0 0 1 1 0 0 1 0 ? 0 0 0 0 ? 0 ? 0 ? 0 0
1 0 0 0 0 0 ? ? ? ? ? ? ? ? ? ? 0 0

*Protocaptorhinus* 1 1 1 1 0 1 0 0 0 0 0 1 0 0 0 1 1 1 0 ? 1 1 0 0 0 1 0 1 ? ? 1 ? 0 0 0 ? 0 ? 1 0 0 0
? 0 0 0 0 1 1 1 ? ? 1 1 1 1 ? ? 0 0

*Rhiodenticulatus* 1 1 0 1 0 1 0 0 0 0 0 1 1 1 0 1 1 0 1 1 0 1 ? ? 0 1 0 1 ? 0 1 0 0 0 0 0 0 0 1 ? ? 0
1 0 0 0 0 ? 1 ? 1 0 ? 1 1 1 ? ? 0 0

*Saurorictus* ? 1 1 ? 1 {12} 0 0 0 0 0 0 0 1 1 1 0 1 1 1 0 ? ? ? ? 1 0 1 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1

*Captorhinus laticeps* 1 1 1 1 1 1 0 0 1 0 0 1 0 0 0 0 1 0 1 1 0 1 0 0 0 1 0 2 1 0 2 0 0 1 1 0 1 0
1 0 0 0 1 1 0 1 0 2 1 1 1 1 0 1 1 1 0 0 0 0

*Captorhinus aguti* 1 1 1 1 1 1 0 1 2 0 1 1 0 0 0 1 1 0 1 1 0 1 0 0 0 1 0 2 1 0 2 0 0 1 1 {0 1} 1
0 0 0 0 0 1 1 0 1 0 2 1 1 1 1 0 1 1 1 0 0 0 0

*Captorhinus magnus* 1 1 1 1 1 1 0 0 1 0 0 1 0 0 0 1 1 1 1 1 0 1 0 0 0 1 0 2 1 0 2 0 0 1 1 0 1
0 ? 0 0 0 1 1 0 1 0 2 1 1 1 ? ? 1 1 1 ? ? 0 0

*Labidosaurus* 1 1 1 1 1 1 1 0 1 0 0 0 0 0 1 1 1 0 1 1 0 1 0 1 0 1 0 2 1 0 1 0 0 1 2 0 1 1 1 1 1 1 1

1 1 1 1 1 1 1 1 1 0 1 1 1 0 1 0 0

*Labidosaurikos* 1 1 1 1 1 1 1 3 3 1 2 0 0 0 1 1 1 0 1 1 1 1 1 1 0 1 1 2 1 1 1 1 1 1 2 0 1 1 1 1 1 1
2 ? 1 1 1 1 ? ? ? ? ? ? ? ? ? ? 1 0

*Moradisaurus* 1 ? 1 1 0 2 0 3 3 0 1 ? 1 ? 1 ? ? ? ? ? ? 1 1 ? ? ? 1 1 1 1 1 1 1 1 2 0 1 1 0 1 1 0 2
1 1 1 1 1 2 1 ? ? ? 1 ? 1 0 ? 1 ?

*Rothianiscus* 1 ? 1 1 0 3 1 2 3 1 2 ? ? ? ? 1 ? ? ? ? ? 1 1 ? ? ? ? 1 1 1 ? 1 2 1 ? 0 1 ? ? ? ? ? 2 ?
1 1 ? 1 2 1 1 ? ? ? ? 1 ? ? 1 ?

*Gansurhinus* 1 ? ? 1 ? 3 1 2 3 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 ? ? ? ? ? ? ? ?
? ? ? 2 1 1 ? ? ? 1 ? ? ? ? ?

*Captorhinikos valensis* ? ? ? ? ? 1 1 2 3 0 2 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 0 0 ? ? ? ? ? ? ?
? 2 ? ? ? ? ? 2 1 ? ? ? ? ? ? ? ? ? ?

*Captorhinikos chozaensis* 1 1 1 1 1 1 1 2 3 0 1 ? 0 ? ? 0 ? ? ? ? ? 1 ? ? ? ? ? ? ? 0 1 0 0 1 ? 0 ? ?
? ? ? 1 2 0 1 1 1 1 1 ? 1 1 1 1 2 1 0 ? 1 ?

*Reiszorhinus* 1 1 1 1 0 1 0 0 0 0 0 0 0 0 0 1 1 1 0 1 0 1 0 0 1 1 0 1 ? ? ? ? ? ? ? ? ? ? ? ? 0 0 1 0
0 0 ? 0 ? ? ? ? ? ? ? ? ? ? 0 0

*Opisthodontosaurus* ? ? 0 1 1 3 0 0 3 0 0 ? ? ? 0 0 1 1 0 ? 0 1 ? ? ? ? ? ? 0 0 2 0 0 0 0 0 1 0 ? ?
? ? 0 1 0 0 1 0 1 ? 0 ? ? 1 1 0 ? ? 0 ?

*Labidosauriscus* 1 1 1 1 1 2 0 0 1 0 0 1 0 0 0 1 ? ? ? ? ? 1 ? ? ? ? ? 2 1 0 2 0 0 1 1 1 1 0 ? ? ? ? 1
0 0 1 1 ? ? ? ? ? ? ? ? ? ? ? ? 1

# Appendix 5

**Data matrix based on the character list present in Appendix 3. Used to generate the phylogeny present in Figure 15. 60 characters. Based on Modesto et al. 2018. *Captorhinus kierani* added.**

*Abbreviation:* polymorphism for {0 1}, {1 2}

*Protorothyris* 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0. 0 0 0 0 0 0 0 0 0 0 0 0 0 0 ? 0 0 0 ? ? 0 ?

*Paleothyris* 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 1 2 0 0 1 0 0 0 0 0 ? 0 0 0 0 1 0 ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 0 0

*Thuringothyris* 0 0 0 0 0 1 1 0 0 0 0 0 1 1 0 1 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 ? ? 0 0 ? 0 0 0 0 ? ? 1 0 1 1 1 0 0

*Euconcordia* 0 1 0 0 1 1 0 0 0 0 0 1 1 1 0 1 1 1 ? ? 0 1 0 0 1 1 0 0 0 0 0 0 0 0 1 0 ? 0 0 0 0 0 0 0 0 0 0 ? ? ? ? ? ? ? ? ? ? ? ? 0

*Romeria prima* 1 1 1 1 0 1 0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 0 0 0 1 1 0 0 1 0 ? ? 0 ? 0 0 0 0 0 0 0 0 1 0 0 0 0 0 ? 1 ? 1 ? 1 ? 1 ? ? 0 0

*Romeria texana* 1 1 1 1 0 1 0 0 0 0 0 ? 0 1 0 0 1 1 0 0 0 1 0 0 1 1 0 0 1 0 ? 0 0 0 0 ? 0 ? 0 ? 0 0 1 0 0 0 0 0 ? ? ? ? ? ? ? ? ? ? 0 0

*Protocaptorhinus* 1 1 1 1 0 1 0 0 0 0 0 1 0 0 0 1 1 1 0 ? 1 1 0 0 0 1 0 1 ? ? 1 ? 0 0 0 ? 0 ? 1 0 0 0 ? 0 0 0 0 1 1 1 ? ? 1 1 1 1 ? ? 0 0

*Rhiodenticulatus* 1 1 0 1 0 1 0 0 0 0 0 1 1 1 0 1 1 0 1 1 0 1 ? ? 0 1 0 1 ? 0 1 0 0 0 0 0 0 0 1 ? ? 0 1 0 0 0 0 ? 1 ? 1 0 ? 1 1 1 ? ? 0 0

*Saurorictus* ? 1 1 ? 1 {12} 0 0 0 0 0 0 0 1 1 1 0 1 1 1 0 ? ? ? ? 1 0 1 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1

*Captorhinus laticeps* 1 1 1 1 1 1 0 0 1 0 0 1 0 0 0 0 1 0 1 1 0 1 0 0 0 1 0 2 1 0 2 0 0 1 1 0 1 0 1 0 0 0 1 1 0 1 0 2 1 1 1 1 0 1 1 1 0 0 0 0

*Captorhinus aguti* 1 1 1 1 1 1 0 1 2 0 1 1 0 0 0 1 1 0 1 1 0 1 0 0 0 1 0 2 1 0 2 0 0 1 1 {0 1} 1 0 0 0 0 0 1 1 0 1 0 2 1 1 1 1 0 1 1 1 0 0 0 0

*Captorhinus magnus* 1 1 1 1 1 1 0 0 1 0 0 1 0 0 0 1 1 1 1 1 0 1 0 0 0 1 0 2 1 0 2 0 0 1 1 0 1 0 ? 0 0 0 1 1 0 1 0 2 1 1 1 ? ? 1 1 1 ? ? 0 0

*Labidosaurus* 1 1 1 1 1 1 1 0 1 0 0 0 0 0 1 1 1 0 1 1 0 1 0 1 0 1 0 2 1 0 1 0 0 1 2 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0 1 1 1 0 1 0 0

| | |
|---|---|
| *Labidosaurikos* | 1 1 1 1 1 1 3 3 1 2 0 0 0 1 1 0 1 1 1 1 1 0 1 1 2 1 1 1 1 1 2 0 1 1 1 1 1 2 ? 1 1 1 1 ? ? ? ? ? ? ? ? ? ? ? 1 0 |
| *Moradisaurus* | 1 ? 1 1 0 2 0 3 3 0 1 ? 1 ? 1 ? ? ? ? ? ? 1 1 ? ? ? 1 1 1 1 1 1 1 2 0 1 1 0 1 1 0 2 1 1 1 1 1 2 1 ? ? ? 1 ? 1 0 ? 1 ? |
| *Rothianiscus* | 1 ? 1 1 0 3 1 2 3 1 2 ? ? ? ? 1 ? ? ? ? ? 1 1 ? ? ? ? 1 1 1 ? 1 2 1 ? 0 1 ? ? ? ? ? ? 2 ? 1 1 ? 1 2 1 1 ? ? ? ? 1 ? ? 1 ? |
| *Gansurhinus* | 1 ? ? 1 ? 3 1 2 3 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 ? ? ? ? ? ? ? ? ? ? ? ? 2 1 1 ? ? ? 1 ? ? ? ? ? |
| *Captorhinikos valensis* | ? ? ? ? ? 1 1 2 3 0 2 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 0 0 ? ? ? ? ? ? ? ? 2 ? ? ? ? ? ? 2 1 ? ? ? ? ? ? ? ? ? ? |
| *Captorhinikos chozaensis* | 1 1 1 1 1 1 1 2 3 0 1 ? 0 ? ? 0 ? ? ? ? ? 1 ? ? ? ? ? ? ? 0 1 0 0 1 ? 0 ? ? ? ? ? 1 2 0 1 1 1 1 1 ? 1 1 1 1 2 1 0 ? 1 ? |
| *Reiszorhinus* | 1 1 1 1 0 1 0 0 0 0 0 0 0 0 1 1 1 0 1 0 1 0 0 1 1 0 1 ? ? ? ? ? ? ? ? ? ? ? ? 0 0 1 0 0 0 ? 0 ? ? ? ? ? ? ? ? ? ? ? 0 0 |
| *Opisthodontosaurus* | ? ? 0 1 1 3 0 0 3 0 0 ? ? ? 0 0 1 1 0 ? 0 1 ? ? ? ? ? ? 0 0 2 0 0 0 0 0 1 0 ? ? ? ? 0 1 0 0 1 0 1 ? 0 ? ? 1 1 0 ? ? 0 ? |
| *Labidosauriscus* | 1 1 1 1 1 2 0 0 1 0 0 1 0 0 0 1 ? ? ? ? ? 1 ? ? ? ? ? 2 1 0 2 0 0 1 1 1 1 0 ? ? ? ? 1 0 0 1 1 ? ? ? ? ? ? ? ? ? ? ? ? ? 1 |
| *Captorhinus kierani* | 1 1 1 1 1 1 0 0 1 0 1 1 0 0 ? 1 1 0 1 1 0 1 1 0 0 1 0 2 1 0 2 0 1 1 ? 1 1 1 1 0 0 0 1 1 0 1 0 1 ? 1 ? ? ? ? ? ? ? ? ? ? |

# Appendix 6

**New and/or redefined morphological characters for phylogenetic analysis.**

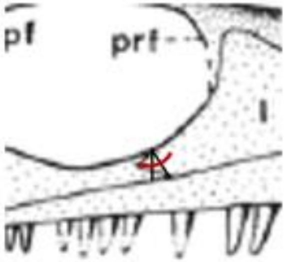
How to read the .ppt file diagrams:

1. Wherever there are ratios or comparisons lengths etc: **RED** compared to **GREEN**.
2. Otherwise, what is being measured is always in **RED**.
3. Auxiliary lines are in **BLACK** or in **BLUE**.

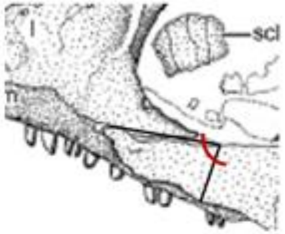
## (13 a) Lacrimal suture with jugal:

Angle with vertical axis < 60º (0)

Angle with vertical axis > 60º (1)

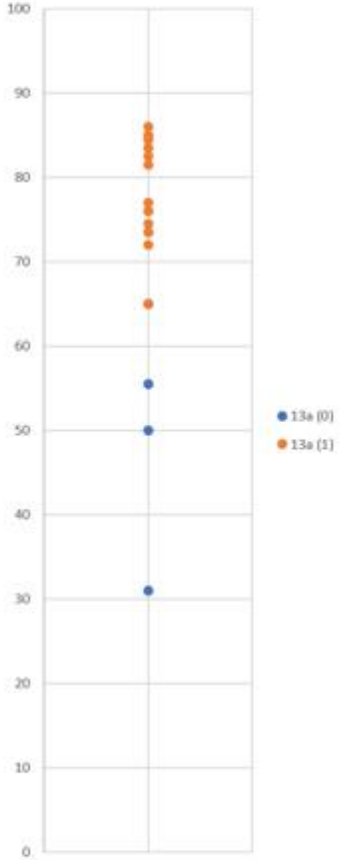


*Thuringothyris mahlendorffae*. Reconstruction. In Boy & Martens 1991.



*Reiszorhinus olsoni*. Reconstruction; holotype; FMNH UC183. In Sumida, Dodick et al 2010.

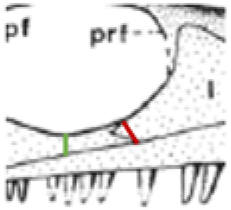
| CHARACTER 13 A | Angle | Character State |
|---|---|---|
| *Protorothyris* | NA | ? |
| *Paleothyris* | NA | ? |
| *Thuringothyris* | 31,0 | 0 |
| *Euconcordia* | 77,0 | 1 |
| *Romeria prima* | 72,0 | 1 |
| *Romeria texana* | 65,0 | 1 |
| *Protocaptorhinus* | 50,0 | 0 |
| *Rhiodenticulatus* | 86,0 | 1 |
| *Saurorictus* | 76,0 | 1 |
| *C. laticeps* | 73,5 | 1 |
| *C. aguti* | 83,5 | 1 |
| *C. magnus* | 84,5 | 1 |
| *Labidosaurus* | 81,5 | 1 |
| *Labidosaurikos* | 74,5 | 1 |
| *Moradisaurus* | No image/data | ? |
| *Rothianiscus* | No image/data | ? |
| *Gansurhinus* | No specimen | ? |
| *Captorhinikos valensis* | No specimen | ? |
| *Captorhinikos chozaensis* | 55,5 | 0 |
| *Reiszorhinus* | 73,5 | 1 |
| *Opisthodontosaurus* | 76,0 | 1 |
| *Labidosauriscus* | 82,5 | 1 |
| *C. kierani* | 85,0 | 1 |



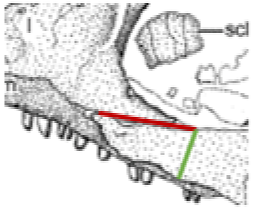
## (13 b) Lacrimal suture with jugal:

Ratio between the L-J suture length, and the jugal width at the orbital midpoint equal or < 2,24 (0)

Ratio between the L-J suture length, and the jugal width at the orbital midpoint > 2,24 (1)

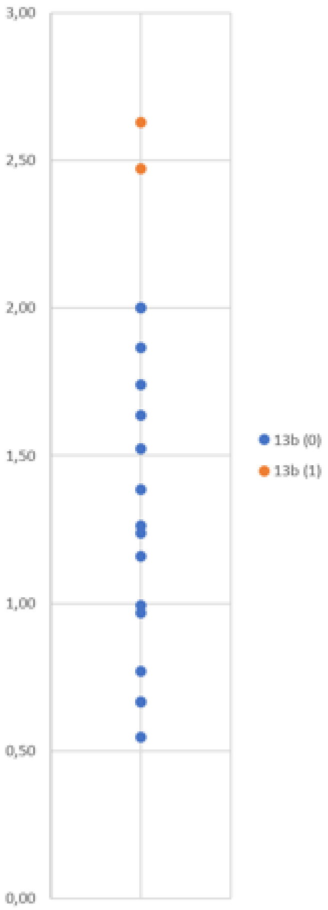


*Thuringothyris mahlendorffae.* Reconstruction. In Boy & Martens 1991.



