A new phylogenetic analysis of Phytosauria (Archosauria: Pseudosuchia) with the application of continuous and geometric morphometric character coding

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Abstract

Phytosauria is a clade of large, carnivorous, semi-aquatic archosauromorphs which reached its peak diversity and an almost global distribution in the Late Triassic (*c.* 230-201 Mya). Previous phylogenetic analyses of Phytosauria have either focused primarily on the relationships of specific subclades, or were limited in taxonomic scope, and no taxonomically comprehensive dataset is currently available. We here present the most taxonomically comprehensive cladistic dataset of phytosaurs to date, based on extensive first-hand study, identification of novel characters and synthesis of previous matrices. This results in an almost two-fold increase in phylogenetic information scored per taxon over previous analyses. Alongside a traditional discrete character matrix, three variant matrices were analysed in which selected characters were coded using continuous and landmarking methods, to more rigorously explore phytosaur relationships. Based on these four data matrices, four tree topologies were recovered. Relationships among non-leptosuchomorph phytosaurs are largely consistent between these four topologies, whereas those of more derived taxa are more variable. *Rutiodon carolinensis* consistently forms a sister relationship with *Angistorhinus*. In three topologies *Nicrosaurus* nests deeply within a group of traditionally non-Mystriosuchini taxa, leading us to redefine Mystriosuchini by excluding *Nicrosaurus* as an internal specifier. Two distinct patterns of relationships within Mystriosuchini are present in the four topologies, distinguished largely by the variable position of *Mystriosuchus*. In two topologies *Mystriosuchus* forms the most basal clade in Mystriosuchini, whilst in the others it occupies a highly derived position within the *Machaeroprosopus* clade. '*Redondasaurus*' is consistently recovered as monophyletic; however, it also nests within the *Machaeroprosopus* clade. The greatest impact on tree topology was associated with the incorporation of continuous data into our matrices, with landmark characters exerting a relatively modest influence. All topologies correlated significantly with stratigraphic

range estimates. Topological variability in our results highlights clades in which further investigation may better elucidate phytosaur relationships.

Introduction

Phytosaurs were a group of large-bodied archosauromorph reptiles that achieved an almost global distribution during the Late Triassic (c. 230–201 Mya; Stocker & Butler, 2013). In overall morphology, they are highly convergent with modern crocodilians, and this observation, in combination with the common recovery of their fossils from fluvial and lacustrine depositional environments, indicates that phytosaurs may have occupied a semi-aquatic niche, with their dentition suggestive of piscivory and carnivory (Stocker & Butler, 2013).

By far the most intensively investigated aspect of Phytosauria is their systematics. The phylogenetic position of phytosaurs within Archosauromorpha remains debated, having been recovered by recent analyses as either the sister group to Archosauria (Nesbitt, 2011), or as the earliest diverging clade within the crocodilian stem-group Pseudosuchia (Ezcurra, 2016). Regardless of their exact phylogenetic position, time-calibration of phylogenies indicates that phytosaurs originated in the Early Triassic, soon after the Permo-Triassic mass extinction, although only one confirmed phytosaur specimen is known prior to the Late Triassic (Stocker *et al.*, 2017). Their abundance, rich fossil record and cosmopolitan distribution indicate that phytosaurs were an important component of Late Triassic ecosystems; as a result, aspects of phytosaur palaeobiology such as ontogeny (Irmis, 2007) and neurosensory adaptions (Holloway, Claeson & O'keefe, 2013; Lautenschlager & Butler, 2016), as well as biogeography (~~e.g.~~e.g., Buffetaut, 1993; Brusatte *et al.*, 2012; Stocker & Butler, 2013), have received considerable interest. Furthermore, phytosaurs have featured heavily in biostratigraphical hypotheses for the Late Triassic terrestrial record (Long & Ballew, 1985; Parrish & Carpenter, 1986; Lucas & Hunt, 1993; Lucas, 1998, 2010; Martz & Parker, 2017). An important factor for these analyses and others is a robust understanding of evolutionary relationships within Phytosauria. Phytosaur taxonomy has long been problematic and

Commented [WGP1]: Lucas 2010 is just a self-plagiarized version of Lucas 1998 with some additional text. You should only cite one.

Commented [WGP2]: Most recent for North America

convoluted, complicating attempts to understand phytosaur evolutionary history (Hungerbühler, 2002; Stocker & Butler, 2013). However, with the advent and continued improvement of cladistic techniques, a more cohesive picture has begun to form.

Most previous phylogenetic analyses of the ingroup relationships of Phytosauria have primarily been focused on elucidating the relationships of individual or specific sets of taxa (Table 1). To achieve this, many analyses have been restricted in their taxonomic scope. These analyses have greatly enhanced current knowledge of many areas in phytosaur systematics; however, there is currently no taxonomically comprehensive cladistic dataset which can be used to investigate relationships across all known phytosaur species and clades. The development of such a dataset is an essential prerequisite for carrying out broader evolutionary analyses. To address this gap, this paper has three primary aims:

1) To present the most taxonomically comprehensive phylogeny of Phytosauria to date, including nearly all currently recognized species;

2) To use this phylogeny to investigate the phylogenetic relationships of a number of species and higher-level taxa that have previously been recognized as problematic;

3) To assess the utility of continuous and geometric morphometric character coding techniques, as tools that can potentially expand the information available to assess phytosaur interrelationships.

Previous work

Previous cladistic analyses. The first cladistic analysis of the ingroup relationships of Phytosauria was performed by Ballew (1989). Her analysis included 11 operational taxonomic units (OTUs) and 64 characters with the aim of establishing character polarity and revising the diagnoses and species assignments of the genera *Rutiodon* and '*Pseudopalatus*'. The analysis generated a tree topology which, in its general structure, has changed relatively little in subsequent analyses. '*Paleorhinus*' and *Angistorhinus*

were recovered at the base of Phytosauria, and a polytomy of taxa which Ballew synonymized into *Rutiodon* was recovered as the sister taxon to a clade consisting of *Nicrosaurus*, '*Pseudopalatus*' and *Mystriosuchus* (Fig. 1A).

Ballew's phylogeny (Fig. 1A) was used as a basis for Long & Murry (1995) to present a comprehensive taxonomic review of Phytosauria, including the erection of three new genera ('*Arganarhinus*', *Smilosuchus*, '*Arribasuchus*') and the identification of numerous new anatomical characters with potential taxonomic or phylogenetic significance. No numerical phylogenetic analysis or phylogenetic tree was presented, but based on the identification of novel characters a taxonomy was constructed, differing from the phylogeny of Ballew (1989) most importantly in the separation of the taxa included in *Rutiodon* by Ballew into *Leptosuchus* Case, 1922 and the new genus *Smilosuchus*, and in the basal position of *Mystriosuchus* as the sister taxon to '*Paleorhinus*' (previously suggested by Gregory [1962] and Hunt & Lucas [1989]).

Hungerbühler (1998) increased taxonomic sampling, including 22 species-level OTUs, and presented a largely novel matrix of 49 characters, of which 12 were based on or reused from previous studies (Ballew, 1989; Long & Murry, 1995). The aims were twofold: to test the concept of a monophyletic '*Paleorhinus*' (Ballew, 1989; Hunt & Lucas, 1991; Long & Murry, 1995), and to more thoroughly assess the phylogenetic position of *Mystriosuchus*. '*Paleorhinus*' was found to be paraphyletic, with the species previously assigned to the genus recovered as a grade of iteratively more derived taxa at the base of Phytosauria. In agreement with Ballew (1989; Fig. 1A), *Mystriosuchus* was found in a more derived position than '*Paleorhinus*', but nested as the sister taxon to '*Pseudopalatus*' rather than within this genus (Fig. 1B).

A heavily revised version of Hungerbühler's (1998) matrix was used by Hungerbühler (2002) to further investigate the relationships of *Mystriosuchus* and assess the phylogenetic position of the newly

described species *Mystriosuchus westphali*. Sampling was reduced to only 11 taxa and 47 characters (of which 16 were taken directly from the previous study), to focus the analysis on the clade formed of *Nicrosaurus*, *Mystriosuchus* and '*Pseudopalatus*', named 'Pseudopalatinae' by Long & Murry (1995). *Mystriosuchus* was again recovered as the sister taxon to '*Pseudopalatus*'; additionally, the genus '*Redondasaurus*' was found to be monophyletic and outside of '*Pseudopalatus*', contra Hungerbühler, Chatterjee & Cunningham (2003), but closer to the latter taxon than to *Mystriosuchus*. *Nicrosaurus* was recovered as the sister-taxon of the *Mystriosuchus* + ('*Redondasaurus*' + '*Pseudopalatus*') clade (Fig. 1C).

The matrix of Hungerbühler (2002) was subsequently used to test the phylogenetic position of '*Pseudopalatus*' *jablonskiae* by Parker & Irmis (2006). This taxon was the only addition to the matrix and was found to occupy the most basal position in the genus '*Pseudopalatus*', with no other changes in tree topology (Fig. 2A).

In order to better resolve the relationships of the stratigraphically important genus *Leptosuchus* (Camp, 1930; Hunt & Lucas, 1991; Lucas, 1998) and other associated taxa (including those that were synonymized into *Rutiodon* by Ballew 1989), Stocker (2010) produced a largely novel matrix, incorporating three characters from the matrix of Sereno (1991), and 18 either directly taken or modified from Hungerbühler (2002). The full matrix consisted of 43 characters scored for 24 OTUs and found *Leptosuchus* to be polyphyletic, with '*Leptosuchus' adamanensis* forming a monophyletic group with *Smilosuchus gregorii* and '*Machaeroprosopus*' *lithodendrorum* (Fig. 2B). As a result, '*Leptosuchus' adamanensis* and '*Machaeroprosopus*' *lithodendrorum* were reassigned to the genus *Smilosuchus*. *Rutiodon* was not found to be synonymous with *Angistorhinus*, *Brachysuchus* or *Leptosuchus*, contra Ballew (1989), Long & Murry (1995) and Hungerbühler & Sues (2001). The new genus and species

Pravusuchus hortus was recovered as the sister taxon to 'Pseudopalatinae', and '*Paleorhinus*' *scurriensis* Langston, 1949 was found to occupy the most basal position within Phytosauria (Fig. 2B).

Following this, Stocker (2012, 2013) presented two further studies in which she first described the new taxon *Protome batalaria* and then redescribed '*Paleorhinus*' *scurriensis*, assigning the latter to the new genus *Wannia*. Phylogenetic aspects of both studies were based entirely on the dataset of Stocker (2010) with no changes or additions to the dataset. In the latter study, Stocker (2013) provided further discussion questioning the existence of a monophyletic '*Paleorhinus*', supporting the findings of Hungerbühler (1998; Fig. 1B).

Although not a phylogenetic study, an important taxonomic alteration was made by Parker, Hungerbühler & Martz (2012). The genus name *Machaeroprosopus* was previously considered invalid because the sole specimen of its presumed type species (*Machaeroprosopus validus*, UW 3807) has been lost (Gregory, 1962); however, Parker, Hungerbühler & Martz (2012) established that the holotype specimen of the species *Machaeroprosopus buceros* actually takes priority. The species *Machaeroprosopus buceros* was initially assigned to the genus '*Belodon*', but subsequently made the type species of the genus *Metarhinus* (Jaekel, 1910); however, when this genus was found to be preoccupied, a replacement genus, *Machaeroprosopus*, was erected by Mehl (1915). Inexplicably, the species *Machaeroprosopus validus* was long used as the genotype of *Machaeroprosopus* despite *Machaeroprosopus buceros* having priority. As the holotype specimen of *Machaeroprosopus buceros* is readily available to study, the genus *Machaeroprosopus* was considered valid by Parker, Hungerbühler & Martz (2012), with the type species being *Machaeroprosopus buceros*. Furthermore, *Machaeroprosopus buceros* has been recovered frequently as the sister taxon to '*Pseudopalatus*' *pristinus*, the type species of '*Pseudopalatus*', and has taxonomic priority over that species. As a result, all of the species previously assigned to '*Pseudopalatus*' were reassigned to *Machaeroprosopus* by Parker, Hungerbühler & Martz

(2012). The clade ‘Pseudopalatinae’ was, however, retained, as its usage lies outside of the remit of the ICZN, although it has subsequently been replaced by Mystriosuchini (see below, but see Martz & Parker, 2017).

The monophyly of the newly diagnosed *Machaeroprosopus* with respect to ‘*Redondasaurus*’ was tested by Hungerbühler *et al.* (2013); the two species of ‘*Redondasaurus*’ were previously found to nest paraphyletically within *Machaeroprosopus* (Hungerbühler, Chatterjee & Cunningham, 2003). The primary purpose of the analysis was, however, to test the phylogenetic position of the newly described species *Machaeroprosopus lottorum*. Taxonomic sampling was restricted to 12 OTUs, focussing entirely on the group ‘Pseudopalatinae’, and 41 characters of which 21 were to some extent based on characters from previous studies (Hungerbühler, 1998; 2002; Stocker, 2010). ‘*Redondasaurus*’ was found to be paraphyletic and nest within *Machaeroprosopus* (Fig. 2C), contra Hungerbühler (2002; Fig. 1C) and Parker & Irmis (2006; Fig. 2A). *Machaeroprosopus lottorum* was also found to nest within *Machaeroprosopus*, bridging the gap between the more derived species and specimens previously referred to ‘*Redondasaurus*’ and the specimens traditionally belonging to *Machaeroprosopus.*

Finally, two further studies were carried out based on the matrix of Stocker (2010, 2012, 2013), both with the aim of redescribing basal phytosaur taxa previously assigned to ‘*Paleorhinus*’ and elucidating the relationships of basal phytosaurs. Butler *et al.* (2014) redescribed the taxa ‘*Paleorhinus*’ *angustifrons* (Kuhn, 1936) (formerly ‘*Francosuchus*’) and *Ebrachosuchus neukami* Kuhn, 1936, and established a robust set of synapomorphies (which were incorporated into the phylogenetic data matrix) to diagnose a revised, restricted definition of ‘*Paleorhinus*’ that included the species ‘*Paleorhinus*’ *bransoni* and ‘*Paleorhinus*’ *angustifrons* (Fig. 3A).

Kammerer *et al.* (2015) produced a redescription of *Parasuchus hislopi* Lydekker, 1885 and found it to be the sister taxon to ‘*Paleorhinus*’ *angustifrons*, supported by two unambiguous synapomorphies.

Commented [WGP3]: Because clade names are not regulated by the ICZN it was unnecessary to replace Pseudopalatinae with Mystriosuchini. Unfortunately, however, there are no rules governing clade names so even priority does apply to retain Pseudopalatinae. However, see the argument for retaining this name in Martz & Parker, 2017.

Given the designation by the ICZN of a neotype for *Parasuchus* (Chatterjee, 2001; ICZN, 2003), this genus takes priority over '*Paleorhinus*' as the senior synonym. As a result, all species in the monophyletic '*Paleorhinus*' group were reassigned to the genus *Parasuchus* (Fig. 3B). Kammerer *et al*. (2015) also presented an update to phytosaur family-level and subfamily groups, including the following groups, from most inclusive to most exclusive: Parasuchidae Lydekker, 1885, Mystriosuchinae von Huene, 1915 (formerly Phytosauridae Jaeger, 1828), Leptosuchomorpha Stocker, 2010, and Mystriosuchini von Huene, 1915 (formerly 'Pseudopalatinae' Long & Murry, 1995). For consistency, the nomenclature used by Kammerer *et al*. (2015) is used henceforth throughout this study, with some minor modification to phylogenetic definitions (Table 2; see below).