*Reiszorhinus olsoni.* Reconstruction; holotype; FMNH UC183. In Sumida, Dodick et al 2010.

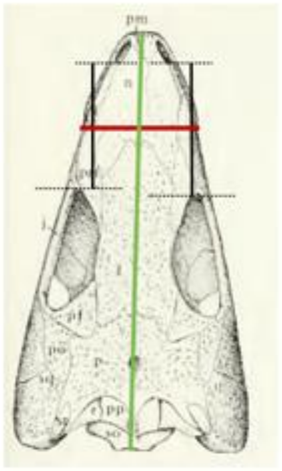
| CHARACTER 13 B | L-J suture length | Orbital midpoint-Jugal height | Ratio | Character state |
|---|---|---|---|---|
| ***Protorothyris*** | 0,04 | 0,07 | 0,55 | 0 |
| ***Paleothyris*** | NA | 0,01 | NA | ? |
| ***Thuringothyris*** | 0,08 | 0,07 | 1,24 | 1 |
| ***Euconcordia*** | 0,32 | 0,13 | 2,47 | 2 |
| ***Romeria prima*** | 0,11 | 0,05 | 2,00 | 2 |
| ***Romeria texana*** | 0,03 | 0,04 | 0,67 | 0 |
| ***Protocaptorhinus*** | 0,03 | 0,04 | 0,67 | 0 |
| ***Rhiodenticulatus*** | 0,43 | 0,26 | 1,64 | 1 |
| ***Saurorictus*** | 0,11 | 0,14 | 0,77 | 0 |
| ***C. laticeps*** | 0,23 | 0,23 | 0,99 | 0 |
| ***C. aguti*** | 0,11 | 0,06 | 2,00 | 2 |
| ***C. magnus*** | 0,79 | 0,68 | 1,16 | 1 |
| ***Labidosaurus*** | 2,50 | 1,98 | 1,26 | 1 |
| ***Labidosaurikos*** | 2,75 | 2,84 | 0,97 | 0 |
| ***Moradisaurus*** | No image/data | No image/data | NA | ? |
| ***Rothianiscus*** | No image/data | No image/data | NA | ? |
| ***Gansurhinus*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos valensis*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos chozaensis*** | 0,98 | 0,71 | 1,39 | 1 |
| ***Reiszorhinus*** | 1,31 | 0,75 | 1,74 | 1 |
| ***Opisthodontosaurus*** | 0,39 | 0,26 | 1,52 | 1 |
| ***Labidosauriscus*** | 0,52 | 0,20 | 2,63 | 2 |
| ***C. kierani*** | 0,76 | 0,41 | 1,87 | 1 |



## (15 a) Snout:

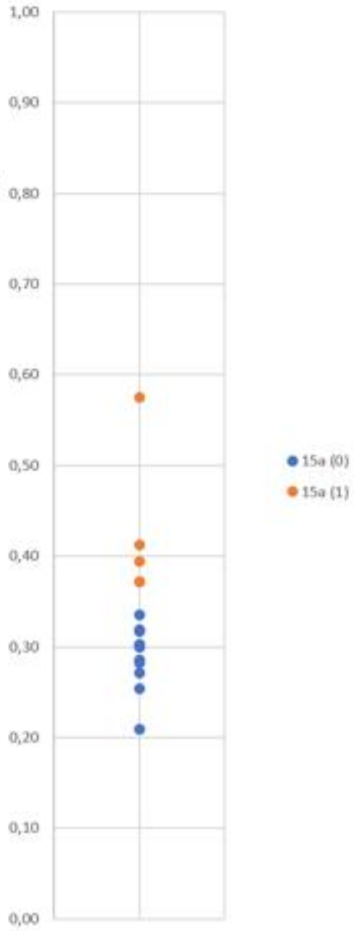
Ratio between ratio between cranium width at nostril-orbital midpoint and total cranium length < 0,36 (0)

Ratio between cranium width at nostril-orbital midpoint and total cranium length > 0,36 (1)



*Protorothyris archeri*. MCZ 2149. In Clark & Carroll 1972.

| CHARACTER 15 A | Width at nostril/orbit midpoint | Cranium length | Ratio | Character state |
|---|---|---|---|---|
| ***Protorothyris*** | 0,27 | 1,01 | 0,27 | 0 |
| ***Paleothyris*** | 0,11 | 0,37 | 0,30 | 0 |
| ***Thuringothyris*** | 0,99 | 2,39 | 0,41 | 1 |
| ***Euconcordia*** | 2,26 | 3,93 | 0,57 | 1 |
| ***Romeria prima*** | 0,29 | 1,04 | 0,28 | 0 |
| ***Romeria texana*** | 0,27 | 0,93 | 0,29 | 0 |
| ***Protocaptorhinus*** | 0,30 | 0,95 | 0,32 | 0 |
| ***Rhiodenticulatus*** | 1,44 | 4,29 | 0,34 | 0 |
| ***Saurorictus*** | 0,88 | 2,37 | 0,37 | 1 |
| ***C. laticeps*** | 1,88 | 5,90 | 0,32 | 0 |
| ***C. aguti*** | 1,95 | 4,96 | 0,39 | 1 |
| ***C. magnus*** | 2,86 | Issue with images/data | NA | ? |
| ***Labidosaurus*** | 4,87 | 19,22 | 0,25 | 0 |
| ***Labidosaurikos*** | 5,81 | 27,81 | 0,21 | 0 |
| ***Moradisaurus*** | Issue with images/data | 40,70 | NA | ? |
| ***Rothianiscus*** | 9,09 | Issue with images/data | NA | ? |
| ***Gansurhinus*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos valensis*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos chozaensis*** | 5,07 | 13,63 | 0,37 | 1 |
| ***Reiszorhinus*** | Issue with images/data | 12,73 | NA | ? |
| ***Opisthodontosaurus*** | Issue with images/data | Issue with images/data | NA | ? |
| ***Labidosauriscus*** | 1,30 | 4,34 | 0,30 | 0 |
| ***C. kierani*** | 2,02 | 6,67 | 0,30 | 0 |

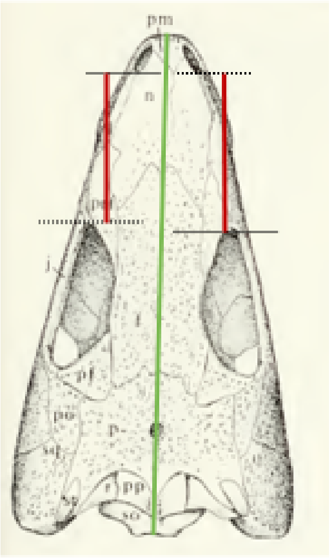


## (15 b) Snout:

Ratio between anterior cranium length at nostril-orbital midpoint and total cranium length > 0,28 (0)

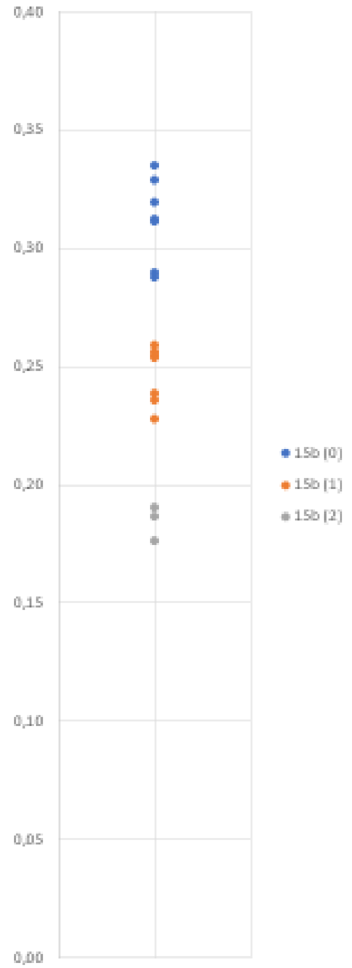
Ratio between anterior cranium length at nostril-orbital midpoint and total cranium length between 0,21 and 0,28 (1)

Ratio between anterior cranium length at nostril-orbital midpoint and total cranium length < 0,21 (2)



*Protorothyris archeri*. MCZ 2149. In Clark & Carroll 1972.

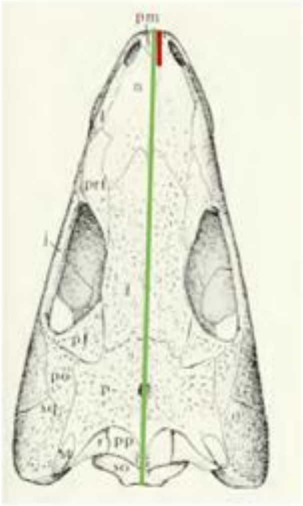
| CHARACTER 15 B | Length nostril/orbit midpoint | Cranium length | Ratio | Character state |
|---|---|---|---|---|
| ***Protorothyris*** | 0,31 | 1,01 | 0,31 | 0 |
| ***Paleothyris*** | 0,11 | 0,37 | 0,29 | 0 |
| ***Thuringothyris*** | 0,57 | 2,39 | 0,24 | 1 |
| ***Euconcordia*** | 0,69 | 3,93 | 0,18 | 2 |
| ***Romeria prima*** | 0,24 | 1,04 | 0,23 | 1 |
| ***Romeria texana*** | 0,27 | 0,93 | 0,29 | 0 |
| ***Protocaptorhinus*** | 0,24 | 0,95 | 0,25 | 1 |
| ***Rhiodenticulatus*** | 0,82 | 4,29 | 0,19 | 2 |
| ***Saurorictus*** | 0,44 | 2,37 | 0,19 | 2 |
| ***C. laticeps*** | 1,50 | 5,90 | 0,25 | 1 |
| ***C. aguti*** | 1,27 | 4,96 | 0,26 | 1 |
| ***C. magnus*** | 2,29 | Issue with images/data | NA | ? |
| ***Labidosaurus*** | 6,14 | 19,22 | 0,32 | 0 |
| ***Labidosaurikos*** | 9,31 | 27,81 | 0,33 | 0 |
| ***Moradisaurus*** | Issue with images/data | 40,70 | NA | ? |
| ***Rothianiscus*** | 5,53 | Issue with images/data | NA | ? |
| ***Gansurhinus*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos valensis*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos chozaensis*** | 4,48 | 13,63 | 0,33 | 0 |
| ***Reiszorhinus*** | 3,97 | 12,73 | 0,31 | 0 |
| ***Opisthodontosaurus*** | Issue with images/data | Issue with images/data | NA | ? |
| ***Labidosauriscus*** | 1,12 | 4,34 | 0,26 | 1 |
| ***C. kierani*** | 1,57 | 6,67 | 0,24 | 1 |



## (15 c) Snout:

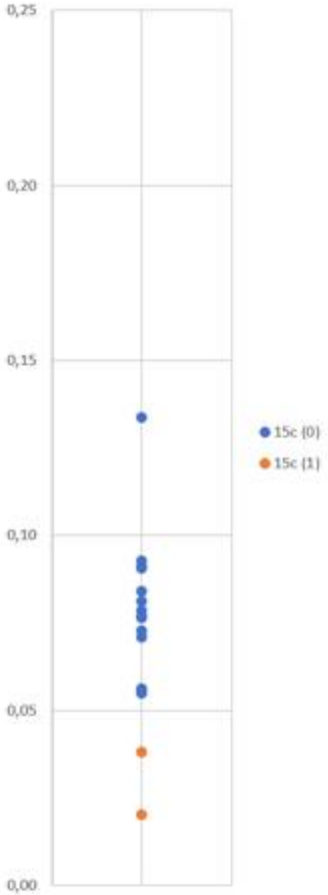
Ratio between premaxilla length in dorsal view and total cranium length > 0,05 (0)

Ratio between premaxilla length in dorsal view and total cranium length < 0,05 (1)



*Protorothyris archeri*. MCZ 2149. In Clark & Carroll 1972.

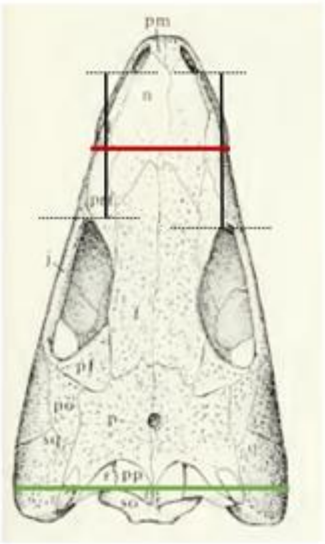
| CHARACTER 15 C | PM (most posterior point) length | Cranium length | Ratio | Character state |
|---|---|---|---|---|
| ***Protorothyris*** | 0,07 | 1,01 | 0,073 | 0 |
| ***Paleothyris*** | 0,02 | 0,37 | 0,055 | 0 |
| ***Thuringothyris*** | 0,19 | 2,39 | 0,081 | 0 |
| ***Euconcordia*** | Issue with images/data | 3,93 | NA | ? |
| ***Romeria prima*** | 0,08 | 1,04 | 0,077 | 0 |
| ***Romeria texana*** | 0,09 | 0,93 | 0,093 | 0 |
| ***Protocaptorhinus*** | 0,05 | 0,95 | 0,056 | 0 |
| ***Rhiodenticulatus*** | 0,24 | 4,29 | 0,055 | 0 |
| ***Saurorictus*** | 0,32 | 2,37 | 0,134 | 0 |
| ***C. laticeps*** | 0,53 | 5,90 | 0,091 | 0 |
| ***C. aguti*** | 0,45 | 4,96 | 0,091 | 0 |
| ***C. magnus*** | 0,64 | Issue with images/data | NA | ? |
| ***Labidosaurus*** | 1,36 | 19,22 | 0,071 | 0 |
| ***Labidosaurikos*** | 0,56 | 27,81 | 0,020 | 1 |
| ***Moradisaurus*** | Issue with images/data | 40,70 | NA | ? |
| ***Rothianiscus*** | Issue with images/data | Issue with images/data | NA | ? |
| ***Gansurhinus*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos valensis*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos chozaensis*** | 0,52 | 13,63 | 0,038 | 1 |
| ***Reiszorhinus*** | 0,97 | 12,73 | 0,077 | 0 |
| ***Opisthodontosaurus*** | Issue with images/data | Issue with images/data | NA | ? |
| ***Labidosauriscus*** | 0,36 | 4,34 | 0,084 | 0 |
| ***C. kierani*** | 0,52 | 6,67 | 0,079 | 0 |



## (15 d) Snout:

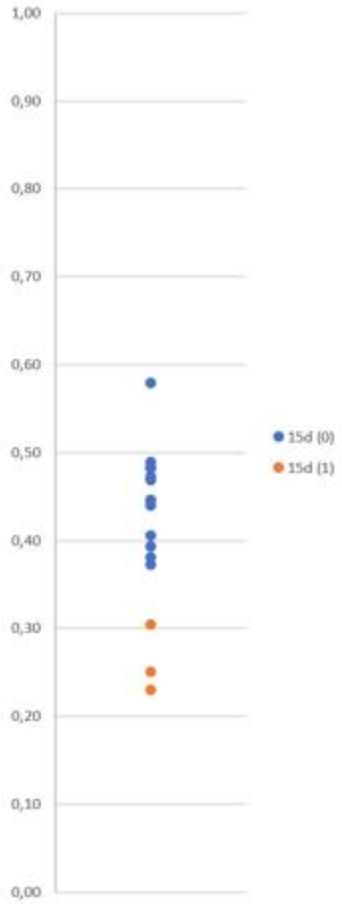
Broad; ratio between cranium width at nostril-orbital midpoint and broadest cranium width > 0,34 (0)

Narrow; ratio between cranium width at nostril-orbital midpoint and broadest cranium width < 0,34 (1)



*Protorothyris archeri*. MCZ 2149. In Clark & Carroll 1972.

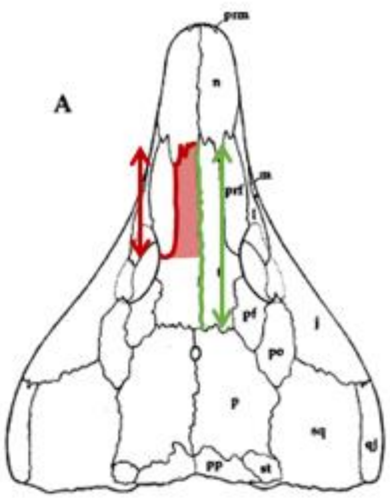
| CHARACTER 15 D | Width at nostril/orbit midpoint | Broadest cranium width | Ratio | Character state |
|---|---|---|---|---|
| ***Protorothyris*** | 0,27 | 0,57 | 0,48 | 0 |
| ***Paleothyris*** | 0,11 | 0,23 | 0,49 | 0 |
| ***Thuringothyris*** | 0,99 | 2,09 | 0,47 | 0 |
| ***Euconcordia*** | 2,26 | 3,90 | 0,58 | 0 |
| ***Romeria prima*** | 0,29 | 0,67 | 0,44 | 0 |
| ***Romeria texana*** | 0,27 | 0,70 | 0,38 | 0 |
| ***Protocaptorhinus*** | 0,30 | 0,67 | 0,45 | 0 |
| ***Rhiodenticulatus*** | 1,44 | 2,98 | 0,48 | 0 |
| ***Saurorictus*** | 0,88 | 1,88 | 0,47 | 0 |
| ***C. laticeps*** | 1,88 | 5,05 | 0,37 | 0 |
| ***C. aguti*** | 1,95 | 2,47 | 0,45 | 0 |
| ***C. magnus*** | 2,86 | Issue with images/data | NA | ? |
| ***Labidosaurus*** | 3,77 | 15,97 | 0,30 | 1 |
| ***Labidosaurikos*** | 0,58 | 2,32 | 0,25 | 1 |
| ***Moradisaurus*** | Issue with images/data | 39,54 | NA | ? |
| ***Rothianiscus*** | 9,09 | 39,55 | 0,23 | 1 |
| ***Gansurhinus*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos valensis*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos chozaensis*** | 5,07 | 12,50 | 0,41 | 0 |
| ***Reiszorhinus*** | Issue with images/data | Issue with images/data | NA | ? |
| ***Opisthodontosaurus*** | Issue with images/data | Issue with images/data | NA | ? |
| ***Labidosauriscus*** | 1,30 | Issue with images/data | NA | ? |
| ***C. kierani*** | 2,02 | 5,13 | 0,39 | 0 |



## (18 a) Frontal – anterior process:

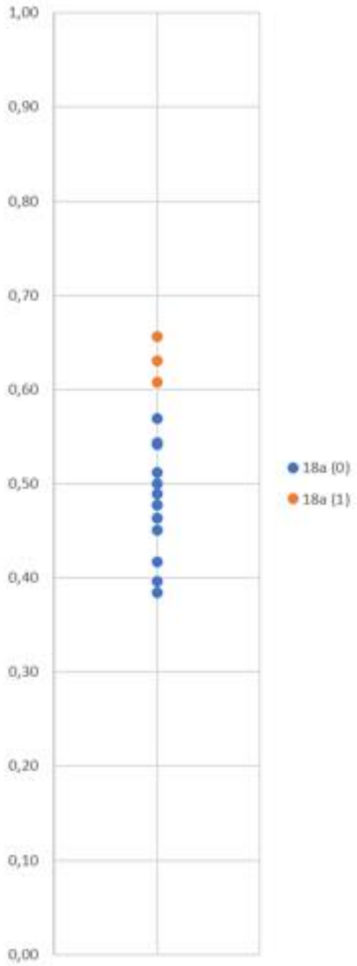
Short, less than 0,59 of the frontal sagittal length (0)

Long, 0,59 or more of the frontal sagittal length (1)



*Labidosaurikos meachami.* Reconstruction; Holotype OMNH 04331. In Dodick & Modesto 1995.

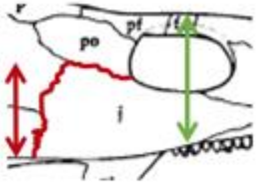
| CHARACTER 18 | Anterior process of the frontal length | Frontal saggital length | Ratio | Character state |
|---|---|---|---|---|
| ***Protorothyris*** | 0,41 | 1,00 | 0,50 | 0 |
| ***Paleothyris*** | 0,15 | 1,00 | 0,42 | 0 |
| ***Thuringothyris*** | 0,94 | 1,00 | 0,51 | 0 |
| ***Euconcordia*** | 1,46 | 1,00 | 0,45 | 0 |
| ***Romeria prima*** | 0,35 | 1,00 | 0,40 | 0 |
| ***Romeria texana*** | 0,36 | Issues with images/data | NA | ? |
| ***Protocaptorhinus*** | 0,37 | 1,00 | 0,46 | 0 |
| ***Rhiodenticulatus*** | 1,68 | 1,00 | 0,61 | 1 |
| ***Sauroricius*** | 0,70 | 1,00 | 0,66 | 1 |
| ***C. laticeps*** | 2,05 | 1,00 | 0,38 | 0 |
| ***C. aguti*** | 1,98 | 1,00 | 0,49 | 0 |
| ***C. magnus*** | 3,27 | 1,00 | 0,54 | 0 |
| ***Labidosaurus*** | 7,53 | 1,00 | 0,54 | 0 |
| ***Labidosaurikos*** | 12,00 | 1,00 | 0,63 | 1 |
| ***Moradisaurus*** | Issue with images/data | Issue with images/data | NA | ? |
| ***Rothianiscus*** | Issue with images/data | Issue with images/data | NA | ? |
| ***Gansurhinus*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos valensis*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos chozaensis*** | Issue with images/data | Issue with images/data | NA | ? |
| ***Reiszorhinus*** | 4,31 | 1,00 | 0,57 | 0 |
| ***Opisthodontosaurus*** | Issue with images/data | Issue with images/data | NA | ? |
| ***Labidosauriscus*** | Issue with images/data | Issue with images/data | NA | ? |
| ***C. kierani*** | 2,37 | 1,00 | 0,48 | 0 |



## (19a) Jugal – subtemporal process height:

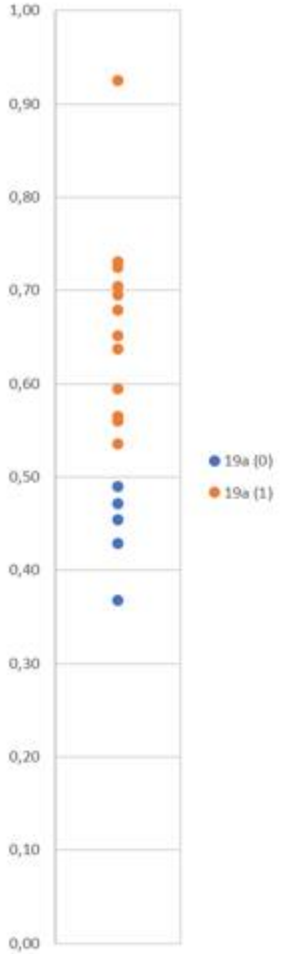
Dorsoventrally low, equal to or less than 0,52 of skull height through orbital midpoint (0)

Dorsoventrally deep, at least 0,52 of skull height through orbital midpoint (1)



*Labidosaurikos meachami.* Reconstruction; Holotype OMNH 04331. In Dodick & Modesto 1995.

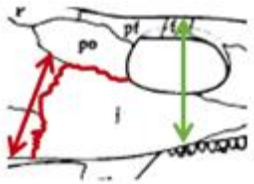
| CHARACTER 19a | Jugal's subtemporal process height | Skull height at orbital midpoint | Ratio | Character status |
|---|---|---|---|---|
| ***Protorothyris*** | 0,17 | 0,340 | 0,49 | 0 |
| ***Paleothyris*** | 0,05 | 0,105 | 0,43 | 0 |
| ***Thuringothyris*** | 0,32 | 0,601 | 0,54 | 1 |
| ***Euconcordia*** | 0,59 | 1,593 | 0,37 | 0 |
| ***Romeria prima*** | 0,25 | 0,347 | 0,73 | 1 |
| ***Romeria texana*** | 0,21 | 0,307 | 0,70 | 1 |
| ***Protocaptorhinus*** | 0,13 | 0,293 | 0,45 | 0 |
| ***Rhiodenticulatus*** | 0,72 | 1,100 | 0,65 | 1 |
| ***Saurorictus*** | 0,30 | 0,430 | 0,70 | 1 |
| ***C. laticeps*** | 0,86 | 1,356 | 0,64 | 1 |
| ***C. aguti*** | 0,18 | 0,296 | 0,59 | 1 |
| ***C. magnus*** | 1,66 | 2,967 | 0,56 | 1 |
| ***Labidosaurus*** | 4,38 | 4,740 | 0,92 | 1 |
| ***Labidosaurikos*** | 4,78 | 6,594 | 0,73 | 1 |
| ***Moradisaurus*** | No image/data | No image/data | NA | ? |
| ***Rothianiscus*** | No image/data | No image/data | NA | ? |
| ***Gansurhinus*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos valensis*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos chozaensis*** | No image/data | 3,821 | NA | ? |
| ***Reiszorhinus*** | 2,53 | 4,481 | 0,57 | 1 |
| ***Opisthodontosaurus*** | 0,91 | 1,936 | 0,47 | 0 |
| ***Labidosauriscus*** | No image/data | 1,528 | NA | ? |
| ***C. kierani*** | 1,25 | 1,844 | 0,68 | 1 |



## (19b) Jugal – subtemporal process length:

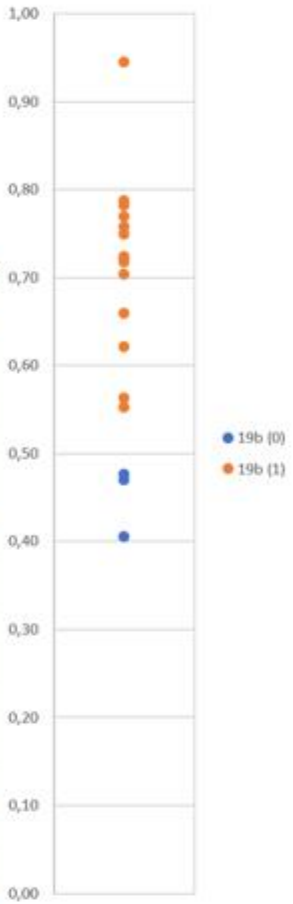
Dorsoventrally low, equal to or less than 0,52 of skull height through orbital midpoint (0)

Dorsoventrally deep, at least 0,52 of skull height through orbital midpoint (1)



*Labidosaurikos meachami.* Reconstruction; Holotype OMNH 04331. In Dodick & Modesto 1995.

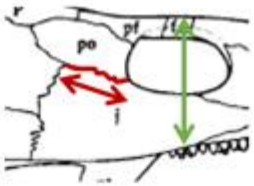
| CHARACTER 19b | Jugal's subtemporal process length | Skull height at orbital midpoint | Ratio | Character status |
|---|---|---|---|---|
| ***Protorothyris*** | 0,16 | 0,340 | 0,47 | 0 |
| ***Paleothyris*** | 0,05 | 0,105 | 0,48 | 0 |
| ***Thuringothyris*** | 0,47 | 0,601 | 0,79 | 1 |
| ***Euconcordia*** | 0,65 | 1,593 | 0,41 | 0 |
| ***Romeria prima*** | 0,27 | 0,347 | 0,77 | 1 |
| ***Romeria texana*** | 0,24 | 0,307 | 0,78 | 1 |
| ***Protocaptorhinus*** | 0,19 | 0,293 | 0,66 | 1 |
| ***Rhiodenticulatus*** | 0,79 | 1,100 | 0,72 | 1 |
| ***Saurorictus*** | 0,30 | 0,430 | 0,70 | 1 |
| ***C. laticeps*** | 1,02 | 1,356 | 0,75 | 1 |
| ***C. aguti*** | 0,18 | 0,296 | 0,62 | 1 |
| ***C. magnus*** | 1,64 | 2,967 | 0,55 | 1 |
| ***Labidosaurus*** | 4,48 | 4,740 | 0,95 | 1 |
| ***Labidosaurikos*** | 5,00 | 6,594 | 0,76 | 1 |
| ***Moradisaurus*** | No image/data | No image/data | NA | ? |
| ***Rothianiscus*** | No image/data | No image/data | NA | ? |
| ***Gansurhinus*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos valensis*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos chozaensis*** | No image/data | 3,821 | NA | ? |
| ***Reiszorhinus*** | 3,25 | 4,481 | 0,72 | 1 |
| ***Opisthodontosaurus*** | 1,09 | 1,936 | 0,56 | 1 |
| ***Labidosauriscus*** | No image/data | 1,528 | NA | ? |
| ***C. kierani*** | 1,32 | 1,844 | 0,72 | 1 |



# (19c) Jugal-Postorbital suture length:

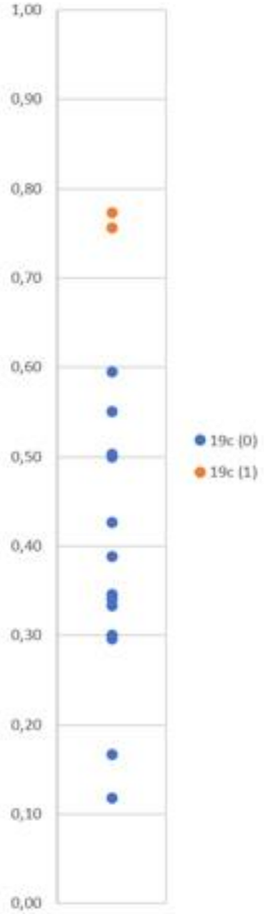
Short, equal to or less than 0,68 of skull height through orbital midpoint (0)

Long, at least 0,68 of skull height through orbital midpoint (1)



*Labidosaurikos meachami*. Reconstruction; Holotype OMNH 04331. In Dodick & Modesto 1995.

| CHARACTER 19c | Length of J-PO suture | Skull height at orbital midpoint | Ratio | Character status |
|---|---|---|---|---|
| ***Protorothyris*** | 0,11 | 0,34 | 0,33 | 0 |
| ***Paleothyris*** | 0,02 | 0,11 | 0,17 | 0 |
| ***Thuringothyris*** | 0,07 | 0,60 | 0,12 | 0 |
| ***Euconcordia*** | NA | 1,59 | NA | ? |
| ***Romeria prima*** | 0,12 | 0,35 | 0,35 | 0 |
| ***Romeria texana*** | 0,15 | 0,31 | 0,50 | 0 |
| ***Protocaptorhinus*** | 0,09 | 0,29 | 0,30 | 0 |
| ***Rhiodenticulatus*** | 0,47 | 1,10 | 0,43 | 0 |
| ***Saurorictus*** | 0,17 | 0,43 | 0,39 | 0 |
| ***C. laticeps*** | 1,03 | 1,36 | 0,76 | 1 |
| ***C. aguti*** | 0,18 | 0,30 | 0,59 | 0 |
| ***C. magnus*** | 0,89 | 2,97 | 0,30 | 0 |
| ***Labidosaurus*** | 2,61 | 4,74 | 0,55 | 0 |
| ***Labidosaurikos*** | 3,31 | 6,59 | 0,50 | 0 |
| ***Moradisaurus*** | No image/data | No image/data | NA | ? |
| ***Rothianiscus*** | No image/data | No image/data | NA | ? |
| ***Gansurhinus*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos valensis*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos chozaensis*** | No image/data | 3,82 | NA | ? |
| ***Reiszorhinus*** | No image/data | 4,48 | NA | ? |
| ***Opisthodontosaurus*** | 0,66 | 1,94 | 0,34 | 0 |
| ***Labidosauriscus*** | No image/data | 1,53 | NA | ? |
| ***C. kierani*** | 1,43 | 1,84 | 0,77 | 1 |



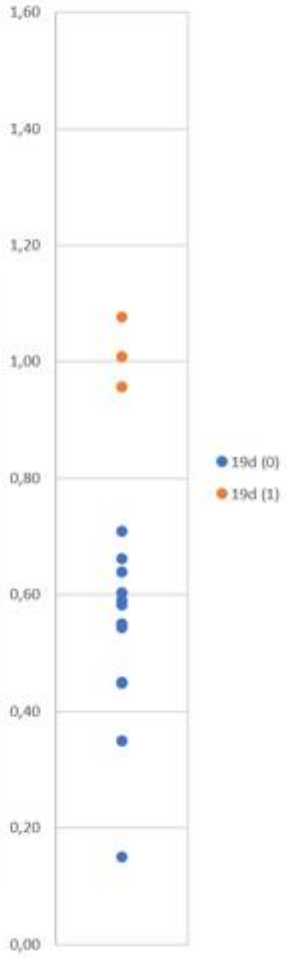
## (19d) Jugal-Postorbital suture length:

Short, less than 0,84 of jugal’s subtemporal process length (0)

Long, equal or more than 0,84 of jugal’s subtemporal process length (1)

*Labidosaurikos meachami.* Reconstruction; Holotype OMNH 04331. In Dodick & Modesto 1995.