~~Weaknesses~~ Limitations of previous work. There are a number of problems with previous phylogenetic analyses, including (i) lack of comprehensive taxonomic sampling and geographic biases; (ii) limited first-hand examination of key specimens; (iii) inclusion of parsimony uninformative characters; (iv) poorly defined characters; (v) outgroup choice. Examples of all these problems are given below.

Limited geographic sampling is one of the predominant biases in phylogenetic analyses of phytosaurs. Previous data sets have often focused on either predominantly North American or predominantly European taxa (only a small number of named phytosaur taxa are known from outside these regions, from Morocco and India); this is particularly noticeable in the studies of Stocker (2010, 2012, 2013) (Fig. 2B). Of the 20 OTUs included by Stocker (2010), only *Mystriosuchus westphali* is from Europe. The exclusion of another key European genus, *Nicrosaurus*, could be problematic for the resulting inferred phylogenetic position of *Pravusuchus*, because *Nicrosaurus* has been recovered by other analyses as the most basal member of Mystriosuchini/'Pseudopalatinae' (Hungerbühler, 2002; Parker & Irmis, 2006) (Fig. 1C, Fig. 2A). Stocker's (2010) placement of *Pravusuchus* as the immediate sister-taxon

Commented [WGP4]: Defined phylogenetically by Parker & Irmis 2006 based on Hungerbuhler 2002.

Commented [WGP5]: The Kammerer et al nomenclature was unnecessary and has not been widely used yet. Consistancy would use Pseudopalatinae, which has been stable and understood since 1995!

Commented [WGP6]: The goal of these previous studies was not an exhaustive phylogenetic study of the phytosaurs so I don't think 'weaknesses' is the right word here.

Commented [WGP7]: This exemplifies how the new nomenclature causes confusion.

to Mystriosuchini/‘Pseudopalatinae’ implies a potential close relationship between *Pravusuchus* and *Nicrosaurus*; however, this remains untested and has the potential to affect the relationships of other closely related species.

Commented [WGP8]: Ditto.

Hungerbühler (1998) scored only four of 22 OTUs based on first-hand study, with the rest scored based upon published figures and descriptions. Hungerbühler (1998) noted that caution should be used when interpreting such data as ‘descriptions of even well-preserved specimens of "well-known" taxa may contain significant misinterpretations’. A consequence of this, not explicitly mentioned by Hungerbühler (1998), relates to character sampling; the majority of Hungerbühler’s characters were novel and were therefore created with first-hand reference to only four taxa. This raises questions regarding the applicability of these characters to the remaining 18 OTUs and the validity of the character states. The matrix of Hungerbühler (2002), which was scored entirely from first-hand study, retained only 16 characters identified in the previous analysis with the states of many having been altered.

The analysis of Ballew (1989) also suffered from issues around choice and definition of characters. As noted by Hungerbühler (1998), of the 64 characters used 39 were autapomorphies of the OTUs and are therefore parsimony uninformative, and five more were characters that describe a clade that is not present in the tree. As a result, the number of phylogenetically informative characters included in this dataset was only 20.

Long & Murry (1995) presented numerous new characters to support various clades identified in their taxonomic review. However, many were criticized for being either plesiomorphic for Phytosauria, susceptible to taphonomic bias, or generally vague (Hungerbühler, 1998). This is especially true of their expansion of the definition of ‘*Paleorhinus*’ given by Hunt & Lucas (1991), which included such characters as ‘external nares anterior to antorbital fenestra,…orbits directed dorsally or

dorsolaterally,…lateral temporal fenestra large', all of which are likely to represent plesiomorphies for Phytosauria.

Finally, the analysis of Hungerbühler (1998) used *Proterochampsa barrionuevoi* as a second outgroup (Fig. 1B); *Proterochampsa* was chosen due to shared cranial similarities with phytosaurs, and historically had been suggested to be the basalmost phytosaur (Walker, 1968). However, its position was subsequently re-evaluated as a derived proterochampsid archosauriform, outside of Archosauria (Romer, 1972; Benton and Clark, 1988; Sereno and Arcucci, 1990; Sereno, 1991; Parrish, 1993; Juul, 1994). This re-evaluation was noted by Hungerbühler (1998); however, the derived morphology of *Proterochampsa* represents homoplastic, rather than plesiomorphic, character states, raising potential problems as an outgroup choice.

Current consensus. Following the revision conducted by Kammerer *et al*. (2015), phytosaurs are currently considered to fall into five successively less inclusive groups: Phytosauria, Parasuchidae, Mystriosuchinae, Leptosuchomorpha and Mystriosuchini (Table 2).

Phytosauria Jaeger, 1828, is a stem-based clade which encompasses all phytosaurs. Previously the membership of the groups Phytosauria and Parasuchidae overlapped completely (Kammerer *et al.*, 2015); however, since the re-evaluation of *Diandongosuchus* (Stocker *et al.*, 2017) this taxon has been included within Phytosauria, but excluded from Parasuchidae. However, this placement remains untested in any analysis of ingroup phylogeny to date.

Parasuchidae Lydekker, 1885 (Chatterjee, 1978; Kammerer *et al*., 2015) contains the basal genera *Parasuchus*, *Ebrachosuchus* and *Wannia*, plus all phytosaurs belonging to Mystriosuchinae, Leptosuchomorpha and Mystriosuchini. Following the work of Stocker (2013), *Wannia* has consistently been recovered as the most basal phytosaur within Parasuchidae (Fig. 2B), being distinct from the more

241 derived *Parasuchus* clade defined by Butler *et al*. (2014) and Kammerer *et al*. (2015). The latter two
242 studies also recovered *Ebrachosuchus* in a more derived position than *Parasuchus* (Fig. 3A,B).
243 Mystriosuchinae von Huene, 1915 excludes basal phytosaurs, being defined as 'the last common
244 ancestor of *Mystriosuchus planirostris* (Meyer, 1863) and *Angistorhinus grandis* Mehl, 1913 and all of its
245 descendants' (Kammerer *et al*., 2015), and is largely equivalent to Phytosauridae of previous analyses. In
246 addition to Leptosuchomorpha and Mystriosuchini, this group may also contain taxa previously
247 synonymized with '*Paleorhinus*', such as '*Paleorhinus*' *sawini*, and other genera, including *Rutiodon*,
248 *Angistorhinus*, *Brachysuchus*, and *Protome*. The relationships between *Angistorhinus*, *Brachysuchus* and
249 '*Paleorhinus*' *sawini* are unresolved, but all of these taxa have been recovered as more derived than
250 *Parasuchus* and basal to *Rutiodon* and *Protome*, with the latter two taxa being placed in a polytomy
251 together with Leptosuchomorpha (Fig. 2B, Fig. 3A,B).
252 Leptosuchomorpha Stocker, 2010, was previously defined as 'the most recent common ancestor of
253 *Leptosuchus studeri* and *Machaeroprosopus pristinus* and all descendants thereof'. We introduce a slight
254 modification to this definition here (Table 2) in response to our phylogenetic results, and include
255 *'Smilosuchus' lithodendrorum* as an additional internal specifier to ensure that minor topological
256 rearrangements between taxa that have consistently been considered as leptosuchomorphs do not
257 jeopardize the stability of the clade. Therefore, in addition to members of Mystriosuchini,
258 Leptosuchomorpha contains all species of *Leptosuchus* and *Smilosuchus*, as well as probably the taxa
259 '*Phytosaurus*' *doughty* and *Pravusuchus hortus*. *Leptosuchus* has been supported as monophyletic by
260 recent analyses, though its possible relationship with '*Phytosaurus*' *doughty* is unresolved. *Smilosuchus*
261 has also been supported as monophyletic, and recovered as the sister taxon to *Pravusuchus* +
262 Mystriosuchini.

Mystriosuchini von Huene, 1915, excludes all but the most derived phytosaurs, and was defined by Kammerer *et al*. (2015) as 'the last common ancestor of *Mystriosuchus planirostris* (Meyer, 1863), *Nicrosaurus kapffi* (Meyer, 1860) and *Machaeroprosopus buceros* (Cope, 1881) and all of its descendants'. We modify this definition here by excluding *Nicrosaurus kapfii* from the list of internal specifiers and introducing *Machaeroprosopus jablonskiae* as a replacement to maximize the taxonomic stability of Mystriosuchini among the trees recovered here (Table 2; see below). Mystriosuchini is largely synonymous with 'Pseudopalatinae' as defined by Long & Murry (1995), with the exception of the inclusion of *Mystriosuchus* and the possible exclusion of *Nicrosaurus*. Although a basal position of *Mystriosuchus* within Phytosauria, such as positioned as the sister taxon to '*Paleorhinus*', has been suggested in multiple studies (Gregory 1962; Hunt & Lucas, 1989; Long & Murry, 1995), this hypothesis has not been supported by quantitative cladistic analyses. A derived position for *Mystriosuchus* within Mystriosuchini has been found in all cladistic analyses thus far (Ballew, 1989; Hungerbühler, 1998; 2002; Parker & Irmis, 2006; Stocker, 2010; 2012; 2013; Hungerbühler *et al.*, 2013; Butler *et al*., 2014; Kammerer *et al*., 2015), and therefore seems relatively uncontroversial. The position of *Mystriosuchus* with respect to other taxa in Mystriosuchini is less well resolved, as discussed below. The European genus *Nicrosaurus* has been included within Mystriosuchini (Long & Murry, 1995; Parker & Irmis, 2006; Kammerer *et al*., 2015); however, the validity of this is also discussed below. The remainder of Mystriosuchini consists of species referred to *Machaeroprosopus* and '*Redondasaurus*', the relationships of which also differ between studies.

Commented [WGP9]: Essentially Pseudopalatinae Parker and Irmis, 2006.

Commented [WGP10]: Parker & Irmis, 2006.

Current uncertainties. Although *Rutiodon* has been consistently found close to, but in a more derived position than, *Angistorhinus*, this relationship has been tested in only three relatively independent matrices (Ballew, 1989; Hungerbühler, 1998; Stocker, 2010), of which the two earliest contain a number of

problems, as described above. It has previously been suggested that *Angistorhinus* and *Rutiodon* may be synonymous (Hungerbühler & Sues, 2001), although this has never been explicitly tested or fully published.

Aside from the study of Hungerbühler (1998), *Angistorhinus* has only been used as a generic-level OTU, or represented by a single species (Kammerer *et al.*, 2015). Kammerer *et al*. (2015) used *Angistorhinus grandis* to score the genus; however, no further discussion of relationships within the genus was presented. The systematics of the genus *Angistorhinus* are another important area which is currently poorly understood within phytosaurs.

Nicrosaurus is generally accepted as the most basal member of Mystriosuchini, and was used as a reference taxon in the previous phylogenetic definition of the group (Kammerer *et al*., 2015; Table 2); however, only the early studies of Ballew (1989) and Hungerbühler (1998) have tested this position. *Nicrosaurus* has been included in two other relatively independent analyses (Hungerbühler, 2002; Hungerbühler *et al*., 2013); however, neither included taxa from outside of Mystriosuchini, and therefore did not test the position of the genus within global phytosaur phylogeny. Therefore, although the position of *Nicrosaurus* has not been contested, it is also not especially well supported by available data.

The position of *Mystriosuchus* within Mystriosuchini remains unclear, having been placed as either sister to the clade of *Machaeroprosopus* + '*Redondasaurus*' (Hungerbühler, 1998; 2002; Parker & Irmis, 2006; Hungerbühler *et al*., 2013) or nested within *Machaeroprosopus* (Ballew, 1989; Stocker, 2010; Butler *et al*., 2014; Kammerer *et al*., 2015). As the genus name *Mystriosuchus* Fraas, 1896 has priority over *Machaeroprosopus* Mehl, 1915, this later relationship may have extensive taxonomic implications.

Commented [WGP11]: This would be unfortunate as the name differences are useful to tell quickly if someone is discussing North American or European taxa.

In multiple studies '*Redondasaurus*' has been found to nest within *Machaeroprosopus* (Ballew, 1989; Hungerbühler, Chatterjee & Cunningham, 2003; Stocker, 2010; Hungerbühler *et al.*, 2013; Butler *et*

al., 2014; Kammerer *et al*., 2015), whereas in others '*Redondasaurus*' is monophyletic to the exclusion of *Machaeroprosopus* (Hungerbühler, 1998; 2002; Parker & Irmis, 2006). In the most recent phylogeny of derived phytosaurs (Hungerbühler *et al*., 2013), '*Redondasaurus*' was found to nest within *Machaeroprosopus* and the two were tentatively synonymized, but this hypothesis requires further testing.

Materials & Methods

Institutional abbreviations

AMNH: American Museum of Natural History, New York, USA; **GPIT**: Institut für Geologie und Paläontologie Tübingen, Tübingen, Germany; **KU**: University of Kansas, Lawrence, USA; **MB**: Museum für Naturkunde, Berlin, Germany; **MNHN**: Muséum National d'Histoire Naturelle, Paris, France; **MU**: University of Missouri, Columbia, Missouri, USA; **NHMW**: Naturhistorisches Museum Wien, Vienna, Austria; **NMMNHS**: New Mexico Museum of Natural History and Science, Albuquerque, USA; **OMNH**: Oklahoma Museum of Natural History, Norman, USA; **PEFO**: Petrified Forest National Park, Arizona, USA; **SMNS**: Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; **TMM**: Texas Memorial Museum, Austin, USA; **TTU-P**: Museum of the University of Texas Tech, Lubbock, USA; **UCMP**: University of California Museum of Paleontology, Berkeley, USA; **UMMP**: University of Michigan Museum of Paleontology, Ann Arbor, USA; **USNM**: National Museum of Natural History, Washington D.C., USA; **UW**: University of Wisconsin Geological Museum, Madison, USA; **YPM**: Yale Peabody Museum, New Haven, USA.

Material

The analysis presented here uses species as OTUs to facilitate comparison with previous phylogenetic analyses. There has been recent interest in specimen-level phylogenetic analyses in vertebrate palaeontology (e.g. e.g., Upchurch, Tomida & Barrett, 2004; Tschopp, Mateus & Benson, 2015), but the validity of this approach and its results remain largely unexplored. We did not use a specimen-level phylogeny here as it would be hampered by the range of intraspecific variation found in most taxa, and would be further compounded by poor preservation in many specimens resulting in high quantities of missing data and widespread polytomies due to unstable terminals.

The OTUs included in this analysis consist of 34 species across 18 genera which are fully detailed in Appendix 1. An additional nine specimen level OTUs were also included to test their affinities. We attempted to sample all phytosaur species currently regarded as taxonomically valid or potentially taxonomically valid, with the exception of a number of problematic species that were excluded for reasons discussed below. *Euparkeria capensis* was used to root the analysis as it displays a generalized archosauriform cranial morphology (Sookias, 2016) which has been used in previous studies for character polarization (Hungerbühler, 2002; Parker & Irmis, 2006; Stocker, 2010; 2012; 2013; Butler *et al.*, 2014; Kammerer *et al.*, 2015). *Diandongosuchus fuyuanensis*, a taxon from the Middle Triassic of China initially identified as a basal poposauroid (Li *et al.*, 2012), was recently re-interpreted as the basal-most phytosaur currently known (Stocker *et al.*, 2017) and is therefore included in this analysis to verify its basal position within Phytosauria.

Of the 43 OTUs included in this analysis, 39 were scored based on first-hand study of at least one of the referred specimens. Photographs and published descriptions and figures were also used where available. The remaining four terminals (*Leptosuchus studeri*, *Diandongosuchus fuyuanensis*, *Euparkeria capensis* and *Parasuchus hislopi*) were not studied first hand for the purposes of this study, and were scored from photographs and/or published descriptions and figures.

Excluded taxa

Although this analysis was designed to be the most comprehensive cladistic dataset for phytosaurs to date, a small number of taxa were excluded for various reasons.