| CHARACTER 19d | Length of J-PO suture | Jugal's subtemporal process length | Ratio | Character status |
|---|---|---|---|---|
| ***Protorothyris*** | 0,113 | 0,160 | 0,71 | 0 |
| ***Paleothyris*** | 0,018 | 0,050 | 0,35 | 0 |
| ***Thuringothyris*** | 0,071 | 0,473 | 0,15 | 0 |
| ***Euconcordia*** | NA | 0,646 | NA | ? |
| ***Romeria prima*** | 0,120 | 0,267 | 0,45 | 0 |
| ***Romeria texana*** | 0,153 | 0,240 | 0,64 | 0 |
| ***Protocaptorhinus*** | 0,087 | 0,193 | 0,45 | 0 |
| ***Rhiodenticulatus*** | 0,469 | 0,794 | 0,59 | 0 |
| ***Saurorictus*** | 0,167 | 0,303 | 0,55 | 0 |
| ***C. laticeps*** | 1,025 | 1,017 | 1,01 | 1 |
| ***C. aguti*** | 0,176 | 0,184 | 0,96 | 1 |
| ***C. magnus*** | 0,891 | 1,641 | 0,54 | 0 |
| ***Labidosaurus*** | 2,610 | 4,481 | 0,58 | 0 |
| ***Labidosaurikos*** | 3,313 | 5,000 | 0,66 | 0 |
| ***Moradisaurus*** | No image/data | No image/data | NA | ? |
| ***Rothianiscus*** | No image/data | No image/data | NA | ? |
| ***Gansurhinus*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos valensis*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos chozaensis*** | No image/data | No image/data | NA | ? |
| ***Reiszorhinus*** | No image/data | 3,25 | NA | ? |
| ***Opisthodontosaurus*** | 0,659 | 1,09 | 0,60 | 0 |
| ***Labidosauriscus*** | No image/data | No image/data | NA | ? |
| ***C. kierani*** | 1,426 | 1,32 | 1,08 | 1 |



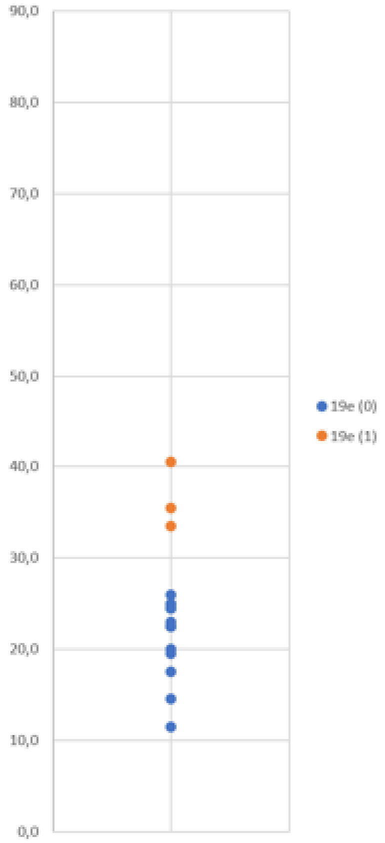
## (19e) Jugal-Postorbital suture:

Angle with lower limit of orbit midpoint smaller than 30º (0)

Angle with lower limit of orbit midpoint equal or bigger than 30º (1)

*Labidosaurikos meachami*.
Reconstruction; Holotype OMNH 04331.
In Dodick & Modesto 1995.

| CHARACTER 19e | Angle | Character status |
|---|---|---|
| *Protorothyris* | 24,5 | 0 |
| *Paleothyris* | 23,0 | 0 |
| *Thuringothyris* | 22,5 | 0 |
| *Euconcordia* | 20,0 | 0 |
| *Romeria prima* | 35,5 | 1 |
| *Romeria texana* | 33,5 | 1 |
| *Protocaptorhinus* | 25,0 | 0 |
| *Rhiodenticulatus* | 24,5 | 0 |
| *Saurorictus* | 11,5 | 0 |
| *C. laticeps* | 22,5 | 0 |
| *C. aguti* | 19,5 | 0 |
| *C. magnus* | 22,5 | 0 |
| *Labidosaurus* | 40,5 | 1 |
| *Labidosaurikos* | 14,5 | 0 |
| *Moradisaurus* | No image/data | ? |
| *Rothianiscus* | No image/data | ? |
| *Gansurhinus* | No specimen | ? |
| *Captorhinikos valensis* | No specimen | ? |
| *Captorhinikos chozaensis* | No image/data | ? |
| *Reiszorhinus* | 26,0 | 0 |
| *Opisthodontosaurus* | 17,5 | 0 |
| *Labidosauriscus* | No image/data | ? |
| *C. kierani* | 25,0 | 0 |

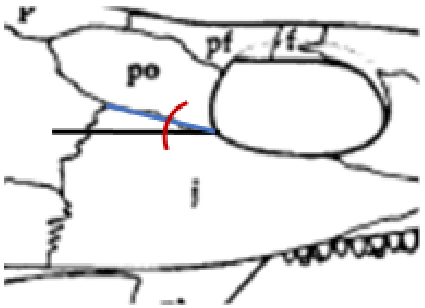


## (19f) Jugal-Postorbital suture:

Angle with dorsal plan bigger than 33º (0)

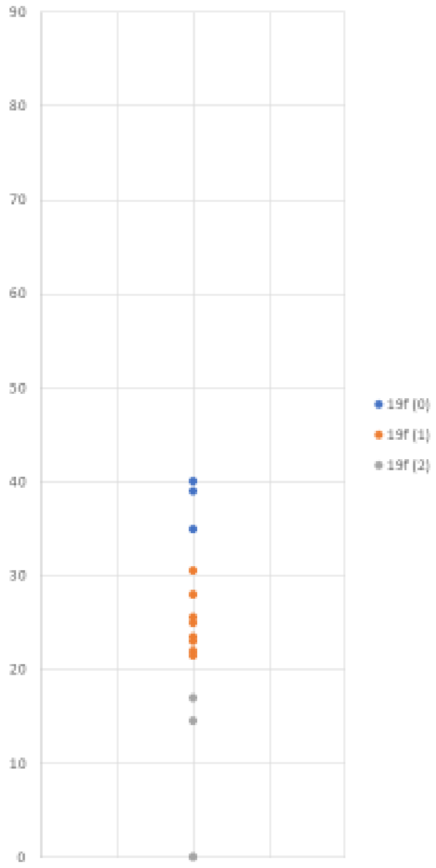
Angle with dorsal plan between 19º and 33º (1)

Angle with dorsal plan smaller than 19º (2)



*Labidosaurikos meachami*.
Reconstruction; Holotype OMNH 04331.
In Dodick & Modesto 1995.

| CHARACTER 19f | Angle | Character status |
|---|---|---|
| *Protorothyris* | 35 | 0 |
| *Paleothyris* | 0 | 2 |
| *Thuringothyris* | 0 | 2 |
| *Euconcordia* | NA | ? |
| *Romeria prima* | 39 | 0 |
| *Romeria texana* | 40 | 0 |
| *Protocaptorhinus* | 22 | 1 |
| *Rhiodenticulatus* | 28 | 1 |
| *Saurorictus* | 0 | 2 |
| *C. laticeps* | 25 | 1 |
| *C. aguti* | 21,5 | 1 |
| *C. magnus* | 23 | 1 |
| *Labidosaurus* | 23,5 | 1 |
| *Labidosaurikos* | 14,5 | 2 |
| *Moradisaurus* | No image/data | ? |
| *Rothianiscus* | No image/data | ? |
| *Gansurhinus* | No specimen | ? |
| *Captorhinikos valensis* | No specimen | ? |
| *Captorhinikos chozaensis* | No image/data | ? |
| *Reiszorhinus* | 30,5 | 1 |
| *Opisthodontosaurus* | 17 | 2 |
| *Labidosauriscus* | No image/data | ? |
| *C. kierani* | 25,5 | 1 |

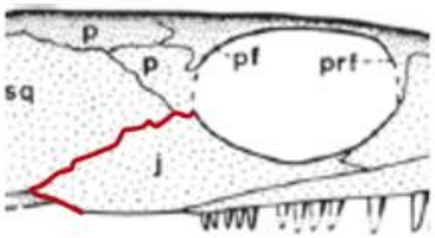


## (19g) Jugal – subtemporal process shape:

Fanning out (0)

Descending (1)

*Labidosaurikos meachami*. Reconstruction; Holotype OMNH 04331. In Dodick & Modesto 1995.



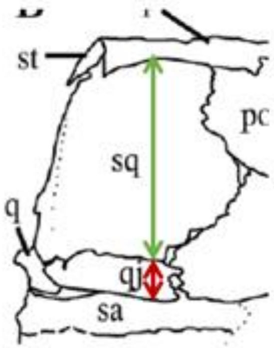
*Thuringothyris mahlendorffae*. Holotype; Museum of Nature in Gotha, Germany, Nr. 7729-1 to 3. In Boy & Martins 1991.

| CHARACTER 19g | Shape | Character status |
|---|---|---|
| ***Protorothyris*** | Fanning out | 0 |
| ***Paleothyris*** | Descending | 1 |
| ***Thuringothyris*** | Descending | 1 |
| ***Euconcordia*** | Descending | 1 |
| ***Romeria prima*** | Fanning out | 0 |
| ***Romeria texana*** | Descending | 1 |
| ***Protocaptorhinus*** | Descending | 1 |
| ***Rhiodenticulatus*** | Fanning out | 0 |
| ***Saurorictus*** | Fanning out | 0 |
| ***C. laticeps*** | Descending | 1 |
| ***C. aguti*** | Fanning out | 0 |
| ***C. magnus*** | Descending | 1 |
| ***Labidosaurus*** | Fanning out | 0 |
| ***Labidosaurikos*** | Fanning out | 0 |
| ***Moradisaurus*** | No image/data | ? |
| ***Rothianiscus*** | No image/data | ? |
| ***Gansurhinus*** | No specimen | ? |
| ***Captorhinikos valensis*** | No specimen | ? |
| ***Captorhinikos chozaensis*** | No image/data | ? |
| ***Reiszorhinus*** | Descending | 1 |
| ***Opisthodontosaurus*** | Descending | 1 |
| ***Labidosauriscus*** | No image/data | ? |
| ***C. kierani*** | Fanning out | 0 |

## (25a) Quadratojugal – maximum height vs squamosal height:

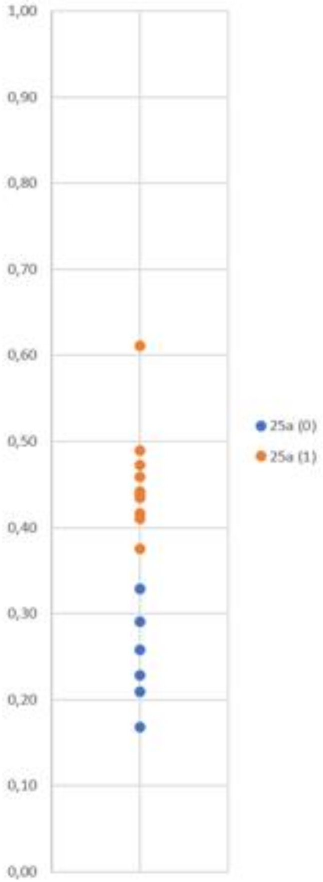
Approximately equal to or less than 0,36 (0)

More than 0,36 (1)



*Captorhinus magnus*. OMNH 56821. In Kissel, Dilkes & Reisz 2002.

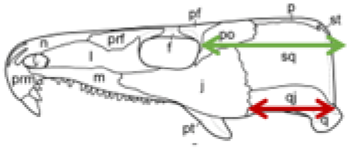
| CHARACTER 25a | Quadratojugal height | Squamosal height | Ratio | Character status |
|---|---|---|---|---|
| ***Protorothyris*** | 0,06 | 0,21 | 0,29 | 0 |
| ***Paleothyris*** | 0,02 | 0,06 | 0,38 | 1 |
| ***Thuringothyris*** | 0,16 | 0,35 | 0,44 | 1 |
| ***Euconcordia*** | No image/data | 0,93 | NA | ? |
| ***Romeria prima*** | 0,11 | 0,24 | 0,47 | 1 |
| ***Romeria texana*** | 0,05 | 0,23 | 0,23 | 0 |
| ***Protocaptorhinus*** | 0,05 | 0,21 | 0,26 | 0 |
| ***Rhiodenticulatus*** | 0,30 | 0,61 | 0,49 | 1 |
| ***Saurorictus*** | 0,11 | 0,32 | 0,33 | 0 |
| ***C. laticeps*** | 0,38 | 0,83 | 0,46 | 1 |
| ***C. aguti*** | 0,08 | 0,18 | 0,43 | 1 |
| ***C. magnus*** | 0,51 | 2,45 | 0,21 | 0 |
| ***Labidosaurus*** | 1,62 | 3,96 | 0,41 | 1 |
| ***Labidosaurikos*** | 2,77 | 4,53 | 0,61 | 1 |
| ***Moradisaurus*** | No image/data | No image/data | NA | ? |
| ***Rothianiscus*** | No image/data | No image/data | NA | ? |
| ***Gansurhinus*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos valensis*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos chozaensis*** |  | No image/data | NA | ? |
| ***Reiszorhinus*** | 1,15 | 2,62 | 0,44 | 1 |
| ***Opisthodontosaurus*** | 0,18 | 1,04 | 0,17 | 0 |
| ***Labidosauriscus*** | No image/data | No image/data | NA | ? |
| ***C. kierani*** | 0,38 | 0,90 | 0,42 | 1 |



# (25b) Quadratojugal – maximum length vs cranium length (posterior to orbit):

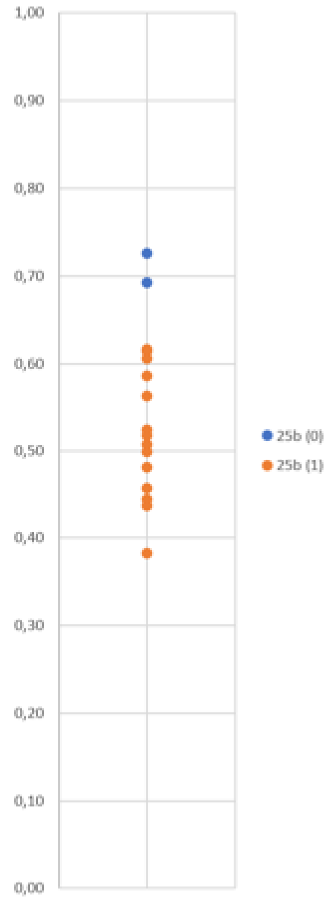
More than 0,66 (0)

Equal to or less than 0,66 (1)



*Labidosaurus hamatus.* Reconstruction. In Modesto, Scott et al 2007.

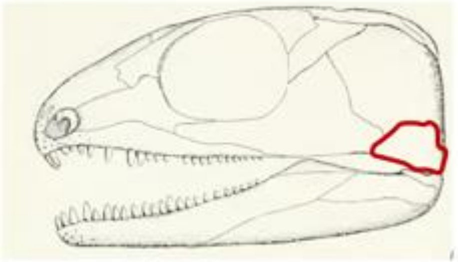
| CHARACTER 25b | QJ length | Cranium length (posterior to orbit) | Ratio | Character status |
|---|---|---|---|---|
| ***Protorothyris*** | 0,25 | 0,34 | 0,73 | 0 |
| ***Paleothyris*** | 0,09 | 0,13 | 0,69 | 0 |
| ***Thuringothyris*** | 0,57 | 1,01 | 0,56 | 1 |
| ***Euconcordia*** | NA | 1,55 | NA | ? |
| ***Romeria prima*** | 0,17 | 0,38 | 0,46 | 1 |
| ***Romeria texana*** | 0,21 | 0,41 | 0,51 | 1 |
| ***Protocaptorhinus*** | 0,16 | 0,36 | 0,44 | 1 |
| ***Rhiodenticulatus*** | 1,21 | 1,96 | 0,62 | 1 |
| ***Saurorictus*** | 0,31 | 0,80 | 0,38 | 1 |
| ***C. laticeps*** | 1,37 | 2,62 | 0,52 | 1 |
| ***C. aguti*** | 0,22 | 0,43 | 0,52 | 1 |
| ***C. magnus*** | 1,85 | 3,85 | 0,48 | 1 |
| ***Labidosaurus*** | 5,45 | 8,88 | 0,61 | 1 |
| ***Labidosaurikos*** | 7,16 | 11,81 | 0,61 | 1 |
| ***Moradisaurus*** | No image/data | No image/data | NA | ? |
| ***Rothianiscus*** | No image/data | No image/data | NA | ? |
| ***Gansurhinus*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos valensis*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos chozaensis*** | No image/data | No image/data | NA | ? |
| ***Reiszorhinus*** | 2,86 | 5,72 | 0,50 | 1 |
| ***Opisthodontosaurus*** | 0,88 | 2,01 | 0,44 | 1 |
| ***Labidosauriscus*** | No image/data | No image/data | NA | ? |
| ***C. kierani*** | 1,70 | 2,91 | 0,59 | 1 |



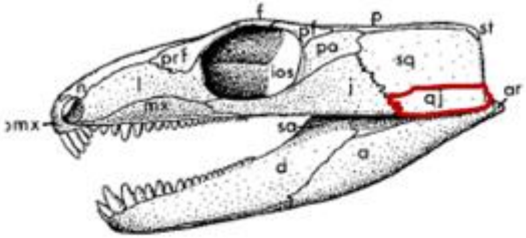
# (25c) Quadratojugal – anterior process shape:

Acuminate (0)

Square (1)



*Romeria prima*. Reconstruction; MCZ 1963. In Clark & Carroll 1972.