Angistorhinus gracilis Mehl, 1915, from the Popo Agie Formation in Wyoming, was only very briefly described in the original paper, and a holotype was not formally designated, despite apparently consisting of a large skull and much of the postcrania of a single phytosaur. When ASJ visited the University of Missouri this material could not be found; however, it may be located in one of many footlockers containing the 'Mehl collection' in the basement of the department (James Schiffbauer, pers. comm. to ASJ, 2016). At present this material is considered lost with no images available other than a line drawing of the antorbital region and two photographs of an anterior thoracic vertebra (Mehl, 1915); because the proportion of missing data would likely hinder any analysis more than its inclusion would contribute, we excluded this taxon.

Angistorhinus maximus Mehl, 1928 is known from the orbital and postorbital portions of a single skull (MU 531) from the top of the Popo Agie Formation in Wyoming. Long & Murry (1995) noted apparent similarities between this species and *Angistorhinus talainti* from Morocco, but also suggested this material may represent a more derived taxon, not referable to *Angistorhinus*. They noted that determining the taxonomic affinities would require detailed study and the type material 'may be lost' (Long & Murry, 1995:42). This material is also suspected to reside in the 'Mehl collection' of the University of Missouri. As this material is considered lost and no images exist aside from the five line drawings in Mehl (1928), it was excluded from analysis.

Angistorhinus alticephalus Stovall and Wharton, 1936 is represented by an incomplete skull, nine vertebrae, rib fragments and osteoderms (OMNH 733) from the Dockum Group of Texas. This species is

differentiated from other *Angistorhinus* species primarily by the more laterally directed orbits, the shape of the squamosal and the straight mediolateral frontal-parietal suture (Stovall and Wharton, 1936). It has been suggested that the direction of the orbits should be used cautiously due to taphonomic distortion (Gregory, 1962; Hungerbühler, 1998) and is 'severely restricted' in practical use due to the difficulty in taking measurements and previous scoring subjectivity (Hungerbühler, 1998: 130); therefore, a more detailed taxonomic analysis of this specimen is required to verify its distinctness, which is beyond the scope of this study. Given the incomplete nature of the type material, the range of better *Angistorhinus* material available to study and the taxonomic uncertainty regarding its validity, *A. alticephalus* was excluded from this study.

Angistorhinus aeolamnis Eaton, 1965 is known from a single skull, lacking approximately its dorsal 50–80 millimetres (KU 11659) from the Dockum Group of Texas. As far as can be seen from its original description, the skull does not preserve any of the features indicative of the genus *Angistorhinus*, such as posterior parietal extensions or the parietal-squamosal bars forming a posterolateral curve when viewed dorsally (Long & Murry, 1995). The loss of the dorsal part of the skull also greatly reduces the number of characters for which this specimen could be scored, making it likely to be problematic in phylogenetic analysis; this combined with its unclear taxonomic affinities leads us to exclude this taxon.

Brachysuchus megalodon Case, 1929 is a very robust taxon, represented by the largely complete, but dorsoventrally crushed holotype skull (UMMP 10336), a likely associated mandible (UMMP 10336a) and a second, well preserved, also largely complete skull (UMMP 14366), from the Dockum Group of Texas. *B. megalodon* has historically been a difficult taxon to interpret, being synonymized with '*Phytosaurus*' (Gregory, 1962) and *Angistorhinus* (Long and Murry, 1995) before being provisionally resurrected by Stocker (2010) pending a full reanalysis of the taxon. *B. megalodon* is excluded here because the material was unavailable for study due to the redevelopment of the UMMP museum.

Although the original description by Case is very detailed and contains many line drawings, it was deemed unfeasible to score such a taxonomically problematic specimen that has been subjected to severe taphonomic distortion from images alone, especially as the less distorted referred specimen has only ever been figured in palatal view (Case & White, 1934).

'*Machaeroprosopus validus*' Mehl *et al*., 1916 was erected on the basis of an incomplete skull (UW 3807) from the Chinle Formation of Arizona ~~or New Mexico~~. This specimen, which has been lost (Westphal, 1979), was long considered to be the holotype specimen for the genus *Machaeroprosopus* (Case, 1920; Camp, 1930; Colbert, 1947; Ballew, 1989; Hungerbühler, 1998). However, the holotype of *Machaeroprosopus buceros* was recently found to take priority (Parker, Hungerbühler & Martz, 2012). Considering the loss of the only specimen and its now decreased taxonomic significance and uncertain taxonomic position this taxon is here excluded.

Mesorhinosuchus fraasi (Jaekel, 1910) was named based on a single partial skull, reportedly from the Middle Buntsandstein of Saxony-Anhalt, Germany. The supposed type locality is dated as Olenekian in age, making this potentially the stratigraphically oldest phytosaur, and predating even *Diandongosuchus* by approximately 10 million years. The specimen, which was housed at the University of Göttingen, was destroyed in WWII and only one photograph exists in the original description by Jaekel (1910); moreover, its stratigraphic provenance has frequently been questioned (Gregory, 1962; 1969; Hunt and Lucas, 1991). In any case this species is excluded due to the loss of the type specimen.

'*Paleorhinus magnoculus*' Dutuit, 1977 is represented by a single, very small (275 mm anteroposterior length) juvenile skull (MNHN ALM 1) from the Argana Formation of Morocco. It was originally described as a unique species of '*Paleorhinus*' due to (among other features) its proportionately enormous orbits and small antorbital fenestrae; however, these putative autapomorphies were later reinterpreted as a reflection of the early ontogenetic stage of the type specimen (Fara and Hungerbühler,

2000) and the species was reclassified as an indeterminate specimen of *Parasuchus*, a view that is shared in this study (but see Kammerer *et al*., 2015). This taxon is therefore excluded from this study because the inclusion of ontogenetically variable features could affect its phylogenetic placement, as has been extensively reported in dinosaurs (Rozhdestvensky, 1965; Dodson, 1975; Sampson, Ryan & Tanke, 1997; Scanella & Horner, 2010; Tsuihiji *et al*., 2011).

Promystriosuchus ehlersi (Case, 1922) is known from a poorly preserved partial skull from the Dockum Group in Texas (UMMP 7487). The specimen displays extensive dorso-ventral crushing with many elements not retaining their original associations; as such, it is a difficult specimen to interpret. It has previously been referred to '*Paleorhinus*' (=*Parasuchus*) (Gregory, 1962; Hunt and Lucas, 1991; Long and Murry, 1995), but more recently its taxonomic position has been seen as uncertain (Kammerer *et al*., 2015). As with *B. megalodon* the sole specimen of this taxon was unavailable for study, and it represents a taxonomically uncertain specimen with challenging morphology and few images available in the literature; for these reasons *Promystriosuchus ehlersi* is not included in this study.

Continuous data in cladistics

The use of continuous characters in cladistics has historically been controversial, with many researchers questioning their validity and appropriateness to cladistic methods (Crisp & Weston, 1987; Pimentel & Riggins, 1987; Cranston & Humphries, 1988; Felsenstein, 1988; Stevens, 1991). The majority of concerns raised have been around the discretization of frequently overlapping taxonomic ranges of continuous measurements into distinct character states using methods often criticized as arbitrary (Poe & Wiens, 2000).

Indeed, techniques such as gap-coding (Mickevich & Johnson, 1976) and segment-coding (Thorpe, 1984; Chappill, 1989) do suffer from elements of arbitrariness: in gap-coding the size of the

fundamental gap, and in segment-coding the number of segments, must be specified by the researchers (Rae, 1998). These metrics may be based on various statistical concepts, such as 95% confidence intervals or standard deviations about the mean, and data may be treated on a linear or logarithmic scale; however, as shown by Gift & Stevens (1997) the choice of which metric to use can have a profound effect on the final character states.

Despite the general rejection of continuous data by many authors, continuous ranges of overlapping data have remained common in cladistic matrices, scored via character states with arbitrary 'discrete' cutoffs, which are generally not explained or justified, ~~e.g.~~e.g., 'ratio of femoral length to width: <6 [0], ≥6 [1]', or 'shape of orbit: circular [0], oval [1]' (Stevens, 1991; Poe & Wiens, 2000; Wiens, 2001). These arbitrary character states have been shown to convey little phylogenetic information compared to identical data ranges coded using gap-weighting (Garcia-Cruz & Sosa, 2006). Despite this, these types of characters are frequently found in modern cladistic datasets, including recent analyses of phytosaur phylogeny (Hungerbühler, 2002; Hungerbühler *et al.*, 2013; Parker & Irmis, 2006; Stocker, 2010; 2012; 2013; Butler *et al.*, 2014; Kammerer *et al.*, 2015). This study aims to incorporate continuous morphological data, including that of 'shape', characterized in a non-arbitrary manner to increase the quantity of phylogenetically useful information available to studies of phytosaur systematics, with the goal of increasing their accuracy and resolution.

As expressed above, the main problem with many continuous coding techniques is the arbitrary splitting of range data into discrete character states. The software package TNT overcomes this problem by employing a similar technique to gap-weighting (Thiele, 1993) and step-matrix gap-weighting (Wiens, 2001). Gap-weighting splits the range of species mean values into as many character states as allowed by the software (32 in PAUP*), thus increasing coding resolution and (as the characters are ordered) ensuring large changes must pass through many steps in comparison to small changes, thus increasing their weight.

This technique is, however, hampered by the limits imposed by the software. Step-matrix gap-weighting follows a similar initial procedure, but circumvents the limit on character weighting by using the sizes of the gaps between unique character states, rescaled along a range from zero to the maximum steps allowed by the software (1000 in PAUP*), to create step-matrix values to weight character state changes. Although gap-weighting provides a higher resolution of states into which measured variation can be categorized, the categorization method is still fundamentally arbitrary and, due to this, taxon ranges that are significantly different may be grouped together and those that are statistically identical may be split up (Farris, 1990).

The techniques developed in TNT (Goloboff, Mattoni & Quinteros, 2006; Goloboff, Farris & Nixon, 2008b), and used in this study, remove arbitrary discretization by analysing the taxon range values as they are, i.e. without being grouped into character states. This is possible through the use of Farris' (1970) down-pass and Goloboff's (1993) up-pass algorithms which are designed to use numerical differences between the states being optimized; therefore, the actual intervals between taxon data ranges, being numerical, are treated in the same way as ordered character states (Goloboff, Mattoni & Quinteros, 2006). As mentioned in Goloboff, Mattoni & Quinteros (2006), step-matrix gap-weighting would produce the same outcome as the TNT technique; however, this approach becomes difficult with a large number of taxa and is not capable of handling ranges of variation. As the scale of the step changes, and therefore weights, are directly proportional to the measured data, the magnitude on which the original measurements were made could have a large (and often unwarranted) influence on character weighting. Goloboff, Mattoni & Quinteros (2006) suggested that implied weighting (re-weighting of characters based on their level of homoplasy) can reduce this issue, however, this was found to be only a partial solution and a combination of implied weighting and re-scaling trait measurement values to unity produced far more satisfactory results (Koch, Soto & Ramírez, 2015).

Geometric morphometric data

Geometric morphometric (GM) characters are a relatively new development in cladistics (Catalano, Goloboff & Giannini, 2010; Goloboff & Catalano, 2011; Goloboff *et al*., 2016). In relation to phylogenetics, the use of geometric morphometrics tends to be equated with phenetic studies and the use of techniques such as principal components analysis to reduce overall morphology to a small number of axes of covariation. The method presented by Catalano, Goloboff & Giannini, (2010) avoids this; x, y and z landmark coordinates are used, without transformation, to generate ancestral state reconstructions using a spatial optimization technique which minimizes displacement between individual, or configurations of, landmarks from two descendants. A thorough discussion of the applicability of geometric morphometrics in phylogeny is given by Catalano, Goloboff & Giannini, (2010) in which previous arguments against its use are also addressed. When integrated into a phylogenetic analysis of Vespinae (Perrard, Lopez- Osorio & Carpenter, 2015), landmark characters were generally found to improve tree resolution when combined with a morphological character matrix. Landmark characters still exerted a noticeable effect with the addition of molecular data, though only four of the ten relationships generated by landmark data were supported in the morphological + landmark + molecular data trees (Perrard, Lopez- Osorio & Carpenter, 2015). In these trees the landmark data mostly affected poorly supported nodes - allowing greater resolution, though possibly only due to over-resolution due to the analysis techniques. It was also found that the landmark data alone were insufficient to reliably resolve relationships, likely due to homoplasy arising from the functional unit in which the landmark characters were placed (Perrard, Lopez- Osorio & Carpenter, 2015). Although the quantity of information may be increased by using landmark characters, not all information is included, which could lead to important features being excluded.

Character coding

The character list (Appendix 2) was constructed by combining those used in previous analyses (Ballew, 1989; Hungerbühler, 2002; Stocker, 2010; Butler *et al*., 2014; Kammerer *et al*., 2015) as well as by identifying new characters based on first-hand study of specimens and published literature. In order to compare the effects of different character types on phylogenetic results, all characters (including continuous and GM) were scored and input into one matrix, each character type as a different data block. The resulting matrix contained three blocks of data: discrete scores, continuous ranges and GM coordinates. Many of the continuous and GM characters were based on discrete characters from previous analyses, for which the categorization of character states seemed inappropriate, ~~e.g.~~e.g., for relative linear measurements of morphological features, or complex morphologies. Therefore, some characters in the discrete data block are discrete versions of continuous or GM characters. Some continuous and GM characters incorporated here were novel; therefore, discrete versions of these were also created in the discrete data block to ensure that where phylogenies were analysed using different data types, any differences in results would not be affected simply by differences in the exact morphological information included. The different combinations of character types were incorporated into different analyses by setting either the continuous, GM, or both character blocks to 'active' or 'inactive' in the phylogenetic software TNT (see below).

The number of characters and proportion of missing data in each data block are summarized in Table S1. No characters were excluded based on quantity of missing data in scored taxa as including more characters, even if this increases the proportion of missing data, has been shown to increase accuracy in phylogenetic analysis (Wiens, 1998). This technique increases the possibility of long branch attraction (Swofford *et al.*, 1996), but is less likely in a dataset where missing data is distributed randomly among all taxa (Poe & Wiens, 2000); in our dataset missing data seem more likely to occur in certain taxa and

certain characters, therefore the possibility of long branch attraction should be kept in mind when interpreting the results.

A consistent discrete matrix was used as a base for each analysis, into which continuous or GM characters were swapped with their discrete counterparts. The discrete data block consisted of 94 characters, the continuous 10 characters and the GM five characters. These were combined in four analyses: 1) discrete characters only (D coding treatment) (94 characters, 21 of which are ordered), 2) discrete + continuous characters (DC coding treatment) (94 characters, 21 ordered), 3) discrete + GM (DM coding treatment) (90 characters, as some GM characters encompass variation described by more than one character in the discrete dataset; 19 ordered), 4) discrete + continuous + GM (DCM coding treatment) (90 characters, 19 ordered). A full list of all characters, ordering and the correspondences of continuous and GM to discrete characters is available in Appendix 2. The coding procedures used here for continuous and GM characters are described below, as are the methods of character state distinction for their discretized counterparts.

It is important to note here that when incorporating continuous and geometric morphometric character scorings for analysis, the format of the TNT data file requires these characters to be presented first in the file. This differs from how the characters are ordered in our character list (Appendix 2). Our character list presents characters in the order in which they occur for the base discrete matrix; where a character possesses a continuous or GM variant this is flagged next to that character. It should also be noted that characters in a TNT file begin at zero, whereas we shift our characters such that the list begins at one.

Continuous characters. Measurements were taken from all referred specimens with the appropriate morphology preserved, either directly, using digital callipers, or from photographs, using the software

ImageJ. Standard error was calculated about the mean score of each species, this was then used to calculate min-max species ranges with statistically meaningful differences (Goloboff, Mattoni & Quinteros, 2006). Min-max species range values were rescaled in each character using the formula: $z_i = x_i - min(x) / max(x) - min(x)$ where z_i is the rescaled value, x_i is the original value and min/max(x) are respectively the minimum and maximum original values in the range of variation across all taxa for that character. This rescales values onto a 0–1 scale, ensuring that magnitudes of interspecific differences within characters are maintained, whilst between-character weighting is standardized. The rescaled range values (and where only one specimen is known, the single values) were input into the data matrix file and treated as ordered.

GM characters. Many features of phytosaur skulls that are appropriate for shape analysis contain few discrete landmark positions, making traditional landmark analysis difficult, and the resolution of the morphology influencing the results would be poor. For example, only two sutures regularly form connections on the border of the antorbital fenestra that could be landmarked in all phytosaurs, and due to the variable shape of the fenestra there are no consistent 'corners' or other morphological features that can be traditionally landmarked on the border, aside from the most anterior and posterior extremities. Conversely, these problems can be resolved by using sliding semi-landmarks to approximate outline shape; this is the technique used here. In techniques such as principal components analysis, semi-landmarks require special treatment, on account of their reduced dimensionality and therefore degrees of freedom (Bookstein, 1996; Zelditch, Swiderski & Sheets, 2012); however, as TNT does not use such analyses and providing the user employs appropriate Procrustes alignment techniques, nothing precludes their use. Semi-landmarks were digitized from photographs using the 'Draw background curves' tool in the software tpsDig2 (Rohlf, 2015) to capture a detailed outline of the structure; this was then resampled

584 to contain a consistent number of equally spaced points which were used for alignment. See Fig. S1 for
585 configurations of landmarks in GM characters. Semi-landmarks were subjected to sliding and Procrustes
586 superimposition to minimize distances between configurations using the R package Geomorph (Adams &
587 Otarola-Castillo, 2013). In TNT, landmark configurations were scaled to unity using the command '*lmark*
588 *rescale* =*;'. Whole configurations of landmarks were used for optimization and to calculate support
589 values, rather than a pairwise approach with each individual landmark, as semi-landmarks define curves
590 and not homologous points.
591
592 **Discrete characters.** Characters consisting of continuous measurements such as ratios were discretized
593 into character states using primarily quantitative, but also qualitative approaches; all measurements from
594 all referred specimens were sorted numerically and character state divisions were introduced where gaps
595 occurred in their sequence. Where no substantial gaps occurred character states were introduced at points
596 between substantial transitions in the data. For example: in a hypothetical dataset of four taxa, A–D, each
597 represented by four specimens which all occupy a 0–10 continuous scale for one of their characters, if all
598 or a substantial majority of specimens from taxa A and B sit between zero and five, whereas those of taxa
599 C and D sit between five and ten, the continuous character range would be divided into two character
600 states at number five. This therefore splits the continuous range into discrete states in the absence of gaps.
601 This treatment was designed to mimic the presumably qualitative techniques for dividing
602 continuous data into discrete states used in previous analyses (although the delimitation technique has
603 never been described in any previous phytosaur phylogeny), and represents a similar treatment to the
604 'arbitrary' method of Garcia-Cruz and Sosa (2006). Discrete characters used as counterparts to implicitly
605 ordered continuous characters were also treated as ordered. This means that different topologies resulting

606 from different combinations of character types reflect changes in character coding approach rather than
607 differences in the approach to character ordering.
608
609 **Implied weighting.** Implied weighting (Goloboff, 1993) is a method of character weighting in which the
610 number of step changes a character undergoes in its current tree topology is compared to the minimum
611 possible for that character, as a metric for homoplasy. Each character in a tree topology is then weighted
612 in inverse proportion to its level of homoplasy, with a concavity constant (k) ascribing the severity of
613 weighting. These weighted scores of 'character fit' are then summed to provide an estimate of character
614 fit for the whole tree; each tree topology in the analysis undergoes the same procedure, with the 'best'
615 overall tree(s) having the best character fit score. We primarily use implied weights here for its apparent
616 advantages in the analysis of matrices high in homoplasy (Goloboff *et al.*, 2008a); a problem well-
617 recognized in Phytosauria (Hungerbühler, 1998, 2002). Although implied weighting has been criticized
618 recently (Congreve & Lamsdell, 2016) it does also have advantages when using continuous and GM
619 character scorings. Continuous characters may be measured on different scales, and this difference in
620 scaling is transferred to a character's step-matrix (arbitrarily increasing the impact of 'large-scale'
621 characters); accordingly, homoplasy in characters measured on large scales tends to be greater and these
622 characters are thus down-weighted in proportion with this (Goloboff, Mattoni & Quinteros, 2006). In this
623 study we further address issues of scaling by standardizing continuous character ranges into a 0–1 range,
624 as described above. Implied weighting also provides a method for weighting landmark-based characters
625 and can be performed either for each individual landmark within a configuration or for whole
626 configurations using the average homoplasy. The latter method is particularly useful in this study as we
627 use semilandmarks; as such the individual landmarks do not necessarily represent homologous points,

rather it is the overall structure that is important - it is therefore the whole configuration of landmarks that should be treated as a single character for weighting.

Analyses

All analyses were performed in the software TNT version 1.5 (Goloboff & Catalano, 2016), under extended implied weighting with the concavity constant 'k' set to vary for each character depending on the quantity of missing entries (using '*xpiwe (**' commands).

Implied weighting requires the minimum possible length for each character coding in order to calculate homoplasy; however, this is problematic in landmark data (Goloboff *et al.*, 2016). Therefore, TNT provides an option to find minimum values for each landmark using heuristic searches; this search function was applied before analysing any dataset incorporating GM characters, then the minima were added to the file for use during tree searching. Furthermore, GM characters were each weighted separately according to the average homoplasy of their landmark configuration (using '*xpiwe [*' commands); therefore, weighting was based on entire configurations rather than the sum of component landmarks, which as stated above, may not be individually homologous.

Analysis parameters. Tree searches were performed using the new technology algorithms in TNT: 10,000 random addition sequences, analysed using TBR swapping with 10 iterations of drift and ratchet, followed by a sectorial search and finally three rounds of tree fusing. The search was performed until the minimum tree length was hit five times. The duration of tree searches dramatically increased with the addition of GM characters; therefore, only 200 random addition sequences were used and minimum length was found only once. Furthermore, because landmark data is relatively unstructured the perturbation phases of ratchet and drifting can produce trees that are 'too suboptimal' and therefore

greatly increase the search time (Goloboff *et al.*, 2016). We therefore followed the suggestion of Goloboff *et al*. (2016) and increased the drift 'xfactor' to 5, decreased the percentage of swapping to be completed to 90%, decreased the number of substitutions to 45, and for ratchet, lowered the probability of reweighting (both up and down) to 3 and decreased the number of substitutions to 30.

Bremer supports were calculated using 10,000 (D and DC) or 1000 (DM and DCM) trees suboptimal by a fit of 10; branch swapping using TBR was performed and absolute supports were calculated based on the results. Robusticity analysis was carried out using symmetric frequencies, with TBR swapping beginning from 10 Wagner trees and 10,000 (D, DC) or 100 (DM, DCM) replicates. As the matrices including GM data were exceptionally computationally heavy and time consuming, parameters were altered such that trees were accepted without consideration of error margin during landmark searches and that swapping distance for branch swapping was reduced (commands respectively: '*lmark errmarg 0*' and '*bbreak : limit 5*').

Output processing and comparisons. Where more than one tree of best character fit resulted from an analysis, a strict consensus was generated. With implied weighting in effect, ties in tree length (resulting in multiple best fitting trees) become very uncommon due to the use of floating-point character-fit calculations. Additionally, continuous data are analysed as actual numerical differences, rather than categorical steps, also reducing the chance of exact ties. To avoid over-resolution due to the acceptance of a single or few trees showing only an extremely small difference in character fit compared to other topologies, an arbitrary Bremer support cut-off value of 0.08 was implemented, below which nodes were judged to be poorly supported and were collapsed. In addition a second cut-off value was used (0.11) which was equal to the average step-length of a single character following weighting. This particular number was used in an attempt to emulate the procedure common in phylogenetics, to collapse nodes with

a Bremer support of less than one step. These cut-offs were maintained throughout the four treatments, allowing the effects on tree resolution to be compared.

Best character fit trees resulting from each of the four analyses using different combinations of character data types (see above) were compared using several techniques. CI and RI were compared to assess the homoplasy present in the trees resulting from each analysis. Maximum agreement subtrees were constructed for each comparison to compare the number of congruent relationships between the trees; this was supplemented with a strict consensus of the two trees in case lower level congruence was masked in the agreement subtree by higher level polytomies (Goloboff, Mattoni & Quinteros, 2006). Subtree pruning and regrafting (SPR) distances were calculated to find the minimum number of changes under the SPR search algorithm required to convert one tree topology into the other - essentially a numerical description of tree similarity. The rooted Robinson-Foulds (RF) distance, which measures the differential presence/absence of phylogenetic relationships between trees, was also used to measure tree-similarity.

The effect of each coding technique was assessed and compared to its alternative counterparts in several ways. Trees were initially compared using mean and summed frequency and Bremer supports across each collapsed tree, alongside the number of nodes retained after collapsing each tree to get a broad view of any major differences. For a more detailed view of the effects of data type on the nodal support each non-collapsed best fit tree was split into five tree-regions; 1) the most basal portion of the tree, including all non-Mystriosuchinae members of Phytosauria; 2) the clade formed by *Rutiodon* and *Angistorhinus*; 3) *Leptosuchus*-grade taxa, here composed of all *Leptosuchus*, *Smilosuchus* and *Nicrosaurus* species, plus PEFO 34852, '*Phytosaurus*' *doughtyi*, *Pravusuchus hortus* and *Coburgosuchus goeckeli*; 4) all members of *Machaeroprosopus* and '*Redondasaurus*', plus USNM V 17098, NMMNHS-P 4256, NMMNHS-P 31094 and *Protome batalaria*; 5) the clade composed of named species of *Mystriosuchus* plus NHMW 1986 0024 0001 and MB.R. 2747. The mean frequency and Bremer supports

were calculated within each region to investigate the effects of different character coding techniques at a greater resolution.

The support for monophyly of groups/taxa of interest was investigated by placing them in alternative positions in a constraint tree, then re-running the analysis whilst imposing those constraints and observing the effect on character fit in the resulting trees.

The accuracy of trees, as denoted by the various nodal support metrics and comparisons described above, is a measure of internal consistency; regardless of a tree's accuracy it may still be spurious. Stratigraphic congruence was used here as an independent estimate of tree-validity; four metrics were employed which measure stratigraphic congruence differently. (1) The stratigraphic consistency index (SCI) (Huelsenbeck, 1994) measures the proportion of nodes within which the first appearance datum is of the same age or younger than the sister node; these nodes are considered stratigraphically consistent. (2) The relative completeness index (RCI) (Benton & Storrs, 1994) reports the ratio between the sum of ranges for taxa in the tree and the sum of ghost-range length within the tree. (3) The Manhattan stratigraphic measure (MSM*) (Siddall, 1998; Pol & Norell, 2001) optimizes the difference in age between the first appearances of taxa (Manhattan distance) as a Sankoff character on the proposed tree. The MSM is the ratio between the minimum possible tree length based on taxon ranges (topology determined by the Manhattan distance character), and the tree length when Manhattan distance is optimized to the original topology. The MSM is basically the consistency index of the distance character (Pol & Norell, 2006). Pol & Norell (2001) introduced a correction to prevent reversals in the Manhattan distance character 'states', presenting the updated metric, MSM*. (4) The gap excess ratio (GER) (Wills, 1999) finds the proportion of ghost range in a tree, relative to the minimum and maximum possible sum of ghost ranges for the corresponding dataset. It also optimizes age range differences on the tree in the same

719 manner as the MSM*, but is calculated as the retention index for the distance character (Pol & Norell,
720 2006).

721 The 'strap' package (Bell & Lloyd, 2014) for the software R version 3.2.5 (R Core Team, 2016)
722 implements all the above metrics, and was used for all analyses of stratigraphic congruence in this study.
723 The strap package also implements a test of statistical significance for each metric, based on random
724 permutations. In calculating significance values we made use of two additional options offered by strap:
725 the first is to generate random trees by swapping OTUs, whilst maintaining tree shape; the second is to fix
726 the outgroup OTU such that it is not randomized. These additions respectively resolve issues of random
727 trees being more symmetrical than commonly found in fossil groups (Wills, Barrett & Heathcote, 2008),
728 and the deliberate assignment of the outgroup prior to analysis, removing the need for its position to be
729 tested (Bell & Lloyd, 2014). The random trees therefore provide a closer estimate of the original tree
730 topology and a more robust test of significance (Bell & Lloyd, 2014). Primarily the P-values from the
731 significance tests are used here for comparisons of stratigraphic congruence, rather than the raw metrics,
732 as the latter are strongly influenced by tree balance, the arrangement of taxon stratigraphic ranges and tree
733 size (Siddall, 1996; Willis, 1999). The results of randomization tests are free from these influences and
734 should therefore be more directly comparable (Wills, 1999; Benton, Hitchin & Wills, 1999).

735 In this study significance tests were carried out with 1000 random permutations. The strict
736 consensus trees resulting from the four data treatments were analysed, as were the three most recent
737 alternative phylogenetic hypotheses of phytosaur relationships (Parker & Irmis, 2006; Hungerbühler *et al*.,
738 2013; Kammerer *et al*., 2015). Where a previous analysis included specimen-level OTUs or taxa not
739 present in this study, these terminals were removed; three terminals were removed from the tree of
740 Kammerer *et al.* (2015) and two from Hungerbühler *et al.* (2013). Three alternate hypotheses of topology
741 were presented by Hungerbühler *et al.* (2013), though with the two terminals missing from this analysis

742 removed, two of the trees become synonymous; therefore, only two hypotheses are tested here from
743 Hungerbühler *et al.* (2013).
744
745 ## Results
746
747 A total of eight best fit trees were found across all four coding variants; in each of the D and DC
748 treatments three equally 'fitting' trees were found, whereas DM and DCM each returned only one best fit
749 tree. Our results are presented as the strict consensus trees of the best fit trees or single best fit trees
750 resulting from each of the four different variants of character coding (D, DC, DM and DCM) with
751 absolute and relative symmetric resampling frequencies above nodes, and Bremer supports below (Figs.
752 4–7). We also present the strict consensus and maximum agreement subtree of these four trees, to
753 summarize the most consistent relationships across all coding treatments (Fig. 8).
754 The tree lengths resulting from the four coding treatments are summarized in Table 3, as are the
755 consistency and retention indices (CI and RI). Tree lengths are not directly comparable between
756 treatments including or excluding GM coding; this arises because the morphology encoded in some GM
757 characters encompasses more than one discretely coded character. Therefore, analyses incorporating GM
758 data contain fewer characters than the other scoring types and will likely show lower tree lengths as a
759 result.
760 Conversely, providing that continuous characters replace their corresponding discrete characters
761 with one-to-one equivalence (which they do here), their alternative coding method alone should not affect
762 tree length. Continuous characters are here scored as ratios and are transformed to occupy a 0–1 scale; the
763 standard treatment of continuous characters by TNT uses the numerical differences between scores to
764 create the step-matrix. As these values are constantly below 1 it may be expected that the greater

765 proportion of continuous characters in a dataset would result in lower tree length. However, due to our use
766 of implied weighting this should not present a problem, as tree length is the sum of homoplasy-adjusted
767 character weight. Homoplasy is, in the simplest sense, calculated as a proportion of the minimum length
768 of a character in topology X, and the minimum possible length of a character in any topology. Character
769 weight is then calculated from this proportion (homoplasy) and is then summed across all characters to
770 generate tree length. As character weight is based on a character-specific proportion, the actual size of
771 changes in the character step-matrix should not affect the final tree length. Simply put, if equivalent
772 discrete and continuous characters share a consistent proportion of homoplasy, their effect on tree-length
773 under implied weighting will be identical regardless of how they are scored.
774
775 **Comparisons of similarity**
776 Comparisons of trees are presented in Tables 4 and 5, using the number of taxa retained by maximum
777 agreement subtrees, the SPR distance and the RF distance as metrics of similarity. Maximum agreement
778 subtrees essentially produce fully resolved consensus trees by pruning taxa in conflict between the input
779 trees; the number of taxa retained in a maximum agreement subtree can be used as a measure of
780 topological similarity between two or more trees.
781 All four trees were found to be significantly similar to each other. For all pairwise comparisons
782 between different coding treatments the number of taxa retained in the maximum agreement subtrees was
783 statistically much greater than expected by chance. Statistical significance was established using 5,000
784 agreement subtrees constructed with randomized tree topologies. None of these subtrees retained more
785 than 14 OTUs and subtrees retaining the highest number of OTUs (14) comprised only 0.96% of the data.
786 All pairwise comparisons yielded multiple maximum agreement subtrees of the same length showing
787 alternative prunings (Table 4).