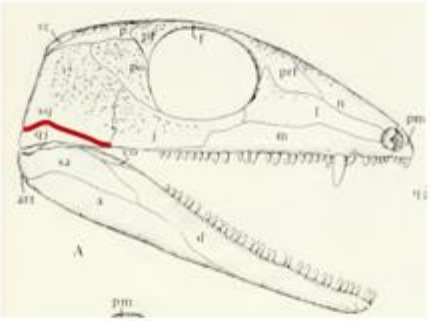
*Captorhinus laticeps*. Reconstruction. In Heaton 1979.

| CHARACTER 25c | Shape | Character status |
|---|---|---|
| ***Protorothyris*** | Acuminate | 0 |
| ***Paleothyris*** | Acuminate | 0 |
| ***Thuringothyris*** | Square | 1 |
| ***Euconcordia*** | NA | NA |
| ***Romeria prima*** | Acuminate | 0 |
| ***Romeria texana*** | Acuminate | 0 |
| ***Protocaptorhinus*** | Acuminate | 0 |
| ***Rhiodenticulatus*** | Square | 1 |
| ***Saurorictus*** | Square | 1 |
| ***C. laticeps*** | Square | 1 |
| ***C. aguti*** | Square | 1 |
| ***C. magnus*** | Square | 1 |
| ***Labidosaurus*** | Acuminate | 0 |
| ***Labidosaurikos*** | Square | 1 |
| ***Moradisaurus*** | No image/data | NA |
| ***Rothianiscus*** | No image/data | NA |
| ***Gansurhinus*** | No specimen | NA |
| ***Captorhinikos valensis*** | No specimen | NA |
| ***Captorhinikos chozaensis*** | No image/data | NA |
| ***Reiszorhinus*** | Acuminate | 0 |
| ***Opisthodontosaurus*** | Square | 1 |
| ***Labidosauriscus*** | No image/data | NA |
| ***C. kierani*** | Square | 1 |

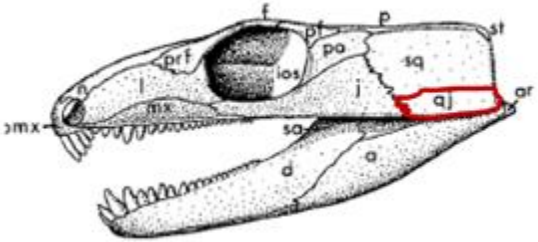
## (25d) Quadratojugal – longitudinal shape:

Elevated (0)

Not elevated/straight (1)



*Protorothyris archeri*. Reconstruction.
In Clark & Carroll 1972.



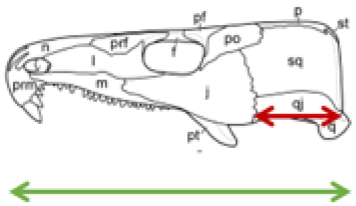
*Captorhinus laticeps*. Reconstruction.
In Heaton 1979.

| CHARACTER 25d | Shape | Character status |
|---|---|---|
| ***Protorothyris*** | Elevated | 0 |
| ***Paleothyris*** | Elevated | 0 |
| ***Thuringothyris*** | Straight | 1 |
| ***Euconcordia*** | NA | NA |
| ***Romeria prima*** | Elevated | 0 |
| ***Romeria texana*** | Elevated | 0 |
| ***Protocaptorhinus*** | Elevated | 0 |
| ***Rhiodenticulatus*** | Straight | 1 |
| ***Sauroictus*** | Straight | 1 |
| ***C. laticeps*** | Straight | 1 |
| ***C. aguti*** | Elevated | 0 |
| ***C. magnus*** | Straight | 1 |
| ***Labidosaurus*** | Straight | 1 |
| ***Labidosaurikos*** | Straight | 1 |
| ***Moradisaurus*** | No image/data | NA |
| ***Rothianiscus*** | No image/data | NA |
| ***Gansurhinus*** | No specimen | NA |
| ***Captorhinikos valensis*** | No specimen | NA |
| ***Captorhinikos chozaensis*** | No image/data | NA |
| ***Reiszorhinus*** | Elevated | 0 |
| ***Opisthodontosaurus*** | Straight | 1 |
| ***Labidosauriscus*** | No image/data | NA |
| ***C. kierani*** | Straight | 1 |

# (25e) Quadratojugal – maximum length vs total cranium length:

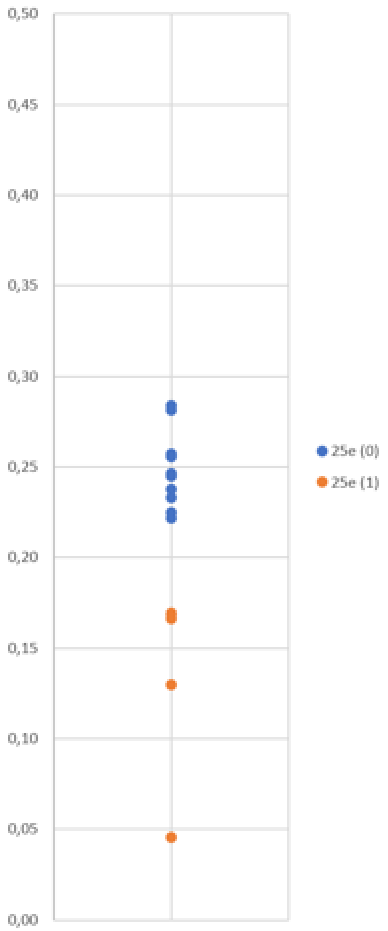
More than 0,2 (0)

Equal to or less than 0,2 (1)



*Labidosaurus hamatus*. Reconstruction. In Modesto, Scott et al 2007.

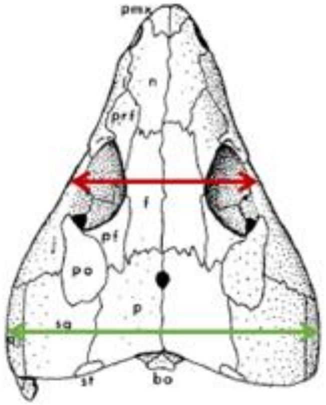
| CHARACTER 25e | QJ length | Cranium length (total | Ratio | Character status |
|---|---|---|---|---|
| ***Protorothyris*** | 0,25 | 1,01 | 0,25 | 0 |
| ***Paleothyris*** | 0,09 | 0,37 | 0,25 | 0 |
| ***Thuringothyris*** | 0,57 | 2,39 | 0,24 | 0 |
| ***Euconcordia*** | NA | 3,93 | NA | ? |
| ***Romeria prima*** | 0,17 | 1,04 | 0,17 | 1 |
| ***Romeria texana*** | 0,21 | 0,93 | 0,22 | 0 |
| ***Protocaptorhinus*** | 0,16 | 0,95 | 0,17 | 1 |
| ***Rhiodenticulatus*** | 1,21 | 4,29 | 0,28 | 0 |
| ***Saurorictus*** | 0,31 | 2,37 | 0,13 | 1 |
| ***C. laticeps*** | 1,37 | 5,90 | 0,23 | 0 |
| ***C. aguti*** | 0,22 | 4,96 | 0,05 | 1 |
| ***C. magnus*** | 1,85 | Issue with images/data | NA | ? |
| ***Labidosaurus*** | 5,45 | 19,22 | 0,28 | 0 |
| ***Labidosaurikos*** | 7,16 | 27,81 | 0,26 | 0 |
| ***Moradisaurus*** | No image/data | 40,70 | NA | ? |
| ***Rothianiscus*** | No image/data | Issue with images/data | NA | ? |
| ***Gansurhinus*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos valensis*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos chozaensis*** | No image/data | 13,63 | NA | ? |
| ***Reiszorhinus*** | 2,86 | 12,73 | 0,22 | 0 |
| ***Opisthodontosaurus*** | 0,88 | Issue with images/data | NA | ? |
| ***Labidosauriscus*** | No image/data | 4,34 | NA | ? |
| ***C. kierani*** | 1,70 | 6,67 | 0,26 | 0 |



## (26a) Postorbital cheek:

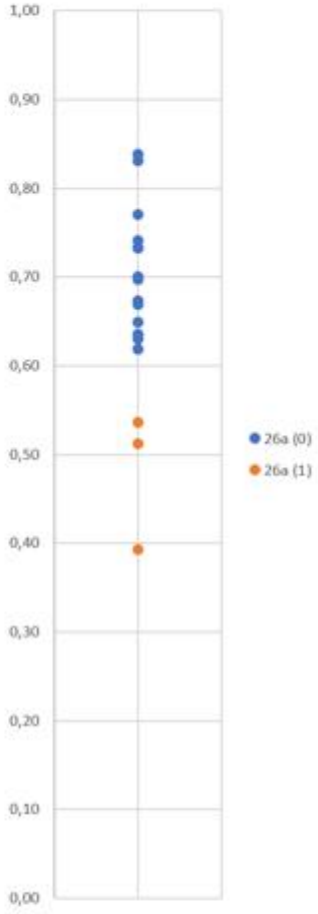
Not expanded laterally: ratio between width of cranium at midorbital point and largest cranium width > 0,58 (0)

Expanded laterally: ratio between width of cranium at midorbital point and largest cranium width < 0,58 (1)



*Captorhinus laticeps*.
Reconstruction. In Heaton 1979.

| CHARACTER 26 a | Cranium width at orbit midpoint | Broadest cranium width | Ratio | Character state |
|---|---|---|---|---|
| ***Protorothyris*** | 0,42 | 0,57 | 0,74 | 0 |
| ***Paleothyris*** | 0,17 | 0,23 | 0,73 | 0 |
| ***Thuringothyris*** | 1,45 | 2,09 | 0,70 | 0 |
| ***Euconcordia*** | 3,24 | 3,90 | 0,83 | 0 |
| ***Romeria prima*** | 0,47 | 0,67 | 0,70 | 0 |
| ***Romeria texana*** | 0,43 | 0,70 | 0,62 | 0 |
| ***Protocaptorhinus*** | 0,45 | 0,67 | 0,67 | 0 |
| ***Rhiodenticulatus*** | 2,18 | 2,98 | 0,73 | 0 |
| ***Saurorictus*** | 1,57 | 1,88 | 0,84 | 0 |
| ***C. laticeps*** | 3,19 | 5,05 | 0,63 | 0 |
| ***C. aguti*** | 3,37 | 4,37 | 0,77 | 0 |
| ***C. magnus*** | Issue with images/data | Issue with images/data | NA | ? |
| ***Labidosaurus*** | 8,57 | 15,97 | 0,54 | 1 |
| ***Labidosaurikos*** | 11,88 | 23,19 | 0,51 | 1 |
| ***Moradisaurus*** | 25,65 | 39,54 | 0,65 | 0 |
| ***Rothianiscus*** | 15,55 | 39,55 | 0,39 | 1 |
| ***Gansurhinus*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos valensis*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos chozaensis*** | 8,36 | 12,50 | 0,67 | 0 |
| ***Reiszorhinus*** | Issue with images/data | Issue with images/data | NA | ? |
| ***Opisthodontosaurus*** | Issue with images/data | Issue with images/data | NA | ? |
| ***Labidosauriscus*** | Issue with images/data | Issue with images/data | NA | ? |
| ***C. kierani*** | 3,26 | 5,13 | 0,64 | 0 |

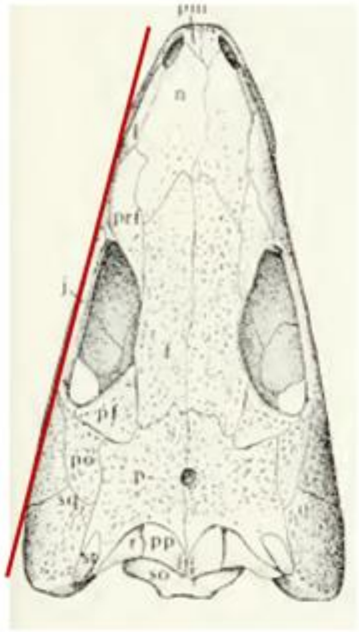


## (26b) Postorbital cheek:

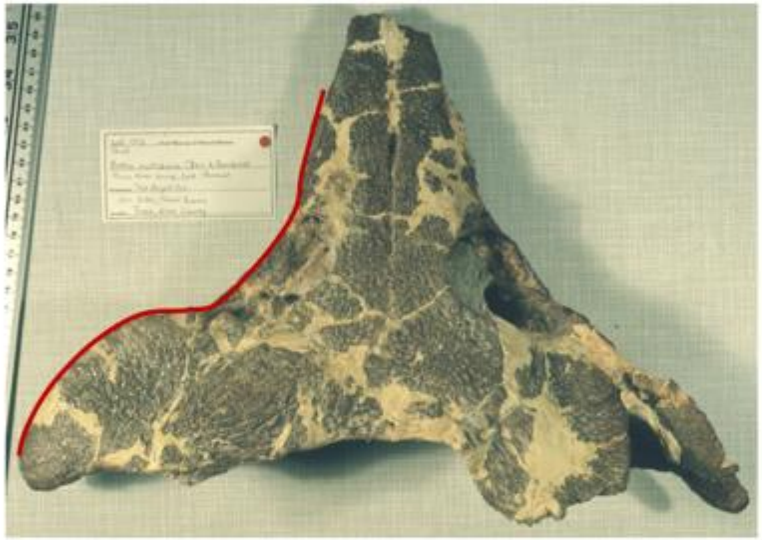
Relatively straight (0)

With sigmoidal shape (1)

| CHARACTER 26 b | Cheek shape |
|---|---|
| *Protorothyris* | 0 |
| *Paleothyris* | 0 |
| *Thuringothyris* | 0 |
| *Euconcordia* | ? |
| *Romeria prima* | 0 |
| *Romeria texana* | 0 |
| *Protocaptorhinus* | 0 |
| *Rhiodenticulatus* | 0 |
| *Saurorictus* | 0 |
| *C. laticeps* | 1 |
| *C. aguti* | 1 |
| *C. magnus* | ? |
| *Labidosaurus* | 1 |
| *Labidosaurikos* | 1 |
| *Moradisaurus* | 1 |
| *Rothianiscus* | 1 |
| *Gansurhinus* | ? |
| *Captorhinikos valensis* | ? |
| *Captorhinikos chozaensis* | 1 |
| *Reiszorhinus* | 0 |
| *Opisthodontosaurus* | 1 |
| *Labidosauriscus* | 1 |
| *C. kierani* | 1 |



*Protorothyris archeri*. Reconstruction. In Clark & Carroll 1972.

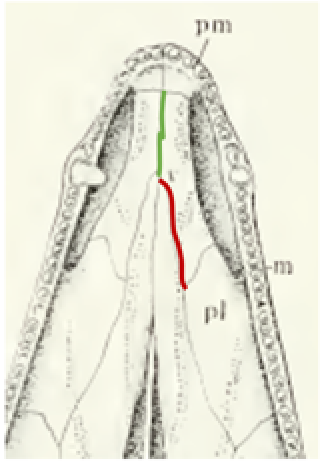


*Rothianiscus multidontus*. Image from Modesto 2018. Personal communication.

## (38a) Vomer-pterygoid contact:

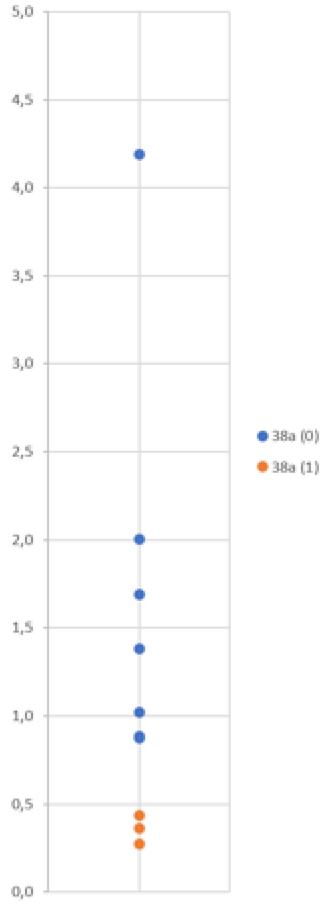
Extensive, at least 0,66 times median border of vomer (0)

Short, no more than 0,66 times median border of vomer (1)



*Protorothyris archeri.* Reconstruction. In Clark & Carroll 1972.