The two coding treatments that utilized continuous data (DC and DCM: Figs. 5, 7) were consistently found to be the most similar tree topologies using all similarity metrics. The trees generated from discrete and discrete + GM coding treatments (D and DM: Figs. 4, 6) also showed a high degree of similarity to each other. However, there is greatly reduced similarity when the DC/DCM trees are compared with the D/DM trees. Broadly speaking, this suggests there are two partially conflicting phylogenetic hypotheses, one represented by the DC and DCM trees and one by the D and DM trees. However, the agreement subtrees suggest that the amount of overlap between these hypotheses is still greater than would be expected to occur by chance.

Consistent relationships

A list of nodal synapomorphies for each tree is presented in Appendix 3. The following relationships were found to be consistent in the trees of all four scoring treatments, and match the topology of the strict consensus tree (Fig. 8).

Diandongosuchus is recovered as the most basal phytosaur in every tree. Its position outside of all other phytosaurs is supported well by frequency and Bremer supports, and two consistent synapomorphies supporting Parasuchidae (Fig. 8, node B) to the exclusion of *D. fuyuanensis* in every tree [13: 0→1; 22: 0→1].

Wannia scurriensis is consistently found as the most basal member of Parasuchidae, outside the clade that includes *Parasuchus* and Mystriosuchinae. The latter clade (Fig. 8, node C) is, however, poorly supported, with only two synapomorphies supporting *Parasuchus* + Mystriosuchinae to the exclusion of *Wannia* in all four trees [36: 0→1; 69: 0→1].

809 *Parasuchus* (Fig. 8, node D) is consistently found to include the species *Parasuchus bransoni*,
810 *Parasuchus hislopi*, and *Parasuchus angustifrons*, and is well supported by frequency and Bremer scores,
811 with three synapomorphies common to all trees [23: 0→1; 26: 0→1; 50: 0→1].
812 '*Paleorhinus*' *parvus*, '*Paleorhinus*' *sawini* and *Ebrachosuchus neukami* are closer to
813 Mystriosuchinae than to *Parasuchus* in all trees; however, the interrelationships of these species and their
814 exact relationships to Mystriosuchinae are variable in the different coding treatments. Mystriosuchinae
815 itself (Fig. 8, node G) is supported by three synapomorphies common to all trees [9: 0→1; 14: 1→2; 80:
816 0→1].
817 *Rutiodon carolinensis* and *Angistorhinus* form a clade at the base of Mystriosuchinae that is
818 consistently well supported by frequency and Bremer supports (Fig. 8, node H) and is united by two
819 synapomorphies in all trees [22: 2→1; 92: 0→1]. Within this clade, *Rutiodon* is consistently the sister
820 taxon to *Angistorhinus;* the clade composed of *Angistorhinus* and *Angistorhinus*-like specimens, to the
821 exclusion of *Rutiodon carolinensis* (Fig. 8, node I), is supported by two synapomorphies [56: 0→1; 58:
822 0→1]. The relationships of the species and specimen-level OTUs within *Angistorhinus* are consistent in
823 all coding treatments: *A. talainti* is the most basal of the two named species and *A. grandis* is more
824 derived, with the specimen-level OTUs representing either potential additional species within the genus,
825 or morphologically diverse representatives of existing *Angistorhinus* species.
826 Leptosuchomorpha (Fig. 8, node M) possesses two synapomorphies common to all tree topologies
827 that separate it from the more basal taxa [16: 1→0; 25: 0→1]. Within Leptosuchomorpha the four
828 phylogenies are more variable (Fig. 8, node M). Among the leptosuchomorph OTUs not included in
829 Mystriosuchini there is only one clade common to all tree topologies: the clade which unites *Nicrosaurus*
830 *kapffi* and *Nicrosaurus meyeri* with *Coburgosuchus goeckeli*, although the relationships between these

three species are variable in the different coding treatments (Fig. 8, node N). This clade is supported by a single synapomorphy [57: 1→2].

Although there are conflicting relationships, the majority of the leptosuchomorph taxa that have been excluded from Mystriosuchini by previous analyses (~~e.g.~~e.g., Kammerer *et al*., 2015) are also consistently excluded from Mystriosuchini as defined in the current analysis (with *Mystriosuchus planirostris*, *Machaeroprosopus jablonskiae* and *Machaeroprosopus buceros* as exemplars of the clade; see Table 2). Non-Mystriosuchini leptosuchomorphs in this analysis include all members of *Smilosuchus*, *Leptosuchus* and *Nicrosaurus* plus '*Phytosaurus*' *doughty*, *Pravusuchus hortus*, *Coburgosuchus goeckeli* and PEFO 34852, as well as *Protome* in some of the coding treatments (see below).

There is only one synapomorphy of Mystriosuchini common to all trees (Fig. 8, node O) [43: 2→0]. Much like the non-Mystriosuchini leptosuchomorphs, interrelationships within Mystriosuchini are generally inconsistent across the different coding treatments; however, as in previous analyses, the clade includes all named species of *Machaeroprosopus*, '*Redondasaurus*' and *Mystriosuchus*, as well as USNM v 17098, NMMNHS P4256, NMMNHS P31094, MB.R. 2747 and NHMW 1986 0024 0001. *Protome batalaria* has been placed close to *Rutiodon* by previous studies (Stocker, 2012; Butler *et al*., 2014; Kammerer *et al*., 2015). In this study it is consistently found to be either nested just inside Mystriosuchini (Fig. 4, Fig. 6) or as the sister taxon to this clade (Fig. 5, Fig. 7).

Commented [WGP12]: What is supporting this placement? What ever it is would finally show that overall squamosal morphology (i.e. isolated squamosals) cannot be used to separate Leptosuchus/Smilosuchus from Machaeroprospus as utilized by Ballew, Long & Murry, Parker and Irmis, etc… Protome has a Smilosuchus/Leptosuchus type squamosal.

Within Mystriosuchini, *Mystriosuchus* (Fig. 8, node P) is the only consistently supported clade. Within this clade MB. R. 2747 and NHMW 1986 0024 0001 form successive sister taxa to *Mystriosuchus planirostris* and *Mystriosuchus westphali*; it is likely that these two specimen-level OTUs also represent unnamed species of *Mystriosuchus*. *Mystriosuchus* and its internal nodes are statistically well supported. The basal node of the clade and the internal nodes are each supported by single synapomorphies common to all trees (Fig. 8, node P) [85: 1→0], (Fig. 8, node Q) [2: 1→2], (Fig. 8, node R) [88: 0→1].

Conflicting relationships

As discussed above, relationships among the non-Mystriosuchinae taxa are almost entirely consistent across all four trees with the exception of '*Paleorhinus*' *parvus*, '*Paleorhinus*' *sawini* and *Ebrachosuchus neukami* (Fig. 8). The relationships between these taxa are poorly supported statistically and variable, and the three form a polytomy together with Mystriosuchinae in the strict consensus trees of the D and DC analyses (Figs. 4, 5). In the DM and DCM analyses (Figs. 6, 7) the relationships are consistent, if not well supported. '*Paleorhinus*' *parvus* is the sister taxon of Mystriosuchinae, with *Ebrachosuchus neukami* and '*Paleorhinus*' *sawini* forming successively more distant sister groups.

Those non-Mystriosuchini members of Leptosuchomorpha in this analysis comprise species assigned to the genera *Smilosuchus*, *Leptosuchus*, '*Phytosaurus*', *Pravusuchus*, *Nicrosaurus* and *Coburgosuchus*. Relationships between these taxa are entirely consistent in the DC and DCM trees (Figs. 5, 7). However, the D and DM trees each show different topologies (Figs. 4, 6). In the DC and DCM trees, *'Smilosuchus' lithodendrorum* is the most basal taxon in Leptosuchomorpha. Within Leptosuchomorpha there are two clades: one containing all species of *Leptosuchus* and *Nicrosaurus*, in addition to *Pravusuchus hortus*, *Coburgosuchus goeckeli* and PEFO 34852; and one containing '*Phytosaurus*' *doughtyi*, *Smilosuchus adamanensis*, *Smilosuchus gregorii*, *Protome* and Mystriosuchini.

In the D tree, all the aforementioned taxa with the exception of *Smilosuchus gregorii* form an unnamed clade (Fig. 4, node 14), which forms a sister relationship within Leptosuchomorpha with *Smilosuchus gregorii* + Mystriosuchini. The basalmost taxon within this unnamed clade is *Smilosuchus adamanensis*, which in the other three trees presented here is recovered as a branch just basal to *S. gregorii*; the next taxon in the clade, '*Phytosaurus*' *doughtyi*, also falls closer to *S. gregorii* than *Leptosuchus* in the DC, DM and DCM trees. Above '*Phytosaurus*' *doughtyi*, two distinct clades are

present as sister taxa. One of these (Fig. 4, node 17) contains *Leptosuchus* spp., plus *'Smilosuchus' lithodendrorum* and PEFO 34852; the second (Fig. 4, node 20) contains *Pravusuchus hortus*, *Nicrosaurus* spp. and *Coburgosuchus goeckeli*. Relationships in both clades have weak Bremer support, with the exception of the node uniting *Nicrosaurus kapffi*, *N. meyeri* and *C. goeckeli* (Fig. 4, node 21), in which frequency supports are generally better.

The topology for this region of the DM tree is very different from that of the D tree (to which it is very similar in most other respects). The taxa that form a distinct clade in the D tree (Fig. 4, node 14) instead form a largely pectinate series of outgroups to Mystriosuchini in the DM tree (Fig. 6, nodes 15–25). The most basally branching taxon is *Leptosuchus studeri*, which falls outside of Leptosuchomorpha in this tree. At the base of Leptosuchomorpha is a relatively poorly supported (according to frequency supports) clade including '*Phytosaurus*' *doughtyi*, *Leptosuchus crosbiensis*, and a sister taxon relationship between *'Smilosuchus' lithodendrorum* and PEFO 34852 (Fig. 6, node 17). *Pravusuchus hortus*, *Smilosuchus adamanensis* and *Smilosuchus gregorii* form a series of outgroups to a clade consisting of Mystriosuchini and the *Nicrosaurus* + *Coburgosuchus* clade. In the DM tree the *Nicrosaurus* species are sister taxa (Fig. 6, node 25). In this topology, *Nicrosaurus* occupies a position consistent with that recovered in previous analyses of Mystriosuchini (Hungerbühler, 2002; Hungerbühler *et al*., 2013) and with the group's previous definition (Kammerer *et al*., 2015).

The main inconsistency within Mystriosuchini is the fluctuating position of the *Mystriosuchus* clade (*Mystriosuchus* spp. plus NHMW 1986 0024 0001 and MB. R. 2747). In both trees incorporating continuously scored data (DC, DCM) this group is recovered as highly derived within Mystriosuchini (Figs. 5, 7), as has previously been found by Stocker (2010, 2012, 2013), Butler *et al.* (2014) and Kammerer *et al.* (2015) (Figs. 2B; 3A, B). In the D and DM coding treatments, however, the *Mystriosuchus* clade forms the sister group to *Protome batalaria* + *Machaeroprosopus* (Figs. 4, 6), as has

been found by Hungerbühler (2002), Parker and Irmis (2006) and Hungerbühler *et al.* (2013) (Figs. 1A; 2A, C).

Relationships among other species within Mystriosuchini are highly variable, though the general pattern is of a highly laddered series of sequentially more derived terminals. Although the order of OTUs varies considerably, there are some similarities across different coding treatments; taxa in the less derived positions are generally *Protome batalaria* and *Machaeroprosopus andersoni*, which are then followed by *Machaeroprosopus pristinus*, *Machaeroprosopus buceros* and *Machaeroprosopus lottorum* and then a clade containing both species of '*Redondasaurus*' (Fig. S2).

As previously mentioned, the two conflicting hypotheses regarding the position of *Mystriosuchus* (basal or derived within Mystiosuchini) split the results of the four coding methods into two alternative topological hypotheses. The positions of *Machaeroprosopus mccauleyi* and *Machaeroprosopus jablonskiae* also consistently differ between these topologies. In the trees in which *Mystriosuchus* occupies a derived position within Mystriosuchini (DC, DCM), *Machaeroprosopus mccauleyi* and *Machaeroprosopus jablonskiae* form successive sister taxa, basal to the clade comprising *Machaeroprosopus pristinus*, *Machaeroprosopus buceros* and *Mystriosuchus*. In topologies where *Mystriosuchus* is recovered basal to *Machaeroprosopus* (D, DM), *Machaeroprosopus mccauleyi* and *Machaeroprosopus jablonskiae* are more derived than the clade composed of *Machaeroprosopus pristinus*, *Machaeroprosopus buceros* and *Machaeroprosopus lottorum*, forming successive sister taxa to '*Redondasaurus*'.

The position of *Machaeroprosopus zunii* is more consistent; in three trees (D, DC and DM) it is recovered basal to the clade composed of *Machaeroprosopus pristinus*, *Machaeroprosopus buceros*, and all more derived taxa. In the DCM results *Machaeroprosopus zunii* is placed more derived than than

Machaeroprosopus pristinus and *Machaeroprosopus buceros*, but less derived than *Machaeroprosopus lottorum*.

Machaeroprosopus lottorum is another taxon which varies consistently between the two broad topological hypotheses presented. In the trees incorporating continuously scored data, in which *Mystriosuchus* is highly derived (DC, DCM), *Machaeroprosopus lottorum* forms a clade with NMMNHS-P 31094 (Figs. 5, 7), closely related to '*Redondasaurus*' and *Mystriosuchus*, as was found by Hungerbühler *et al*. (2013). In the alternative topologies (D, DM) *Machaeroprosopus lottorum* nests with *Machaeroprosopus pristinus*, to the exclusion of *Machaeroprosopus buceros* (Figs. 4, 6). Both positions are similarly poorly supported by Bremer analyses, but possess relatively good frequency scores. In this topology NMMNHS-P 31094 is consistently found within '*Redondasaurus*', as the sister taxon of '*Redondasaurus*' *gregorii*, to the exclusion of '*Redondasaurus*' *bermani*.

Commented [WGP13]: Does not support proposed conspecific hypothesis for M. pristinus and M. buceros as sexual dimorphs.