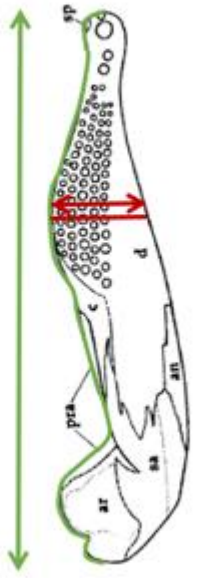
| CHARACTER 38a | V-Pt suture length | Median border of vomer length | Ratio | Character state |
|---|---|---|---|---|
| ***Protorothyris*** | 0,16 | 0,11 | 1,38 | 0 |
| ***Paleothyris*** | 0,06 | 0,22 | 0,27 | 1 |
| ***Thuringothyris*** | 0,35 | 0,34 | 1,02 | 0 |
| ***Euconcordia*** | 0,16 | 0,36 | 0,44 | 1 |
| ***Romeria prima*** | 0,10 | 0,11 | 0,88 | 0 |
| ***Romeria texana*** | 0,22 | 0,05 | 4,19 | 0 |
| ***Protocaptorhinus*** | 0,15 | 0,09 | 1,69 | 0 |
| ***Rhiodenticulatus*** | No image/data | No image/data | NA | ? |
| ***Saurorictus*** | No image/data | No image/data | NA | ? |
| ***C. laticeps*** | 0,38 | 1,06 | 0,36 | 1 |
| ***C. aguti*** | No image/data | No image/data | NA | ? |
| ***C. magnus*** | No image/data | No image/data | NA | ? |
| ***Labidosaurus*** | 3,58 | 1,79 | 2,00 | 0 |
| ***Labidosaurikos*** | 3,83 | 4,38 | 0,88 | 0 |
| ***Moradisaurus*** | No image/data | No image/data | NA | ? |
| ***Rothianiscus*** | No image/data | No image/data | NA | ? |
| ***Gansurhinus*** | No image/data | No image/data | NA | ? |
| ***Captorhinikos valensis*** | No image/data | No image/data | NA | ? |
| ***Captorhinikos chozaensis*** | No image/data | No image/data | NA | ? |
| ***Reiszorhinus*** | No image/data | No image/data | NA | ? |
| ***Opisthodontosaurus*** | No image/data | No image/data | NA | ? |
| ***Labidosauriscus*** | No image/data | No image/data | NA | ? |
| ***C. kierani*** | No image/data | No image/data | NA | ? |



## (59a) Mandibular ramus:

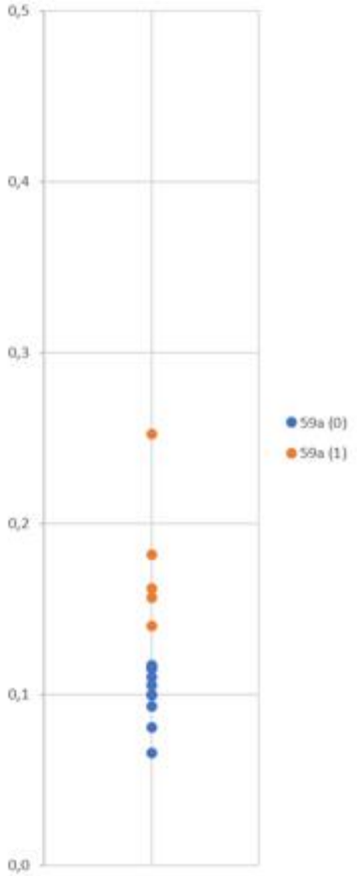
Narrow, 0,13 or less of total jaw length (0)

Broad, more than 0,13 of total jaw length (1)



*Labidosaurikos meachami*. Reconstruction. In Dodick & Modesto 1995.

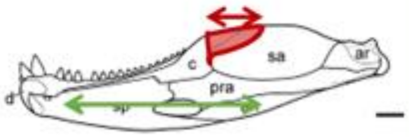
| CHARACTER 59a | Mandibular ramus length | Mandibular ramus width | Ratio | Character state |
|---|---|---|---|---|
| ***Protorothyris*** | 1,02 | 0,07 | 0,07 | 0 |
| ***Paleothyris*** | 0,38 | NA | NA | ? |
| ***Thuringothyris*** | 2,72 | 0,30 | 0,11 | 0 |
| ***Euconcordia*** | 3,47 | 0,36 | 0,10 | 0 |
| ***Romeria prima*** | 1,00 | 0,10 | 0,10 | 0 |
| ***Romeria texana*** | 0,58 | 0,07 | 0,11 | 0 |
| ***Protocaptorhinus*** | 0,93 | 0,11 | 0,12 | 0 |
| ***Rhiodenticulatus*** | 3,71 | 0,43 | 0,12 | 0 |
| ***Saurorictus*** | NA | NA | NA | ? |
| ***C. laticeps*** | 6,15 | 0,72 | 0,12 | 0 |
| ***C. aguti*** | 6,45 | 0,52 | 0,08 | 0 |
| ***C. magnus*** | 6,47 | 0,64 | 0,10 | 0 |
| ***Labidosaurus*** | 23,34 | 3,66 | 0,16 | 1 |
| ***Labidosaurikos*** | 27,19 | 4,94 | 0,18 | 1 |
| ***Moradisaurus*** | 44,75 | 11,28 | 0,25 | 1 |
| ***Rothianiscus*** | NA | NA | NA | ? |
| ***Gansurhinus*** | NA | 2,10 | NA | ? |
| ***Captorhinikos valensis*** | NA | NA | NA | ? |
| ***Captorhinikos chozaensis*** | 14,13 | 2,29 | 0,16 | 1 |
| ***Reiszorhinus*** | 11,51 | NA | NA | ? |
| ***Opisthodontosaurus*** | 4,96 | 0,69 | 0,14 | 0 |
| ***Labidosauriscus*** | 3,31 | 0,39 | 0,12 | 0 |
| ***C. kierani*** | 6,62 | 0,61 | 0,09 | 0 |



## (62a) Coronoid – posterior process:

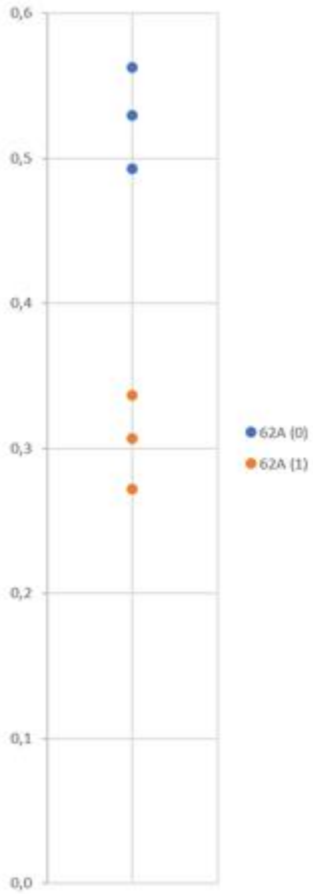
Equal to or longer than 0,42 of total coronoid length (0)

Shorter than 0,42 of total coronoid length (1)



*Labidosaurus hamatus.* Reconstruction. In Modesto, Scott et al 2007.

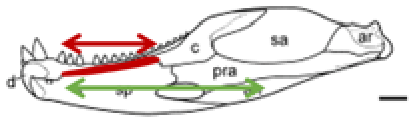
| CHARACTER 62a | Coronoid (posteral process) | Coronoid (total length) | Ratio | Character state |
|---|---|---|---|---|
| ***Protorothyris*** | 0,12 | 0,21 | 0,56 | 0 |
| ***Paleothyris*** | NA | NA | NA | ? |
| ***Thuringothyris*** | NA | NA | NA | ? |
| ***Euconcordia*** | NA | NA | NA | ? |
| ***Romeria prima*** | NA | NA | NA | ? |
| ***Romeria texana*** | NA | NA | NA | ? |
| ***Protocaptorhinus*** | NA | NA | NA | ? |
| ***Rhiodenticulatus*** | NA | NA | NA | ? |
| ***Saurorictus*** | NA | NA | NA | ? |
| ***C. laticeps*** | 1,03 | 1,95 | 0,53 | 0 |
| ***C. aguti*** | NA | NA | NA | ? |
| ***C. magnus*** | NA | NA | NA | ? |
| ***Labidosaurus*** | 2,86 | 10,52 | 0,27 | 1 |
| ***Labidosaurikos*** | 4,25 | 8,63 | 0,49 | 0 |
| ***Moradisaurus*** | NA | NA | NA | ? |
| ***Rothianiscus*** | NA | NA | NA | ? |
| ***Gansurhinus*** | NA | NA | NA | ? |
| ***Captorhinikos valensis*** | NA | NA | NA | ? |
| ***Captorhinikos chozaensis*** | NA | NA | NA | ? |
| ***Reiszorhinus*** | 0,91 | 2,96 | 0,31 | 1 |
| ***Opisthodontosaurus*** | NA | NA | NA | ? |
| ***Labidosauriscus*** | NA | NA | NA | ? |
| ***C. kierani*** | 1,36 | 4,04 | 0,34 | 1 |



## (62b) Coronoid – anterior process:

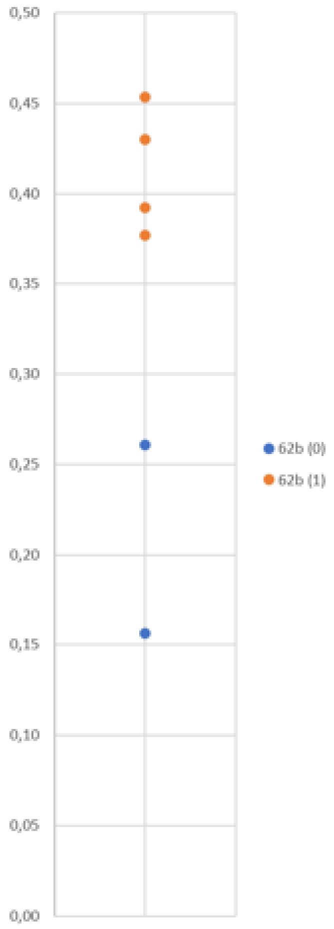
Equal to or longer than 0,32 of total coronoid length (0)

Shorter than 0,32 of total coronoid length (1)



*Labidosaurus hamatus.* Reconstruction. In Modesto, Scott et al 2007.

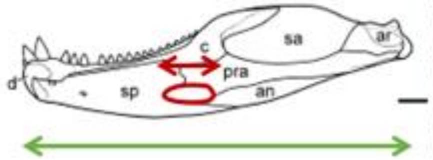
| CHARACTER 62a | Coronoid (anterior process) | Coronoid (total length) | Ratio | Character state |
|---|---|---|---|---|
| ***Protorothyris*** | 0,03 | 0,21 | 0,16 | 0 |
| ***Paleothyris*** | NA | NA | NA | ? |
| ***Thuringothyris*** | NA | NA | NA | ? |
| ***Euconcordia*** | NA | NA | NA | ? |
| ***Romeria prima*** | NA | NA | NA | ? |
| ***Romeria texana*** | NA | NA | NA | ? |
| ***Protocaptorhinus*** | NA | NA | NA | ? |
| ***Rhiodenticulatus*** | NA | NA | NA | ? |
| ***Saurorictus*** | NA | NA | NA | ? |
| ***C. laticeps*** | 0,51 | 1,95 | 0,26 | 0 |
| ***C. aguti*** | NA | NA | NA | ? |
| ***C. magnus*** | NA | NA | NA | ? |
| ***Labidosaurus*** | 4,77 | 10,52 | 0,45 | 1 |
| ***Labidosaurikos*** | 3,25 | 8,63 | 0,38 | 1 |
| ***Moradisaurus*** | NA | NA | NA | ? |
| ***Rothianiscus*** | NA | NA | NA | ? |
| ***Gansurhinus*** | NA | NA | NA | ? |
| ***Captorhinikos valensis*** | NA | NA | NA | ? |
| ***Captorhinikos chozaensis*** | NA | NA | NA | ? |
| ***Reiszorhinus*** | 1,27 | 2,96 | 0,43 | 1 |
| ***Opisthodontosaurus*** | NA | NA | NA | ? |
| ***Labidosauriscus*** | NA | 1,76 | NA | ? |
| ***C. kierani*** | 1,59 | 4,04 | 0,39 | 1 |



## (63a) Meckelian foramen:

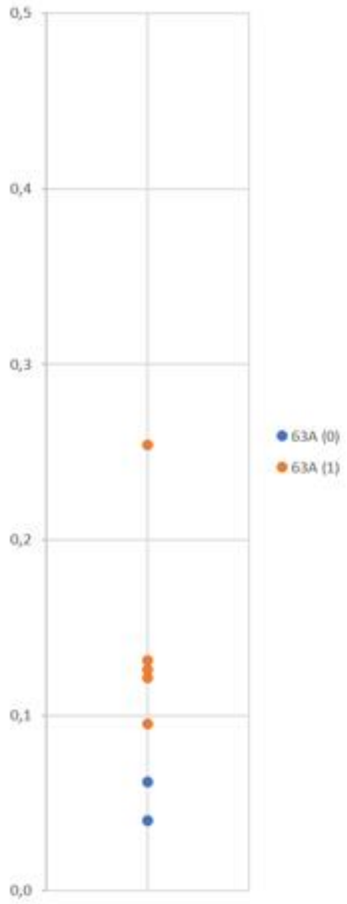
Small, anteroposterior length roughly or less 0,08 of total jaw length (0)

Large, anteroposterior length greater than or equal to 0,08 of total jaw length (1)



*Labidosaurus hamatus.* Reconstruction. In Modesto, Scott et al 2007.

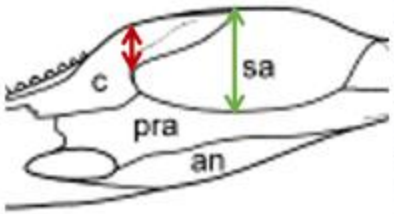
| CHARACTER 63a | Total jaw length (lateral) | Meckelian foramen length | Ratio | Character state |
|---|---|---|---|---|
| ***Protorothyris*** | 1,00 | 0,04 | 0,04 | 0 |
| ***Paleothyris*** | 0,38 | NA | NA | ? |
| ***Thuringothyris*** | NA | NA | NA | ? |
| ***Euconcordia*** | NA | NA | NA | ? |
| ***Romeria prima*** | 0,93 | NA | NA | ? |
| ***Romeria texana*** | 0,56 | NA | NA | ? |
| ***Protocaptorhinus*** | 0,85 | NA | NA | ? |
| ***Rhiodenticulatus*** | 3,48 | NA | NA | ? |
| ***Saurorictus*** | 2,04 | NA | NA | ? |
| ***C. laticeps*** | 5,87 | 0,36 | 0,06 | 0 |
| ***C. aguti*** | 5,42 | NA | NA | ? |
| ***C. magnus*** | 5,94 | NA | NA | ? |
| ***Labidosaurus*** | 19,29 | 2,53 | 0,13 | 1 |
| ***Labidosaurikos*** | 27,19 | 2,59 | 0,10 | 1 |
| ***Moradisaurus*** | 44,75 | 5,44 | 0,12 | 1 |
| ***Rothianiscus*** | NA | NA | NA | ? |
| ***Gansurhinus*** | NA | NA | NA | ? |
| ***Captorhinikos valensis*** | NA | NA | NA | ? |
| ***Captorhinikos chozaensis*** | 13,58 | NA | NA | ? |
| ***Reiszorhinus*** | 11,51 | 2,92 | 0,25 | 1 |
| ***Opisthodontosaurus*** | 4,96 | NA | NA | ? |
| ***Labidosauriscus*** | 3,31 | NA | NA | ? |
| ***C. kierani*** | 6,15 | 0,78 | 0,13 | 1 |



## (64a) Coronoid – posterodorsal process:

Slender, < 0,25 of lateral wall of adductor fossa (0)

Deep, > 0,25 of lateral wall of adductor fossa (1)



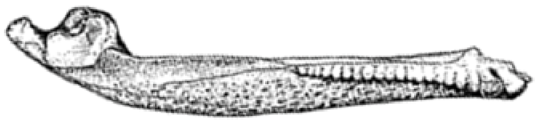
*Labidosaurus hamatus.* Reconstruction. In Modesto, Scott et al 2007.

| CHARACTER 64a | Addutor fossa height | Posterodorsal process of coronoid height | Ratio | Character state |
|---|---|---|---|---|
| ***Protorothyris*** | 0,13 | 0,02 | 15,0 | 0 |
| ***Paleothyris*** | NA | NA | NA | ? |
| ***Thuringothyris*** | NA | NA | NA | ? |
| ***Euconcordia*** | NA | NA | NA | ? |
| ***Romeria prima*** | NA | NA | NA | ? |
| ***Romeria texana*** | NA | NA | NA | ? |
| ***Protocaptorhinus*** | NA | NA | NA | ? |
| ***Rhiodenticulatus*** | NA | NA | NA | ? |
| ***Saurorictus*** | NA | NA | NA | ? |
| ***C. laticeps*** | 0,91 | 0,08 | 8,4 | 0 |
| ***C. aguti*** | NA | NA | NA | ? |
| ***C. magnus*** | NA | NA | NA | ? |
| ***Labidosaurus*** | 2,86 | 1,27 | 44,3 | 1 |
| ***Labidosaurikos*** | 2,84 | 1,88 | 65,9 | 1 |
| ***Moradisaurus*** | NA | 2,31 | NA | ? |
| ***Rothianiscus*** | NA | NA | NA | ? |
| ***Gansurhinus*** | NA | NA | NA | ? |
| ***Captorhinikos valensis*** | NA | NA | NA | ? |
| ***Captorhinikos chozaensis*** | NA | NA | NA | ? |
| ***Reiszorhinus*** | 1,48 | 0,21 | 14,0 | 0 |
| ***Opisthodontosaurus*** | 0,72 | 0,15 | 21,3 | 0 |
| ***Labidosauriscus*** | 0,35 | 0,10 | 28,8 | 1 |
| ***C. kierani*** | 0,74 | 0,22 | 30,2 | 1 |

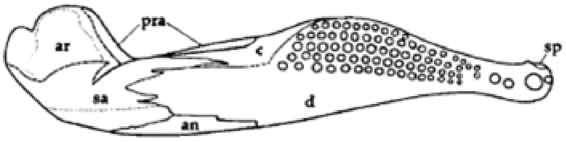
## (76) Dentary – lingual shelf:

Absent (0)

Present (1)



*Labidosaurus hamatus*. CM76876. In Modesto, Scott et al. 2007.



*Labidosaurikos meachami*. Reconstruction; OMNH 4331. In Dodick & Modesto 1995.

### Status 76(0)

- *Protorothyris archeri*
- *Paleothyris acadiana*
- *Thuringothyris mahlendorffae*
- *Romeria prima*
- *Romeria texana*
- *Protocaptorhinus pricei*
- *Rhiodenticulatus heatoni*
- *Captorhinus laticeps*
- *Captorhinus aguti*
- *Captorhinus magnus*
- *Labidosaurus hamatus*
- *Reiszorhinus olsoni*
- *Opisthodontosaurus carrolli*

### Status 76(1)

- *Labidosaurikos meachami*
- *Moradisaurus grandis*
- *Rothianiscus multidontus*
- *Captorhinikos chozaensis*

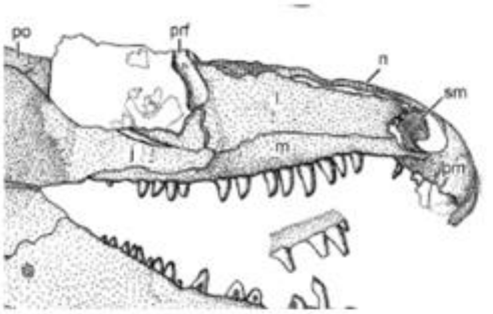
### Status 76(?)

- *Euconcordia cunninghami*
- *Sauroríctus australis*
- *Gansurhinus qingtoushanensis*
- *Captorhinikos valensis*
- *Labidosauriscus richardi*
- *Captorhinus kierani*

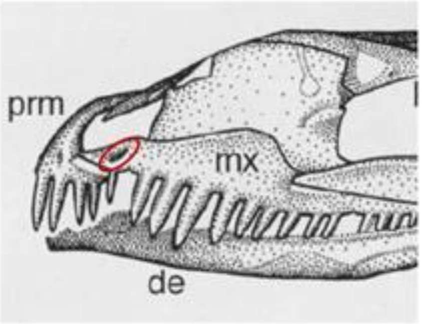
**(77) Anterior maxillary foramen:**

Absent (0)

Present (1)



*Reiszorhinus olsoni*. Holotype FMNH UC183. In Sumida, Dodick et al 2010.



*Saurorictus australis*. Holotype; SAM PK-8666. In Modesto & Smith 2001.

## Status 77(0)

- *Paleothyris acadiana*
- *Thuringothyris mahlendorffae*
- *Euconcordia cunninghami*
- *Romeria prima*
- *Romeria texana*
- *Protocaptorhinus pricei*
- *Rhiodenticulatus heatoni*
- *Captorhinus laticeps*
- *Captorhinus aguti*
- *Captorhinus magnus*
- *Labidosaurus hamatus*
- *Labidosaurikos meachami*
- *Reiszorhinus olsoni*

## Status 77(1)

- *Saurorictus australis*
- *Labidosauriscus richardi*

## Status 77(?)

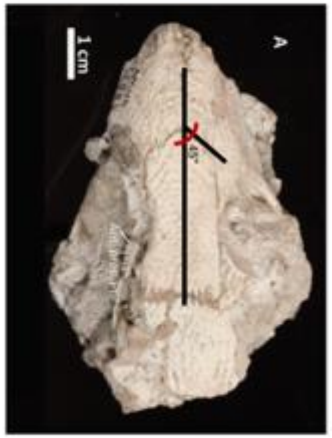
- *Protorothyris archeri*
- *Moradisaurus grandis*
- *Rothianiscus multidontus*
- *Gansurhinus qingtoushanensis*
- *Captorhinikos valensis*
- *Captorhinikos chozaensis*
- *Opisthodontosaurus carrolli*
- *Captorhinus kierani*

## (78a) Nasal-frontal:

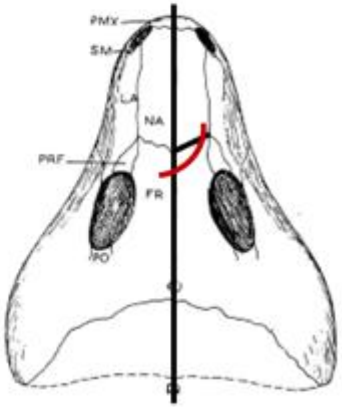
Angle of suture between nasal and frontals < 70º (0)

Angle of suture between nasal and frontals between 70º and 90º (1)

Angle of suture between nasal and frontals > 90º (2)

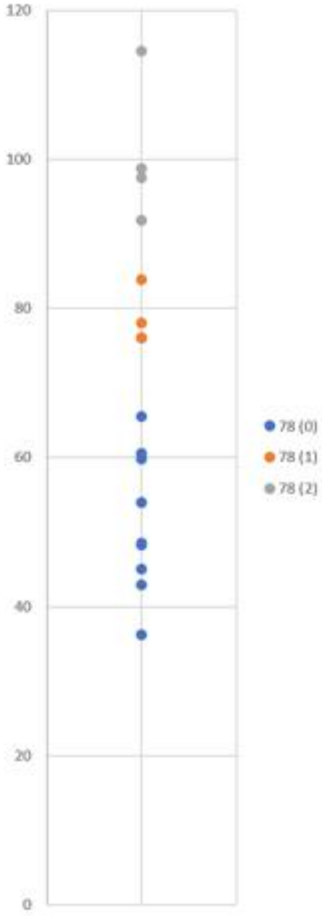


*Captorhinus magnus*. OMNH 56820. In deBraga, Bevitt & Reisz 2019.



*Captorhinus chozaensis*. Reconstruction. In Olson 1962.

| CHARACTER 78 | Angle | Character status |
|---|---|---|
| ***Protorothyris*** | 49 | 0 |
| ***Paleothyris*** | 98 | 2 |
| ***Thuringothyris*** | 76 | 1 |
| ***Euconcordia*** | 60 | 0 |
| ***Romeria prima*** | 99 | 2 |
| ***Romeria texana*** | 92 | 2 |
| ***Protocaptorhinus*** | 78 | 1 |
| ***Rhiodenticulatus*** | 43 | 0 |
| ***Saurorictus*** | 61 | 0 |
| ***C. laticeps*** | 84 | 1 |
| ***C. aguti*** | 76 | 1 |
| ***C. magnus*** | 48 | 0 |
| ***Labidosaurus*** | 54 | 0 |
| ***Labidosaurikos*** | 36 | 0 |
| ***Moradisaurus*** | Issue with images/data | ? |
| ***Rothianiscus*** | Issue with images/data | ? |
| ***Gansurhinus*** | No specimen | ? |
| ***Captorhinikos valensis*** | No specimen | ? |
| ***Captorhinikos chozaensis*** | 115 | 2 |
| ***Reiszorhinus*** | 45 | 0 |
| ***Opisthodontosaurus*** | Issue with images/data | ? |
| ***Labidosauriscus*** | 66 | 0 |
| ***C. kierani*** | 71 | 1 |



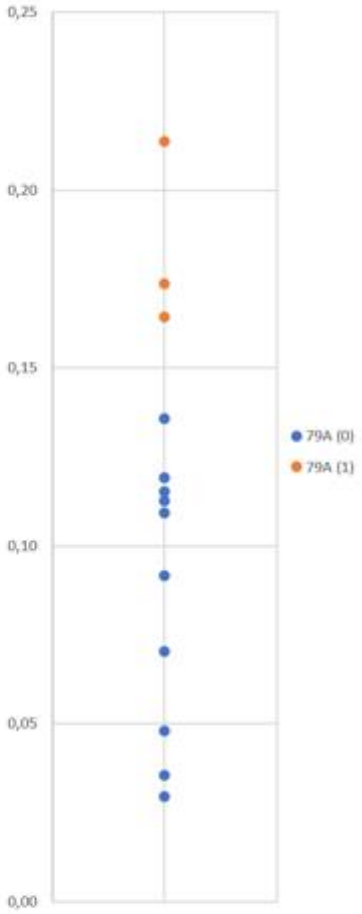
# (79a) Postorbital-Jugal suture:

Ratio with cranium length < 0,15 (0)

Ratio with cranium length > 0,15 (1)

*Labidosaurus hamatus.* Reconstruction. In Modesto, Scott et al 2007.

| CHARACTER 79a | Length of J-PO suture | Cranium length | Ratio | Character state |
|---|---|---|---|---|
| ***Protorothyris*** | 0,11 | 1,01 | 0,11 | 0 |
| ***Paleothyris*** | 0,02 | 0,37 | 0,05 | 0 |
| ***Thuringothyris*** | 0,07 | 2,39 | 0,03 | 0 |
| ***Euconcordia*** | NA | 3,93 | NA | ? |
| ***Romeria prima*** | 0,12 | 1,04 | 0,12 | 0 |
| ***Romeria texana*** | 0,15 | 0,93 | 0,16 | 1 |
| ***Protocaptorhinus*** | 0,09 | 0,95 | 0,09 | 0 |
| ***Rhiodenticulatus*** | 0,47 | 4,29 | 0,11 | 0 |
| ***Saurorictus*** | 0,17 | 2,37 | 0,07 | 0 |
| ***C. laticeps*** | 1,03 | 5,90 | 0,17 | 1 |
| ***C. aguti*** | 0,18 | 4,96 | 0,04 | 0 |
| ***C. magnus*** | 0,89 | Issue with images/data | NA | ? |
| ***Labidosaurus*** | 2,61 | 19,22 | 0,14 | 0 |
| ***Labidosaurikos*** | 3,31 | 27,81 | 0,12 | 0 |
| ***Moradisaurus*** | No image/data | 40,70 | NA | ? |
| ***Rothianiscus*** | No image/data | Issue with images/data | NA | ? |
| ***Gansurhinus*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos valensis*** | No specimen | No specimen | NA | ? |
| ***Captorhinikos chozaensis*** | No image/data | 13,63 | NA | ? |
| ***Reiszorhinus*** | No image/data | 12,73 | NA | ? |
| ***Opisthodontosaurus*** | 0,66 | Issue with images/data | NA | ? |
| ***Labidosauriscus*** | No image/data | 4,34 | NA | ? |
| ***C. kierani*** | 1,43 | 6,67 | 0,21 | 1 |



# Appendix 7

**Updated list and definition of phylogenetic characters used in the phylogenetic analysis for phylogeny present in Figure 16. 89 characters in total.**

This character list is formed by the addition of characters present in Appendix 6 with the characters present in Appendix 3.

# Appendix 8

**Updated list and definition of phylogenetic characters used in the phylogenetic analysis for phylogeny present in Figure 16. 89 characters in total.**

Modified from Modesto *et al*. (2018). *Abbreviation*: polymorphism for {0 1}, {1 2}

*Protorothyris* 0 0 0 0 0 0 0 0 0 0 0 ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 ? 0 0 0 ? ? 0 ? ? 0 0

*Paleothyris* 0 0 0 0 0 0 0 0 0 0 0 ? ? 0 0 0 0 0 0 1 0 0 0 0 0 0 2 1 0 0 0 0 1 1 0 0 0 0 0 0 1
2 0 0 1 0 0 0 0 1 0 0 0 0 0 0 1 0 ? 0 0 0 0 0 0 0 0 ? 0 ? ? ? ? ? 0 0 0 0 1 0 0 0 1 1 0 0 0 2 0

*Thuringothyris* 0 0 0 0 0 1 1 0 0 0 0 0 1 0 1 1 0 0 1 1 0 1 1 0 0 0 2 1 1 0 1 0 1 1 1 1 1 0 0 0 0
1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 ? ? 0 0 0 ? ? ? ? ? ? 0 0 0 ? ? 1 0 1 1 1 0 0 0 1 0

*Euconcordia* 0 1 0 0 1 1 0 0 0 0 0 1 2 1 1 2 ? 0 1 1 0 0 0 ? ? 0 ? 1 1 1 1 ? ? ? ? ? ? ? 0 ? 0 1
0 0 1 1 0 0 0 1 0 0 0 0 0 0 1 0 ? 0 0 0 0 0 0 0 0 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 0 0 ?

*Romeria prima* 1 1 1 1 0 1 0 0 0 0 0 1 2 0 0 1 0 0 0 0 0 1 1 0 0 1 0 0 0 1 1 0 0 1 1 0 0 1 0 0 1
0 0 0 1 1 0 0 1 0 0 ? ? 0 ? 0 0 0 0 0 0 0 0 1 0 0 0 0 0 ? ? ? ? ? ? 1 ? 1 ? 1 ? 1 ? ? 0 0 0 2 0

*Romeria texana* 1 1 1 1 0 1 0 0 0 0 0 1 0 ? 0 0 0 0 0 1 ? 1 1 0 0 1 0 1 0 1 1 0 0 0 1 0 0 0 0 0 0
1 0 0 1 1 0 0 1 0 0 ? 0 0 0 0 ? 0 ? 0 ? 0 0 1 0 0 0 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 0 0 2 1

*Protocaptorhinus* 1 1 1 1 0 1 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0 1 0 0 0 1 1 1 1 1 0 ? 0 1 0 0 1 0 0 1
1 0 0 0 1 0 1 ? 0 ? 1 ? 0 0 0 ? 0 ? ? 0 0 0 ? 0 0 0 0 0 ? ? ? ? ? 1 1 ? ? 1 1 1 1 ? ? 0 0 0 1 0

*Rhiodenticulatus* 1 1 0 1 0 1 0 0 0 0 0 1 1 1 0 2 0 0 1 1 1 1 1 0 0 0 1 0 1 1 0 1 1 1 1 1 1 0 0 0 0
1 ? ? 0 1 0 1 ? ? 0 1 0 0 0 0 0 0 0 0 ? ? 0 1 0 0 0 0 0 1 ? ? ? ? 1 ? 1 0 ? 1 1 1 ? ? 0 0 0 0 0

*Saurorictus* ? 1 1 ? 1 {1 2} 0 0 0 0 0 1 0 0 1 2 0 0 0 1 1 1 1 0 0 0 2 0 1 0 0 1 1 0 1 1 1 1 0
0 0 ? ? ? ? 1 0 1 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 1 0 0

*Captorhinus laticeps* 1 1 1 1 1 1 0 0 1 0 0 1 0 1 0 1 0 0 0 0 0 1 1 1 1 0 1 1 0 1 0 1 1 1 1 1 1 0 0 1 0
1 0 0 0 1 0 2 1 1 0 2 0 0 1 1 0 1 0 0 0 0 0 1 1 0 0 0 0 1 0 0 0 0 1 1 1 1 0 1 1 1 0 0 0 0 0 1 1

*Captorhinus aguti* 1 1 1 1 1 1 0 1 2 0 1 1 2 1 1 1 0 0 0 0 0 1 1 0 1 0 1 0 1 1 0 1 1 1 1 1 1 0 1 0 1 0

1 0 0 0 1 0 2 1 ? 0 2 0 0 1 1 ? 1 0 0 0 0 0 1 1 0 0 0 0 1 ? ? ? ? 1 1 1 1 0 1 1 1 0 0 0 0 0 1 0

*Captorhinus magnus* 1 1 1 1 1 1 0 0 1 0 0 1 1 1 ? ? ? ? 0 0 0 1 1 0 0 0 1 1 1 1 0 1 1 0 1 1 1 ? ? ? 0

1 0 0 0 1 0 2 1 ? 0 2 0 0 1 1 0 1 0 0 0 0 0 1 1 0 0 0 0 1 ? ? ? ? 1 1 1 ? ? 1 1 1 ? ? 0 0 0 0 ?