Accuracy and validity

Bremer supports. With poorly supported nodes collapsed below Bremer values of 0.08, the DM condition produced greatest tree resolution, retaining 23 nodes; however, its mean Bremer score is one of the lowest among the four trees, suggesting that the additional nodes supported in this tree only exceed the cut-off by a small amount (Table 6). When using the mean step length of a single character (0.11) as a cut-off for node-collapsing, the DM and DCM conditions were found to perform more poorly than the D and DC conditions in terms of nodes retained and total Bremer support. Mean Bremer values for the retained nodes remained almost consistent across all trees (Table 6).

When broken down into regions, it appears that the extra support in the DM tree is added in regions three and four, which are almost consistently the worst supported in all trees. Despite this extra

support, relationships within these regions are still relatively poorly supported in the DM condition, and the support for region one also becomes among the poorest in both GM trees (DM and DCM) (Table 7).

The best condition for overall Bremer support was the DC tree (Fig. 5), achieving the highest, or equal highest support in all regions except three and four, with a sum of mean support equalling 0.75. Conversely, despite maximizing support in the poorest regions of the tree, the DM condition scored second worst for overall support, with a sum total of 0.60; this was followed by the DCM condition with a score of 0.58 (Table 7).

Frequency supports. With a cut-off for node collapsing of <10, symmetric frequency support produced broadly similar results for all the trees, with the DC condition producing a marginally higher resolution and mean support value. Conversely to the results from Bremer supports, the DM condition was the poorest supported topology based on symmetric resampling, although the difference between 'best' and 'worst' is minor (Table 6).

Split into regions, the overall sum of mean supports follows the same trend as that of the Bremer supports; DC is best, with a sum of 240.56, then D (229.47), DM (213.16) and finally DCM (199.11). The DC tree holds the highest mean support compared to the other trees in regions one, three and five. The DM tree only holds the highest support value in region four; however this is one of the two poorest supported regions (three and four), and is therefore important in achieving the best possible resolution in all parts of the tree (Table 8).

Stratigraphic congruence. All tree topologies recovered under the four data conditions tested in this analysis were found to be significantly better correlated with stratigraphy than would be expected of random data. Among the raw results from each correlation metric, there is no consistent trend indicating

one or more of the four topologies are optimal. The SCI metric suggests the D and DM topologies (in which *Mystriosuchus* is basal to *Machaeroprosopus*) to be better stratigraphically correlated than the DC and DCM topologies (in which *Mystriosuchus* is the most derived member of Mystriosuchini); however, this finding is not borne out by any other metric. Among the other three metrics the only consistent trend is the slightly worse performance of the two datasets incorporating GM characters (DM and DCM); however, the difference in fit is almost negligible (Table 9).

The previous phylogenetic analyses of Parker & Irmis (2006) and Kammerer *et al.* (2015) (based respectively on the original matrices of Hungerbühler [2002] and Stocker [2010]), also correlate well with the stratigraphic data used in this study, generally achieving significance values equal to those of the current study. The topologies of Hungerbühler *et al.* (2013) were found to correlate poorly with stratigraphy and were not statistically differentiable from random data; however the analysis of Hungerbühler *et al.* (2013) focuses only on one area of the tree, roughly corresponding to 'region four' in this study. This region is poorly supported in terms of accuracy and robusticity. The poor stratigraphic correlation of the analysis of Hungerbühler *et al.* (2013) may indicate that this region has poor stratigraphic support, but this is masked in the stratigraphic correlations of other studies by good correlation overall in other areas of the tree.

Tree choice

In order to carry out further investigations into the effects of alternative, or previously reported topologies, it was decided to select only two of the four topologies presented above to avoid unnecessarily long comparisons of fit between multiple alternative taxonomic relationships within multiple tree topologies. As there is a general dichotomy in tree topology within the four trees, it would be inappropriate to arbitrarily favour one topology over the other, so a representative of each topology was chosen.

The DC condition exhibits an almost identical topology to the DCM condition, but consistently outperforms the latter in the various robusticity analyses described above. Comparisons of topological similarity do not assist in selecting one of these topologies over the other as they are shown to be almost identical, with neither being more representative of all topologies.

The D and DM conditions are less similar to each other than are the DC and DCM conditions, though they show largely the same topology. Between the Bremer and frequency analyses the D and DM conditions outperform each other in various aspects; when the trees are regionalized the DM condition generally provides slightly better support in the worst-supported areas of the tree, but is poorly supported in most other areas. The sum of Robinson-Foulds distances for the D tree in comparison to all others suggests that it is the most representative topology of the four trees recovered in this study; this was never found to be the case with the DM topology.

Ultimately the D and DC trees (Figs. 4, 5) were selected for further analysis based partially on the above metrics, but partially due to the relative difficulty of undertaking multiple further GM analyses. Continuous and discrete characters boast substantial advantages in analysis duration, and the comparative simplicity of data acquisition and processing, over GM characters. Because of these reasons continuous and discrete data are far more accessible and provide a better basis on which future studies can build.

Alternative taxonomic relationships

The consistent recovery of a sister-relationship between *Rutiodon carolinensis* and the genus *Angistorhinus* makes the decision of whether or not to synonymize these taxa entirely arbitrary (see below); therefore, to test for their synonymy would also be meaningless and as such these taxa were excluded from these analyses.

Nicrosaurus was previously found as the basal-most member of Mystriosuchini (Hungerbühler, 2002; Hungerbühler *et al*., 2013) and was therefore used as an internal specifier for the previous phylogenetic definition of the clade (Kammerer *et al*., 2016); however, as described in the introduction little data has been provided to support this. Here we find *Nicrosaurus* to group closer to *Leptosuchus* than to *Mystriosuchus* or *Machaeroprosopus*, and thus outside of Mystriosuchini according to our redefinition of the clade (Table 2). We tested the previously proposed position of *Nicrosaurus*, i.e. as the most basal group within Mystriosuchini (Kammerer *et al*., 2016). To achieve this, the clade of *Nicrosaurus* and *Coburgosuchus* was constrained to its previous position in relation to Mystriosuchini, such that all members of *Machaeroprosopus* and *Mystriosuchus* fell in a more derived position. Additionally *Pravusuchus hortus* was constrained as the basal sister taxon to *Nicrosaurus*, *Coburgosuchus* and Mystriosuchini, to replicate the previous hypothesis that *Pravusuchus* is the immediate sister taxon to Mystriosuchini (Stocker, 2010). Under these topological constraints tree character fit worsened by 0.693 in the D condition, and 1.013 in the DC condition.

The tree topology resulting from the D condition places *Mystriosuchus* as the sister clade to *Machaeroprosopus*; for this analysis we constrained *Mystriosuchus* to nest within *Machaeroprosopus* as found by Stocker (2010), although its exact position within the clade was left flexible. Under this condition the tree-fit worsens by 0.584. In contrast, in the DC condition *Mystriosuchus* was found to occupy a position within the *Machaeroprosopus* clade; therefore, we constrained it as sister to this clade, leading to a decline in tree fit by 0.714.

Unlike the findings of Hungerbühler *et al*. (2013), in our phylogenies the two species of '*Redondasaurus*' do appear to form a sister taxon relationship; however, in accordance with their findings and those of other studies (Ballew, 1989; Hungerbühler, Chatterjee & Cunningham, 2003; Stocker, 2010; Butler *et al*., 2014; Kammerer *et al*., 2015) '*Redondasaurus*' remains nested within *Machaeroprosopus*.

Commented [WGP14]: For Pseudopalatinae.

When the two genera are forced into a sister group relationship the tree fit deteriorated considerably by a score of 0.857 under the D condition, and 1.004 in the DC condition.

Discussion

Higher-level taxonomy

The recently revived family-level name Parasuchidae Lydekker, 1885, (Kammerer *et al*., 2015) was suggested by Stocker *et al*. (2017) to exclude the proposed basal phytosaur *Diandongosuchus fuyuanensis*. Our analysis corroborates the hypothesis of Stocker *et al*. (2017) that *Diandongosuchus* is the most basal phytosaur, and the only taxon to fall outside of Parasuchidae but within Phytosauria using current definitions.

The taxonomic content of Mystriosuchinae von Huene, 1915, defined as the last common ancestor of *Angistorhinus grandis* and *Mystriosuchus planirostris* and all its descendants by Kammerer *et al*. (2015), is largely compatible between the phylogenetic hypotheses presented here and that presented by Kammerer *et al*. (2015). However, in the phylogeny of Kammerer *et al.* (2015) '*Paleorhinus*' *sawini* falls within Mystriosuchinae whereas here it is excluded from this clade.

Stocker (2010) erected the clade Leptosuchomorpha, defined as the most recent common ancestor of *Leptosuchus studeri* and *Machaeroprosopus pristinus*, and all descendants thereof. In the D and DM trees presented here this definition is perfectly compatible with previous definitions of the clade; however in the DC and DCM conditions *'Smilosuchus' lithodendrorum* is recovered in a more basal position than all other previous members of Leptosuchomorpha, and would thus be excluded from the group based on the definition of Stocker (2010), despite exhibiting numerous similarities with other members. We therefore redefine Leptosuchomorpha such that it includes the latest common ancestor of *'Smilosuchus'*

lithodendrorum, *Leptosuchus studeri* and *Machaeroprosopus pristinus*, and all of its descendants (Table 2). In addition, *Protome batalaria* and '*Machaeroprosopus*' *zunii* are consistently recovered within Leptosuchomorpha in the analyses presented here, whereas they were previously excluded (Stocker, 2010; Butler *et al.*, 2014; Kammerer *et al.*, 2015).

The definition of Mystriosuchini von Huene, 1915 proposed by Kammerer *et al.* (2015) is problematic with regard to the results presented here, due to our general result that *Nicrosaurus* is deeply nested with taxa such as *Leptosuchus* and *Smilosuchus* that are traditionally excluded from Mystriosuchini. This problem is especially pronounced in the D tree (Fig. 4), in which the previous definition of Mystriosuchini renders the group entirely synonymous with Leptosuchomorpha; the DC and DCM trees produce a very similar result, though excluding *'Smilosuchus' lithodendrorum* from Mystriosuchini (Figs. 5, 7). In the DM tree (Fig. 6) the taxonomic content of Mystriosuchini using the previous phylogenetic definition is essentially the same as in previous studies, with the inclusion of a few additional taxa such as *Protome batalaria*.

To resolve this taxonomic issue we propose that *Nicrosaurus kapffi* is removed from the definition of Mystriosuchini due to its conflicting phylogenetic position, and is replaced with *Machaeroprosopus jablonskiae* to stabilize the taxonomic content of the clade (see above; Table 2). Without the addition of *Machaeroprosopus jablonskiae* as a specifier, *Machaeroprosopus mccauleyi* and *Machaeroprosopus jablonskiae* would be variably excluded from Mystriosuchini, despite consistent previous findings of their inclusion in the clade. A number of other taxa would also be variably included in Mystriosuchini, leading to increased instability of the clade.

Machaeroprosopus jablonskiae is recovered in a similar position to that found by previous phylogenetic analyses (Parker & Irmis, 2006; Hungerbühler *et al.*, 2013; Butler *et al.*, 2014; Kammerer *et al.*, 2015) in all of our trees. In the DC and DCM trees *Machaeroprosopus jablonskiae* is recovered as one

of the most basal taxa within *Machaeroprosopus* (Figs. 5, 7), as in the studies of Parker & Irmis (2006) and Hungerbühler *et al.* (2013) (Fig. 2A,C). In the D and DM trees *Machaeroprosopus jablonskiae* is placed in a more derived position in the *Machaeroprosopus* clade (Figs. 4, 6), similar to the findings of Butler *et al*. (2014) and Kammerer *et al*. (2015) (Fig. 3A,B); however, as this coincides with the migration of *Mystriosuchus* to a more basal position with respect to *Machaeroprosopus*, the taxa retained in Mystriosuchini remain largely identical among our four trees. Crucially, *Machaeroprosopus jablonskiae* consistently nests within Mystriosuchini in previous studies (Parker & Irmis, 2006; Hungerbühler *et al.*, 2013; Butler *et al.*, 2014; Kammerer *et al*., 2015), and in this sense our proposed definition errs on the side of caution in ensuring the definition of Mystriosuchini used here is as compatible as possible with the phylogenetic topologies of previous studies. This being the first investigation of this dataset, it seems likely that future analyses of this data could disagree with our findings, in which case a definition that maximizes compatibility between recent studies may be the most useful. We therefore tentatively suggest Mystriosuchini should henceforth be defined as the most recent common ancestor of *Mystriosuchus planirostris*, *Machaeroprosopus jablonskiae* and *Machaeroprosopus buceros*, and all its common ancestors (Table 2).

Lower-level taxonomy

Synonymy of *Rutiodon* and *Angistorhinus.* The results of this analysis depart from both previously proposed hypotheses of the relative phylogenetic positions of these taxa: that *Rutiodon* occupies a derived position within the monophyletic clade of *Angistorhinus* (Hungerbühler and Sues, 2001), or that *Rutiodon* sits in a more derived position than *Angistorhinus*, closer to *Leptosuchus* (Hungerbühler, 1998; Stocker, 2010). Supporting character data was not provided for the proposal of synonymy made by Hungerbühler & Sues (2001), which was published in an abstract only. In our results the two taxa form a monophyletic

group, supported by two synapomorphies common to all four best-fit trees [22: 2→1; 92: 0→1]. However, the fact that *Rutiodon* consistently forms the sister group to *Angistorhinus* makes the decision of whether or not to synonymize the genera entirely arbitrary. Unfortunately we were unable to study any material of *Brachysuchus megalodon*, which has been suggested to be synonymous with *Angistorhinus* (Long & Murry, 1995), but which was also found to be distinct by Stocker (2010).

Angistorhinus. In her discussion of the relationships of *Angistorhinus*, Stocker (2010) advocated the necessity for future in-depth analysis of *Angistorhinus* and its affinities. We do not present a detailed analysis or redescription of any species within *Angistorhinus*; however, our analysis is only the second to include more than one species (Hungerbühler, 1998), and the first to incorporate further specimens that have been identified previously as *Angistorhinus*. Our results provide a stable and consistently well-supported phylogenetic position for *Angistorhinus* that future descriptive and taxonomic work can build on. Furthermore we provide additional synapomorphies for both the *Angistorhinus* clade, and relationships within it.

The *Angistorhinus* clade (Figs. 4, 5, node 9; Figs. 6, 7, node 11) is distinguished by two unambiguous synapomorphies common to all trees, pertaining to the parietal/squamosal bars being medially convex, and at least as wide as the postorbital/squamosal bars [56: 0→1; 58: 0→1]. Both of these characters have previously been suggested to be diagnostic features of *Angistorhinus* Mehl, 1913 (Mehl, 1915; Gregory, 1962; Stocker, 2010) or 'Angistorhininae' Camp, 1930 (Long & Murry, 1995).

The next most inclusive clade contains *Angistorhinus talainti*, *A. grandis*, TMM 31100-1332 and USNM V 21376. This group is distinguished by the presence of a sulcus running longitudinally along the postorbital/squamosal bar [42: 0→1], and the partial or total squaring of the medial rim of the postorbital/squamosal bar and posterior process [51: 0→1].