*Labidosaurus* 1 1 1 1 1 1 1 0 1 0 0 1 1 0 0 0 0 1 0 0 0 1 1 0 0 1 1 0 1 1 0 1 1 1 1 0 1 0 1 1 0

1 0 1 0 1 0 2 1 0 0 1 0 0 1 2 0 1 1 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0 1 1 1 0 1 0 0 0 0 0

*Labidosaurikos* 1 1 1 1 1 1 1 3 3 1 2 1 0 0 0 0 1 1 0 0 1 1 1 0 0 0 2 0 1 1 0 1 1 1 1 1 1 0 1 1 1

1 1 1 0 1 1 2 1 0 1 1 1 1 1 2 0 1 1 0 1 1 1 2 ? 1 1 1 1 0 0 1 1 1 ? ? ? ? ? ? ? ? ? ? 1 0 0 0 0

*Moradisaurus* 1 ? 1 1 0 2 0 3 3 0 1 ? ? ? ? ? ? ? 1 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 1 ? 1 1

? ? ? 1 1 1 ? 1 1 1 1 1 2 0 1 1 1 1 1 0 2 1 1 1 1 1 0 ? ? 1 ? 2 1 ? ? ? 1 ? 1 0 ? 1 ? ? ? ?

*Rothianiscus* 1 ? 1 1 0 3 1 2 3 1 2 ? ? ? ? ? ? 1 ? ? ? ? ? ? ? ? ? ? 1 ? ? ? ? ? ? ? ? ? 1 1 ? 1

1 ? ? ? ? 1 1 ? 1 ? 1 2 1 ? 0 1 ? ? ? ? ? 2 ? 1 1 ? ? ? ? ? ? ? 2 1 1 ? ? ? ? 1 ? ? 1 ? ? ? ?

*Captorhinikos valensis* ? ? ? ? ? 1 1 2 3 0 2 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?

? ? ? ? ? ? ? ? ? 0 0 0 ? ? ? ? ? ? ? ? 2 ? ? ? ? ? ? ? ? ? ? 2 1 ? ? ? ? ? ? ? ? ? ? ? ? ?

*Gansurhinus* 1 ? ? 1 ? 3 1 2 3 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?

? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 2 1 1 ? ? ? 1 ? ? ? ? ? ? ? ?

*Captorhinikos chozaensis* 1 1 1 1 1 1 1 2 3 0 1 0 1 ? 1 0 1 0 0 ? ? ? ? ? ? ? ? ? 0 ? ? ? ? ? ? ? ? ?

0 1 ? 1 ? ? ? ? ? ? ? ? 0 1 0 0 1 ? 0 ? ? ? ? ? 1 2 0 1 1 1 1 ? ? ? ? ? 1 ? 1 1 1 1 2 1 0 ? 1 ? ? 2 ?

*Reiszorhinus* 1 1 1 1 0 1 0 0 0 0 0 1 1 0 ? 0 0 ? 0 0 0 1 1 ? ? 0 1 1 1 1 0 0 1 1 1 0 0 0 ? 0 0

1 0 0 1 1 0 1 ? ? ? ? ? ? ? ? ? ? ? ? ? 0 0 1 0 0 1 ? ? 1 1 1 1 0 ? ? ? ? ? ?? ? ? ? 0 0 0 0 ?

*Opisthodontosaurus* ? ? 0 1 1 3 0 0 3 0 0 1 1 ? ? ? ? ? ? ? ? 0 1 0 0 0 2 1 0 1 1 0 ? 0 1 1 1 ? ? 1 0 1

? ? ? ? ? ? 0 ? 0 2 0 0 0 0 0 1 0 ? ? ? ? 0 1 0 0 0 1 1 ? ? ? 0 1 ? 0 ? ? 1 1 0 ? ? 0 ? ? ? ?

*Labidosauriscus* 1 1 1 1 1 2 0 0 1 0 0 1 2 1 0 1 0 ? 0 0 ? ? ? ? ? ? ? ? 1 ? ? ? ? ? ? ? ? ? ? 1 ? 1

? ? ? ? ? 2 1 ? 0 2 0 0 1 1 1 1 0 ? ? ? ? 1 0 0 0 0 1 1 ? ? ? 1 ? ? ? ? ? ? ? ? ? ? ? ? 1 0 ?

*Captorhinus kierani* 1 1 1 1 1 1 0 0 1 0 1 1 1 1 0 1 0 0 0 0 0 1 1 1 1 0 1 0 1 1 0 1 1 1 1 1 1 0 0 1 0

1 1 0 0 1 0 2 1 ? 0 2 0 1 1 ? 1 1 1 0 0 0 0 1 1 0 0 0 0 1 1 1 1 1 ? 1 ? ? ? ? ? ? ? ? ? ? ? 1 1

# Appendix 9

**Updated list and definition of phylogenetic characters used in the phylogenetic analysis for phylogeny present in Figure 20. 100 characters total.**

This character list is formed by the addition of characters present in Appendix 6 with the characters present in Table 2, Section 3. h.

# Appendix 10

**New data matrix used to generate the phylogeny present in Figure 20; skull sculpturing characters included. Total of 100 characters.**

Modified from Modesto *et al*. (2018). *Abbreviation*: polymorphism for {0 1}, {1 2}.

*Protorothyris* 0 0 0 0 0 0 0 0 0 0 0 ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 ? 0 0 ? ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 ? 0 0 0 ? ? 0
? ? 0 0

*Paleothyris* 0 0 0 0 0 0 0 0 0 0 0 ? ? 0 0 0 0 0 0 1 0 0 0 0 0 0 2 1 0 0 0 0 1 1 0 0 0 0 0 0 1
2 ? 1 1 ? ? 0 1 0 0 0 1 0 0 1 0 0 0 0 1 0 0 0 0 0 0 1 0 ? 0 0 0 0 0 0 0 0 ? 0 ? ? ? ? ? 0 0 0 0 1 0 0 0 1 1 0
0 0 2 0

*Thuringothyris* 0 0 0 0 0 1 1 0 0 0 0 0 1 0 1 1 0 0 1 1 0 1 1 0 0 0 2 1 1 0 1 0 1 1 1 1 1 0 0 0 0
1 0 1 0 ? ? 0 2 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 ? ? 0 0 0 ? ? ? ? ? ? 0 0 0 ? ? 1 0 1 1 1 0
0 0 1 0

*Euconcordia* 0 1 0 0 1 1 0 0 0 0 0 1 2 1 1 2 ? 0 1 1 0 0 0 ? ? 0 ? 1 1 1 1 ? ? ? ? ? ? ? 0 ? 0 1
1 0 0 0 0 ? 0 0 0 0 0 0 0 1 1 0 0 0 1 0 0 0 0 0 0 1 0 ? 0 0 0 0 0 0 0 0 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0
0 0 ?

*Romeria prima* 1 1 1 1 0 1 0 0 0 0 0 1 2 0 0 1 0 0 0 0 0 1 1 0 0 1 0 0 0 1 1 0 0 1 1 0 0 1 0 0 1
0 ? ? ? ? ? ? ? ? ? ? ? 0 0 1 1 0 0 1 0 0 ? ? 0 ? 0 0 0 0 0 0 0 0 1 0 0 0 0 0 ? ? ? ? ? ? 1 ? 1 ? 1 ? 1 ? ? 0 0
0 2 0

*Romeria texana* 1 1 1 1 0 1 0 0 0 0 0 1 0 ? 0 0 0 0 0 1 ? 1 1 0 0 1 0 1 0 1 1 0 0 0 1 0 0 0 0 0 0
1 ? ? ? ? ? ? ? ? ? ? ? 0 0 1 1 0 0 1 0 0 ? 0 0 0 0 ? 0 ? 0 ? 0 0 1 0 0 0 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 0
0 2 1

*Protocaptorhinus* 1 1 1 1 0 1 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0 1 0 0 0 1 1 1 1 1 0 ? 0 1 0 0 1 0 0 1

1 1 0 1 0 1 1 0 1 0 1 0 0 0 0 1 0 1 ? 0 ? 1 ? 0 0 0 ? 0 ? ? 0 0 0 ? 0 0 0 0 0 ? ? ? ? ? 1 1 ? ? 1 1 1 1 ? ? 0

0 0 1 0

*Rhiodenticulatus* 1 1 0 1 0 1 0 0 0 0 0 1 1 1 0 2 0 0 1 1 1 1 1 0 0 0 1 0 1 1 0 1 1 1 1 1 1 0 0 0 0

1 ? ? ? ? ? ? ? ? ? ? ? ? ? 0 1 0 1 ? ? 0 1 0 0 0 0 0 0 0 0 ? ? 0 1 0 0 0 0 0 1 ? ? ? ? 1 ? 1 0 ? 1 1 1 ? ? 0 0

0 0 0

*Saurorictus* ? 1 1 ? 1 {1 2} 0 0 0 0 0 1 0 0 1 2 0 0 0 1 1 1 1 0 0 0 2 0 1 0 0 1 1 0 1 1 1 1 0

0 0 ? ? 0 0 ? ? 0 1 0 0 0 1 ? ? ? 1 0 1 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?

1 1 0 0

*Captorhinus laticeps* 1 1 1 1 1 1 0 0 1 0 0 1 0 1 0 1 0 0 0 0 0 1 1 1 1 0 1 1 0 1 0 1 1 1 1 1 1 0 0 1 0

1 1 0 1 1 1 0 1 {0 1} 0 0 0 0 0 0 1 0 2 1 1 0 2 0 0 1 1 0 1 0 0 0 0 0 1 1 0 0 0 0 1 0 0 0 0 1 1 1 1 0 1 1 1

0 0 0 0 0 1 1

*Captorhinus aguti* 1 1 1 1 1 1 0 1 2 0 1 1 2 1 1 1 0 0 0 0 0 1 1 0 1 0 1 0 1 1 0 1 1 1 1 1 0 1 0 1 0

1 1 0 1 1 1 1 1 0 1 0 0 0 0 0 1 0 2 1 ? 0 2 0 0 1 1 ? 1 0 0 0 0 0 1 1 0 0 0 0 1 ? ? ? ? 1 1 1 1 0 1 1 1 0 0 0

0 0 1 0

*Captorhinus magnus* 1 1 1 1 1 1 0 0 1 0 0 1 1 1 ? ? ? ? 0 0 0 1 1 0 0 0 1 1 1 1 0 1 1 0 1 1 1 ? ? ? 0

1 1 0 1 1 ? 0 1 ? 1 0 0 0 0 0 1 0 2 1 ? 0 2 0 0 1 1 0 1 0 0 0 0 0 1 1 0 0 0 0 1 ? ? ? ? 1 1 1 ? ? 1 1 1 ? ? 0

0 0 0 ?

*Labidosaurus* 1 1 1 1 1 1 1 0 1 0 0 1 1 0 0 0 0 1 0 0 0 1 1 0 0 1 1 0 1 1 0 1 1 1 1 0 1 0 1 1 0

1 1 0 0 1 1 1 1 0 0 0 0 0 1 0 1 0 2 1 0 0 1 0 0 1 2 0 1 1 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0 1 1 1 0 1

0 0 0 0 0

*Labidosaurikos* 1 1 1 1 1 1 1 3 3 1 2 1 0 0 0 0 1 1 0 0 1 1 1 0 0 0 2 0 1 1 0 1 1 1 1 1 1 0 1 1 1

1 0 1 0 1 ? 1 1 0 0 0 0 1 1 0 1 1 2 1 0 1 1 1 1 1 2 0 1 1 0 1 1 1 2 ? 1 1 1 1 0 0 1 1 1 ? ? ? ? ? ? ? ? ? ? 1

0 0 0 0

*Moradisaurus* 1 ? 1 1 0 2 0 3 3 0 1 ? ? ? ? ? ? ? 1 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 1 ? 1 0

1 0 1 0 1 0 1 1 0 0 1 ? ? ? 1 1 1 ? 1 1 1 1 1 2 0 1 1 1 1 0 2 1 1 1 1 1 0 ? ? 1 ? 2 1 ? ? ? 1 ? 1 0 ? 1 ? ?

? ?

*Rothianiscus* 1 ? 1 1 0 3 1 2 3 1 2 ? ? ? ? ? ? 1 ? ? ? ? ? ? ? ? ? ? 1 ? ? ? ? ? ? ? ? ? 1 1 ? 1

0 1 0 0 0 0 0 0 1 0 0 1 ? ? ? ? 1 1 ? 1 ? 1 2 1 ? 0 1 ? ? ? ? ? 2 ? 1 1 ? ? ? ? ? ? ? 2 1 1 ? ? ? ? 1 ? ? 1 ? ?

? ?

*Captorhinikos valensis* ? ? ? ? ? 1 1 2 3 0 2 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?

0 ? ? ? ? 2 ? 0 1 ? ? ? ? ? ? ? ? ? ? ? 0 0 0 ? ? ? ? ? ? ? ? 2 ? ? ? ? ? ? ? ? ? ? 2 1 ? ? ? ? ? ? ? ? ? ? ? ? ?

*Gansurhinus* 1 ? ? 1 ? 3 1 2 3 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?

? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 2 1 1 ? ? ? 1 ? ? ? ? ? ? ? ?

*Captorhinikos chozaensis* 1 1 1 1 1 1 1 2 3 0 1 0 1 ? 1 0 1 0 0 ? ? ? ? ? ? ? ? ? 0 ? ? ? ? ? ? ? ? ?

0 1 ? 1 ? ? ? ? ? ? 0 ? 0 0 ? ? ? ? ? ? ? ? ? 0 1 0 0 1 ? 0 ? ? ? ? ? 1 2 0 1 1 1 1 ? ? ? ? ? 1 ? 1 1 1 1 2 1 0

? 1 ? ? 2 ?

*Reiszorhinus* 1 1 1 1 0 1 0 0 0 0 0 1 1 0 ? 0 0 ? 0 0 0 1 1 ? ? 0 1 1 1 1 0 0 1 1 1 0 0 0 ? 0 0

1 ? ? ? ? ? ? 2 ? 1 0 0 0 0 1 1 0 1 ? ? ? ? ? ? ? ? ? ? ? ? ? 0 0 1 0 0 1 ? ? 1 1 1 1 0 ? ? ? ? ? ? ?? ? ? ? 0 0

0 0 ?

*Opisthodontosaurus* ? ? 0 1 1 3 0 0 3 0 0 1 1 ? ? ? ? ? ? ? ? 0 1 0 0 0 2 1 0 1 1 0 ? 0 1 1 1 ? ? 1 0 1

1 2 1 ? ? ? 2 0 0 0 1 ? ? ? ? ? ? 0 ? 0 2 0 0 0 0 0 1 0 ? ? ? ? 0 1 0 0 0 1 1 ? ? ? 0 1 ? 0 ? ? 1 1 0 ? ? 0 ? ?

? ?

*Labidosauriscus* 1 1 1 1 1 2 0 0 1 0 0 1 2 1 0 1 0 ? 0 0 ? ? ? ? ? ? ? ? 1 ? ? ? ? ? ? ? ? ? ? 1 ? 1

1 2 1 ? ? ? {1 2} 0 0 0 1 ? ? ? ? ? 2 1 ? 0 2 0 0 1 1 1 1 0 ? ? ? ? 1 0 0 0 0 1 1 ? ? ? 1 ? ? ? ? ? ? ? ? ? ? ?

? 1 0 ?

*Captorhinus kierani* 1 1 1 1 1 1 0 0 1 0 1 1 1 1 0 1 0 0 0 0 0 1 1 1 1 0 1 0 1 1 0 1 1 1 1 1 1 0 0 1 0

1 1 0 1 1 1 1 1 1 0 0 1 0 0 1 0 2 1 ? 0 2 0 1 1 ? 1 1 1 0 0 0 0 1 1 0 0 0 0 1 1 1 1 1 ? 1 ? ? ? ? ? ? ? ? ?

? ? 1 1

# Appendix 11 (digital)

**Visual guide to morphological characters in captorhinids.**

*Available in digital format.*

# Appendix 12

**Strict consensus phylogenetic tree of captorhinomorphs, based on the new matrix presented in Appendix 9 and 10.**