The next most inclusive clade excludes *A. talainti*, leaving only *A. grandis*, TMM 31100-1332 and USNM V 21376. This clade is well supported by four unambiguous synapomorphies, though within the clade the basal-most member (TMM 31100-1332) shows no autapomorphies and the sister grouping of *A. grandis* with USNM V 21376 is supported by only one synapomorphy [69: 2→1] and displays poor support values. Given the strong support for the wider clade, but the relatively poor differentiation of the OTUs within it, there may be a case for referring both TMM 31100-1332 and USNM V 21376 to *A. grandis*. The synapomorphies of this clade are: the division of the narial openings into an anterior 'anteriorly opening' section and a posterior 'dorsally opening' section [12: 0→1]; the raising of the external nares above the level of the skull roof [17: 0→1]; the posttemporal fenestra being moderately wide and dorsoventrally compressed [66: 0→1]; and the presence of an anteroposteriorly oriented ridge on the midline of the basioccipital between the basitubera [70: 0→1].

Based on these results we suggest *A. grandis* to be one of the most derived members of *Angistorhinus*, and *A. talainti* to be less derived. At face value there does not appear to be any clear relationship between palaeogeography and phylogeny; *A. talainti*, from Morocco, nests amongst the specimens known from the west and south central USA. This finding should be expected as these locations were placed at broadly similar palaeolatitudes and were closely connected in the Late Triassic.

Monophyly of *Leptosuchus.* Stocker (2010) found a strongly supported monophyletic relationship between *Leptosuchus crosbiensis* and *Leptosuchus studeri*; here, we found almost all nodes relating to *Leptosuchus*-grade taxa were extremely poorly supported in each tree. Only in the D tree did we find an arrangement approaching a monophyletic *Leptosuchus* (Fig. 4, node 17), though with the addition of *'Smilosuchus' lithodendrorum* and PEFO 34852 as a sister clade to *L. crosbiensis*. In the DC and DCM trees *Leptosuchus studeri* forms the sister group to a clade containing *Leptosuchus crosbiensis*, but also

Pravusuchus, *Coburgosuchus* and *Nicrosaurus* (Fig. 5, node 15; Fig. 7, node 17). Support values are generally poor. In the DM tree *Leptosuchus*-grade taxa occur as a paraphyletic grade of sequentially more derived branches (Fig. 6).

Stocker (2010) found one synapomorphy to support the monophyly of *Leptosuchus* and one further potential apomorphy under DELTRAN optimization.

Distal end of paroccipital process of opisthotic rounded, distal edge is curved rather than straight (36: 1→2). This character was excluded from analysis here as the associated morphology appears to be highly variable both inter- and intraspecifically, is often subject to damage, and scoring may change depending on small differences in viewing angle.

Jugal contributing to antorbital fenestra (4: 0→1) (potential apomorphy under DELTRAN). In our analysis this character state is optimized as basal to the entire tree, and is found in the vast majority of taxa. In this position the character does not provide unambiguous support for the monophyly of *Leptosuchus.*

Monophyly of *Smilosuchus.* The previously proposed taxonomic content of *Smilosuchus* is not monophletic in any of our best-fit trees. In the D tree (Fig. 4) all three species are found in different locations: *S. adamanensis* forms the basal-most taxon in a clade containing all leptosuchomorph taxa excluded from Mystriosuchini except *S. gregorii* (Fig. 4, node 14); *'S'. lithodendrorum* is deeply nested within this group, forming a close relationship with *Leptosuchus crosbiensis* (Fig. 4, node 18); *S. gregorii* forms its own distinct branch forming a sister relationship with Mystriosuchini (Fig. 4, node 23).

In none of the trees presented here does *'Smilosuchus' lithodendrorum* form a close relationship with any other member of *Smilosuchus*. Instead, its relationships are divergent, being recovered in two trees as the most basal member of the newly defined Leptosuchomorpha (DC & DCM; Figs. 5, 7) and in

the other two nesting closely with *Leptosuchus crosbiensis* (D & DM; Figs. 4, 6). The similarity to *Leptosuchus crosbiensis* has previously been noticed, leading Long & Murry (1995) to regard *'S'. lithodendrorum* as a junior synonym of the former taxon, though without a written justification (see Appendix 1 for more details). We do not here revise the taxonomy of *'S'. lithodendrorum*, as the instability of its position does not allow any consistent hypothesis of its relationships to be reached. Instead, we consider the phylogenetic position of this taxon as uncertain pending a more detailed investigation into its similarity to *L. crosbiensis*.

In Stocker's (2010) analysis, the monophyly of *Smilosuchus* was supported on the basis of two synapomorphies and a further possible apomorphy under ACCTRAN optimization.

Ventral margin of squamosal gently sloping anteroventrally from posterior edge of posterior process to opisthotic process (28: 1→0). In contrast to the scorings of Stocker (2010), no specimen of *'S'. lithodendrorum* was found with a gently sloping posteroventral squamosal margin. This state was, however, found to be present in both *S. adamanensis* and *S. gregorii*. The latter taxon displays polymorphism for this character as AMNH D. VP. 3060 displays a morphology that is neither a gentle slope, nor a sharp shelf, but sits somewhere between.

In the D and DM trees (Figs. 4, 6) *S. adamanensis* and *S. gregorii* apparently gain this character state (0) independently, though because the latter taxon is polymorphic for this character, the ancestral state (1) is partially retained. In the DC and DCM trees (Figs. 5, 7) the ancestral state is polymorphic; therefore, depending on the tree in question this character is either partially consistent or inconsistent with the hypothesis of monophyly between *S. adamanensis* and *S. gregorii*.

Interestingly, if *S. gregorii* is scored as '0' rather than as polymorphic, both taxa consistently form a monophyly in the D tree, whereas they were previously relatively distant phylogenetically from each other. This was also tested in the DC tree (which shares the same relative phylogenetic positions of *S.*

adamanensis and *S. gregorii* as in the DM and DCM trees). However, the phylogenetic positions of these two taxa were not modified, and state '0' was also reconstructed as ancestral to the clade including *Protome batalaria* and Mystriosuchini.

Squamosal fossa extends to posterior edge of squamosal (30: 1→0). The scores for this character in the current analysis are inconsistent with those of Stocker (2010); we observed a polymorphic state in both *'S'. lithodendrorum* (TMM 31173-121: 0; UCMP 26688: 1) and *S. gregorii* (UCMP 27200: 0; AMNH 3060: 1). Our character optimization is inconsistent with the hypothesis of a monophyletic *Smilosuchus*, given that character state '0' is ancestral to the majority of taxa (excluding many basal taxa for which the character is inapplicable and most species of *Machaeroprosopus*) in all four of our trees.

Commented [WGP15]: Is this really S. lithodendrorum? Based on whose assessment?

Lateral border of posttemporal fenestra formed by the contact of the parietal process of the squamosal and the paroccipital process of the opisthotic (37: 1→0) (potential apomorphy under ACCTRAN). Our scoring for this character differs from that of Stocker (2010); we concur that *'S'. lithodendrorum* displays state '0', whereas both *S. adamanensis* and *S. gregorii* are scored as possessing a thin lamina of squamosal that slightly undercuts the border of the fenestra ventrolaterally (character state '2'). The latter condition is ancestral to both species of *S. adamanensis* and *S. gregorii*, all species of *Machaeroprosopus* and closely related taxa in all four trees (though in the D tree the ancestral state is polymorphic '0, 2'). In trees D, DC and DCM character state '2' independently characterizes the clade formed by *Nicrosaurus* and *Coburgosuchus*. Character state '0' is the ancestral condition for *'Smilosuchus' lithodendrorum* in all four trees presented here. None of the optimizations of this character presented here support the monophyly of *Smilosuchus*.

Position of *Pravusuchus hortus.* *Pravusuchus hortus* has previously been indirectly implied to potentially form a close relationship with *Nicrosaurus*: *Pravusuchus* was found to form the immediate

outgroup to Mystriosuchini by Stocker (2010), while *Nicrosaurus* has long been hypothesized to form a close relationship with *Mystriosuchus* and *Machaeroprosopus* (Ballew, 1989) as the most basal taxon within Mystriosuchini (Long & Murry, 1995; Hungerbühler, 2002; Parker & Irmis, 2006; Hungerbühler *et al.*, 2013). Thus our a priori assumption was that these taxa would be closely related. Our results corroborate this view, with *Pravusuchus* forming the outgroup to a clade containing *Nicrosaurus* and *Coburgosuchus* in three of the four analyses (D, DC, DCM); however, these taxa are found here to nest deeply within a clade of non-Mystriosuchini leptosuchomorph taxa in all but the DM analysis.

The analysis of Stocker (2010) identified a single synapomorphy in support of a clade containing *Pravusuchus*, *Machaeroprosopus mccauleyi*, *Machaeroprosopus pristinus* and *Mystriosuchus westphali*. In the three trees in which *Pravusuchus* is the immediate outgroup of *Nicrosaurus* we found two consistent synapomorphies supporting the clade of *Pravusuchus, Nicrosaurus* and *Coburgosuchus*: presence of an infranasal recess, and absence of a furrow or ridge on the lateral surface of the squamosal/post-orbital bar [21: 0→1; 29: 1→0]. The synapomorphy identified by Stocker (2010) is discussed below.

Subsidiary opisthotic process of the squamosal present (29: 0→1). Our scores for this character are partially inconsistent with those of Stocker (2010); we found *Pravusuchus* to be polymorphic for this character (PEFO 31218: 0; AMNH FR. 30646:1), as was the case in *Machaeroprosopus mccauleyi* (UCMP 126999: 0; PEFO 31219: 1), *Machaeroprosopus pristinus* (PEFO 382: 0; MU 525: 1; AMNH FR. 7222: 1; NMMNHS P50040: 1), and *Mystriosuchus westphali* (AMNH FR. 10644: 0; GPIT 261/001: 1).

Commented [WGP16]: Preservation?

In all four trees presented here, the most exclusive clade that contains *Pravusuchus* is not supported by the synapomorphy of Stocker (2010); instead, character optimization finds the absence of the subsidiary opisthotic process [47: 0] to be symplesiomorphic for this clade. Here we find that the presence of a subsidiary opisthotic process of the squamosal [47: 1] primarily optimizes in two alternative

positions depending on tree topology. In the D and DM trees (in which *Mystriosuchus* is basal within Mystriosuchini), the presence of this character is a synapomorphy of the clade formed by USNM v 17098 and all more derived taxa. This clade includes *Machaeroprosopus mccauleyi* and *Machaeroprosopus pristinus*, but excludes *Mystriosuchus westphali* and *Pravusuchus hortus*. Therefore in these topologies, this synapomorphy is partially consistent with the aforementioned clade of Stocker (2010), though fundamentally excludes *Pravusuchus* and therefore does not provide support for its position in our trees. In the DC and DCM trees (in which *Mystriosuchus westphali* occupies a more derived position within the *Machaeroprosopus* clade), the presence of a subsidiary opisthotic process is optimized as polymorphic for the clade that includes *Machaeroprosopus mccauleyi* and all more derived taxa (including *Machaeroprosopus pristinus* and *Mystriosuchus westphali*, but excluding *Pravusuchus*). At the node one step more derived, (thus excluding *Machaeroprosopus mccauleyi*) the character is optimized as 'present' (1) however cannot be regarded as a synapomorphy due to the uncertain optimization of the previous node. This is also partially consistent with the optimization of this character by Stocker (2010); however, the clade supported by this character state excludes *Pravusuchus*, and is inconsistent with the phylogenetic hypothesis of Stocker (2010).

Position of *Nicrosaurus*. The most recent novel cladistic analysis to investigate the position of *Nicrosaurus* was that of Hungerbühler (2002). The analysis found *Nicrosaurus* as the sister taxon to a clade formed by *Mystriosuchus*, '*Redondasaurus*' and *Machaeroprosopus* - congruent with the later definition of Mystriosuchini by Kammerer *et al*. (2015); however, no synapomorphies were reported in support of this clade.

In three of the four trees identified in this study (D, DC, DCM) *Nicrosaurus* groups more closely with a number of non-Mystriosuchini leptosuchomorph taxa than with Mystriosuchini. *Nicrosaurus*

differs from Mystriosuchini in all trees due to the possession of a relatively long free-section of the postorbital/squamosal bar, rather than a short bar as is synapomorphic for the latter clade [43: 2→0] (although *Nicrosaurus meyeri* independently acquires a short postorbital/squamosal bar). Character optimization suggests that the relatively long 'free-section' is plesiomorphic to almost all phytosaurs. This character therefore provides no support for the hypothesized position of *Nicrosaurus* suggested by Hungerbühler (2002).

Position of *Mystriosuchus.* The dichotomy of topologies regarding the position of *Mystriosuchus*, as presented in the results section, reflects the dichotomy seen in the literature. The two most recent hypotheses of the position of *Mystriosuchus*, based on independent datasets, are those of Hungerbühler (2002) and Stocker (2010), which respectively place *Mystriosuchus* in the less and more derived positions found in this analysis.

Less derived position. In the analysis of Hungerbühler (2002), the clade in which *Mystriosuchus* is the basal member is diagnosed with three synapomorphies.

Presence of a pre-infratemporal shelf (18: 1). We find this character in three trees (D, DC, DCM) to be a synapomorphy of the clade containing *Mystriosuchus*, '*Redondasaurus*' and many members of *Machaeroprosopus* - generally matching the clade membership of Mystriosuchini as it was previously defined in both Hungerbühler (2002) and Stocker (2010). This character is therefore largely unaffected by the placement of *Mystriosuchus*, and thus supports both hypotheses.

Presence of the pre-infratemporal shelf is restricted in our analysis almost exclusively to the clade discussed above, however this character state independently arises as a polymorphic state in *Nicrosaurus* and *Pravusuchus*, and also in *Parasuchus hislopi*.

Presence of a parietal ledge (21: 2). This character was not included in this analysis as the morphology described is dependent on the morphology of the depressed squamosal processes of the parietal, which is scored elsewhere (character 75). The morphology of this area of the skull is partially considered in character 74, which scores the ratio of width to length of the parietals between the supratemporal fenestrae. Regardless, this morphology appears to be present in all leptosuchomorph phytosaurs, and would thus be unlikely to support the clade detailed above.

Parieto/squamosal bar is strongly depressed (23: 2). We find this character to be synapomorphic for a more inclusive group than that of Hungerbühler (2002), consisting of *Smilosuchus gregorii*, *Mystriosuchus planirostris*, their common ancestor and all its descendants [49: 1→2]. In three of the trees presented here (D, DC and DCM) this transformation independently occurs in *Nicrosaurus* and *Coburgosuchus*, whereas in the DM tree *Nicrosaurus* and *Coburgosuchus* are included in the clade described above. This character distribution therefore is not found here to support the clade described by Hungerbühler (2002).

No synapomorphies were listed by Hungerbühler (2002) for the clade from which *Mystriosuchus* was immediately excluded; therefore, we are unable to comment of the consistency of our synapomorphies with those of Hungerbühler (2002), for a clade containing *Machaeroprosopus* and '*Redondasaurus*' but excluding *Mystriosuchus.* The characters supporting this phylogenetic arrangement in our study are detailed in the results section.

More derived position. Stocker (2010) identified eight synapomorphies (and two potential synapomorphies under ACCTRAN) supporting a clade consisting of *Machaeroprosopus mccauleyi*, *Machaeroprosopus pristinus* and *Mystriosuchus westphali*, which, in her analysis, represented Mystriosuchini.

Interpremaxillary fossa present - narrow slit (8: 1→2). Here this character state is restricted only to *Mystriosuchus* and NHMW 1986 0024 0001, which consistently sits within the same clade as *Mystriosuchus* (and probably represents an unnamed species within this this genus), and is a synapomorphy of the node uniting these taxa in all four trees [2: 1→2]. It therefore provides no support for the topology hypothesized by Stocker.

Alveolar ridges not visible in lateral view (9: 0→1). We find this character to optimize as a synapomorphy in multiple locations across our four trees; however, these are mostly inconsistent with Stocker's hypothesis of this character's optimization.

In both trees which present the same topological hypothesis of the relationships of *Mystriosuchus* as Stocker (2010) (DC, DCM), this character is found as a synapomorphy of a clade containing *Machaeroprosopus pristinus*, *Machaeroprosopus buceros*, *Machaeroprosopus lottorum*, both species of '*Redondasaurus*', and *Mystriosuchus* [3: 0→1]. This synapomorphy, however, describes a morphological reversal, i.e. state 1→0, rather than 0→1 as suggested by Stocker. In the two trees in which *Mystriosuchus* occupies a more basal position (D, DM), this character is optimized as a 0→1 synapomorphy, as suggested by Stocker (2010), of a clade similar to that described above, though differing by containing all members of *Machaeroprosopus* and excluding *Mystriosuchus.* In summary, we find this character to contradict the hypothesized optimization of Stocker (2010), in that a 0→1 change is only found when *Mystriosuchus* is one of the sister taxa to *Machaeroprosopus*, rather than nesting within the clade.

Postorbital squamosal articulation approximately transverse (22: 1→2). The distribution of character state (2) is here restricted to members of *Machaeroprosopus*, *Mystriosuchus* and '*Redondasaurus*', though it twice arises independently in the *Leptosuchus*-grade OTUs PEFO 34852 and *Coburgosuchus.* Despite its restricted occurrence, this trait change [33: 1→2] is not optimized as a synapomorphy here, though the change from 0→1 is optimized in two trees (DC, DCM) as a

synapomorphy of the node linking *Smilosuchus adamanensis* with all more derived members of Leptosuchomorpha. In the DM tree a 0→1 change is a defining feature of the most recent node linking the clade of *Nicrosaurus* and *Coburgosuchus* with all more derived members of Leptosuchomorpha.

Although not optimized as a synapomorphy, the distribution of this character state is broadly supportive of not only the hypothesis of Stocker (2010), but also that of Hungerbühler (2002), as in both topologies, character state (2) is optimized as being plesiomorphic to the clade containing *Machaeroprosopus* and *Mystriosuchus.*

Lateral ridge from postorbital/squamosal bar continues strongly on lateral surface of squamosal as two raised ridges (23: 1→2). This character state was removed from the analysis as it could not be reliably identified in any species of phytosaur. A similar character state was added by Butler *et al*. (2014), referring specifically to the bifurcation of the lateral ridge in species of *Parasuchus*, though this state has not been observed in any other phytosaurs. Here we find the presence of a ridge to occur sporadically throughout the tree, though with a greater frequency in more derived members of *Machaeroprosopus.* In *Mystriosuchus* a ridge is only found as a polymorphism within *Mystriosuchus westphali*, and it is otherwise entirely absent within the genus. In topologies in which *Mystriosuchus* is a sister group of *Machaeroprosopus* the absence state is plesiomorphic to the group. When *Mystriosuchus* is found within *Machaeroprosopus*, the clade containing *Machaeroprosopus mccauleyi*, *Machaeroprosopus pristinus* and *Mystriosuchus westphali* is plesiomorphically polymorphic for this character. Furthermore, the presence of any form of ridge is only found as a synapomorphy of derived members of *Machaeroprosopus* in the D tree; in this topology *Mystriosuchus* is in any case excluded from the *Machaeroprosopus* clade.

Posterior process of squamosal dorsoventrally expanded in lateral view (25: 2→1). This character was altered to use the terminology of Ballew (1989) and Hungerbühler (2002) for the ‘knob-like’

posterior process found in *Machaeroprosopus pristinus*, *Machaeroprosopus buceros* and some specimens of *Machaeroprosopus mccauleyi*; this was done to reduce ambiguity in character scoring.

This character is not optimized as a synapomorphy of any node close to either the base of *Mystriosuchus* or *Machaeroprosopus* in any of the trees presented here. State (1) (which here refers to the same morphology as Stocker's character) is here found to be more frequent in derived members of *Machaeroprosopus*, (excluding *Machaeroprosopus pristinus* and *Machaeroprosopus buceros* which are characterized by a state change of 1→2) and is plesiomorphic for the clade. Although the general character distribution generally supports Stocker's (2010) topological hypothesis for all other members of Stocker's '*Pseudopalatus*' clade, this character does not convey any information regarding the position of *Mystriosuchus* as the taxon lacks a posterior process and optimization of this character at the base of *Mystriosuchus* relies entirely on its position in the phylogeny. This character therefore provides no support for the inclusion of *Mystriosuchus* within *Machaeroprosopus*.

Supratemporal fenestrae fully depressed, posterior process of parietal and entire parietal/squamosal bar below level of skull roof (32: 1→2). Rather than forming a synapomorphy of only the Mystriosuchini clade used by Stocker (2010), we find this character to be synapomorphic for the node uniting *Smilosuchus gregorii* with all more derived taxa (D, DC: node 23; DM: node 22; DCM: node 25) [49: 1→2]. *Mystriosuchus* is included within this clade regardless of its position with respect to *Machaeroprosopus*, thus this character does not provide any support for the inclusion of *Mystriosuchus* within *Machaeroprosopus.*

Border of posttemporal fenestra formed laterally and slightly ventrally by process of squamosal that extends onto paroccipital process (37: 1→2). Mystriosuchus is scored here as polymorphic for this character. In the trees in which it occupies a more derived position *Mystriosuchus* forms a sister group to '*Redondasaurus*', which consistently displays character state (0); the plesiomorphic state is, in this

situation, also polymorphic - providing only limited support for the hypothesis of a derived placement for *Mystriosuchus*. This character is more consistent here with the hypothesis that *Mystriosuchus* is sister to *Machaeroprosopus*, as character state (2) alone is plesiomorphic for *Mystriosuchus* in this position, and forms a synapomorphy in three of our trees (DC, DM and DCM) for the clade formed by all descendants of the common ancestor of *Smilosuchus adamanensis* and *Mystriosuchus planirostris* [67: 0→2].

Skull shape boxy in posterior view, width across squamosals approximately equal to width across ventral edge of quadrates (38: 1→0). This character was excluded in this analysis as it is extremely sensitive to taphonomic distortion, and is highly subjective. The most basal taxon in Mystriosuchini identified by Stocker (2010) is *Machaeroprosopus mccauleyi*, which contrary to Stocker's scoring would here be considered to possess a trapezoidal skull shape, as would *Machaeroprosopus buceros* and all taxa in '*Redondasaurus*', none of which were included in Stocker's analysis. Despite the exclusion of this character, the inclusion of multiple additional taxa in this analysis may have affected the optimization of synapomorphies in the clade.

Rostral crest present, continuous and sloping steeply anteroventrally from nares to terminal rosette (19: 0→1) (Possibly additional apomorphy under ACCTRAN). The above character was altered slightly in this analysis (Appendix 2); however, character state (1) of Stocker (2010) is still represented by character state (2) here. We find a wide range of synapomorphy optimizations of this character in our trees, none of which are consistent with the results of Stocker (2010).

In the DCM tree a clade containing *Mystriosuchus*, '*Redondasaurus*' and more derived members of *Machaeroprosopus* are partially defined by this character as a synapomorphy; however, *Machaeroprosopus mccauleyi* is excluded from the group and the state transformation is from the presence of a steep, continuous slope posteriorly from the terminal rosette, to the presence of a narial crest

- the relatively abrupt rise from a thin, tubular snout to the nares [7: 2→1]. Within this clade, '*Redondasaurus*' undergoes a state reversal back to the morphology of a steep, continuous crest [7: 1→2].

The D and DM trees both optimize this character as a synapomorphy of a clade including all species of *Machaeroprosopus* and '*Redondasaurus*'; in these trees, the state transformation is from the presence of a narial crest, to the presence of a partial rostral crest [7: 1→4]. A more exclusive clade within the former, containing *Machaeroprosopus mccauleyi*, *Machaeroprosopus jablonskiae* and '*Redondasaurus*' again features this character as a synapomorphy, with a state change from a partial rostral crest, to presence of a continuous steep slope [7: 4→2]. *Mystriosuchus*, however, occurs in none of these clades in the two trees and this character is not found to support any relatively exclusive clade containing *Mystriosuchus*.

Commented [WGP17]: Crest is not preserved in the holotype specimen.

In the DC tree this character is not found to define any clade in which *Mystriosuchus* is placed; within close proximity to *Mystriosuchus* the only clade featuring this as a synapomorphy is '*Redondasaurus*', displaying a change from a narial crest to a continuous, steep rostral crest [7: 1→2].

Supratemporal fenestrae mostly covered/completely closed dorsally, at most only anteromedial corners of supratemporal fenestrae visible in dorsal view (33: 1→2) (Possible additional apomorphy under ACCTRAN). In the trees in which *Mystriosuchus* is recovered in a derived position this character was only found as a synapomorphy of the clade of *Mystriosuchus* + NHMW 1986 0024 0001 + MB.R. 2747; specifically, the synapomorphy denotes a character transformation from state (2) to state (1) [57: 2→1]. This does not provide support for the hypothesis of relationships within Mystriosuchini proposed by Stocker (2010); however, the majority of nodal optimizations and scorings for this character in the other members of Mystriosuchini (and for all those included in Stocker's analysis), display character state (2). The state change observed by Stocker (2010) is likely not found here due to a polymorphic optimization of states (1) and (2) at the base of the *Machaeroprosopus* clade (*Machaeroprosopus*

andersoni and all more derived taxa); at the node one step more derived (*Machaeroprosopus jablonskiae* and all more derived taxa) the character is optimized as state (2), as are the majority of following nodes. It is therefore likely that a state change of (1) to (2) [57: 1→2] is synapomorphic at the base of *Machaeroprosopus* which, in the DC and DCM topologies, is consistent with the phylogenetic hypothesis of Stocker's 'Mystriosuchini' clade.

In the D and DM trees (i.e. where *Mystriosuchus* occupies a less derived position), this character is only optimized as a synapomorphy of '*Redondasaurus*' + NMMNHS P31094, as a state change from the supratemporal fenestrae being mostly covered (state 2), to being fully covered (state 3). However, the synapomorphy suggested by Stocker (2010) is probably again suppressed due to two nodes optimized as polymorphisms bracketing the base of *Machaeroprosopus*. Using the D tree as an example: the two nodes directly basal to *Machaeroprosopus* (Fig. 4, nodes 28, 29) are optimized as state (1) and (1 or 2) respectively; in the following node (the most basal in *Machaeroprosopus* [node 30]), this character is again optimized as (1 or 2). In the next node (node 31) the character is optimized as state (2), as are the majority of other nodes within the clade. Therefore, we suggest that the topology in the D and DM trees is also mostly consistent with the reduction in supratemporal fenestra visibility identified by Stocker (2010), except that *Mystriosuchus* is excluded from the supported clade in the D and DM trees.

Relatively few of the synapomorphies identified in previous analyses to support particular clades containing *Mystriosuchus* are corroborated here, despite the dichotomy of tree topologies presented in this analysis being broadly consistent with each of the previous studies discussed above.

Monophyly of '*Redondasaurus*'

'*Redondasaurus*' was originally diagnosed by Hunt & Lucas (1993) solely on the basis of the lack of visibility of the supratemporal fenestrae in dorsal view. The genus was re-diagnosed by Spielmann &

Lucas (2012) with a broader complement of characters: 1) supratemporal fenestrae concealed in dorsal view; 2) reduced antorbital fenestrae; 3) a prominent pre-infratemporal shelf at the anteroventral margin of the lateral temporal fenestra; 4) septomaxillae wrap around the outer margin of the external narial opening; 5) thickened orbital margin; 6) inflated posterior nasal behind the external narial opening; 7) thickened dorsal osteoderms.

Hungerbühler *et al.* (2013) were unable to recover '*Redondasaurus*' *gregorii* and '*Redondasaurus*' *bermani* as a monophyletic group in any of their trees; however, we find a monophyletic '*Redondasaurus*' (albeit nested within *Machaeroprosopus*) in all of our trees. Many of the characters proposed by Spielmann & Lucas (2012) were not implemented in the analysis of Hungerbühler *et al.* (2013); however, in this analysis we included some of these characters that were used in previous phylogenetic studies and independently identified others which overlap to a considerable extent with those proposed synapomorphies of '*Redondasaurus*'. The consistency of the characters included in our analysis with the hypothesis of a monophyletic '*Redondasaurus*' are discussed below.

Supratemporal fenestrae concealed in dorsal view. As was briefly mentioned above, this character is found as a synapomorphy of the '*Redondasaurus*' clade in all trees presented in this study [57: 2→3], and is therefore entirely consistent with the hypothesis of Hunt & Lucas (1993). This character state occurs in no other taxon, though is found in NMMNHS P31094 (referred to '*Redondasaurus*' *gregorii* by Spielmann & Lucas 2012), which in the D and DM trees is included within the '*Redondasaurus*' clade, but in the other trees is recovered as the sister taxon of *Machaeroprosopus lottorum*, the character state having arisen independently of '*Redondasaurus*'.

Anteriormost border of pre-infratemporal shelf terminates anterior of the posteriormost corner of the antorbital fenestra. The presence of this character state is restricted almost entirely to '*Redondasaurus*' and *Mystriosuchus*; unsurprisingly, where these two groups form a clade this character

is consistently optimized as a synapomorphy. However, in the D and DM trees, where *Mystriosuchus* is placed basally, distant from '*Redondasaurus*', the character only constitutes a synapomorphy for *Mystriosuchus* rather than '*Redondasaurus*'; this may be due to the polymorphic condition of '*Redondasaurus*' *gregorii* for this character. Despite this inconsistency between trees the distribution of this character still broadly supports a monophyletic '*Redondasaurus*'.

The diagnostic characters proposed by Spielmann & Lucas (2012) for '*Redondasaurus*' but not included in our analysis are discussed briefly below. We agree that several of these support a sister taxon relationship between '*Redondasaurus*' *gregorii* and '*Redondasaurus*' *bermani*, and are therefore consistent with our results.

Reduced antorbital fenestrae. Whether or not the antorbital fenestrae are substantially reduced may be subjective; in more robust specimens of '*Redondasaurus*' (NMMNHS P-4256) the antorbital fenestra does appear smaller than in closely related taxa. However, in more gracile specimens (YPM 3294) the fenestra appears similar in proportions to those of other phytosaurs such as *Mystriosuchus.* The antorbital fenestrae do appear to exhibit a unique shape in most specimens of '*Redondasaurus*'; the general shape is roughly triangular, as is common in *Mystriosuchus* and *Machaeroprosopus*, but the anterior- and posterior-most corners of the fenestra are sharp angles, rather than smooth curves.

Septomaxillae wrap around the outer margin of the external narial opening. No taxon studied was observed to possess 'septomaxillae' that extend onto the lateral surface of the external nares. Stocker (2010) noted the presence of this character state in '*Redondasaurus*' and suggested it may also occur in *Pravusuchus hortus*; however, upon inspection of the holotype and referred specimens of *Pravusuchus hortus* it seems equally likely that the morphology described by Stocker pertains to cracks on the holotype, with the true sutures covered by iron oxide. Rather than a lateral extension of the

1492 ‘septomaxillae’ the feature identified in ‘*Redondasaurus*’ and *Pravusuchus* may represent the paranasals,
1493 identified in *Machaeroprosopus lottorum* by Hungerbühler *et al.* (2013).
1494 *Thickened orbital margin.* We here concur with Spielmann & Lucas (2012); in all specimens of
1495 ‘*Redondasaurus*’ examined by us, the descending process of the postorbital appears to be greatly
1496 thickened to an extent not seen in any other group. For this particular character Spielmann & Lucas (2012)
1497 suggested it is also shared with *Coburgosuchus*; however, we see no observable expansion of the
1498 postorbital in the latter taxon to distinguish it from the condition present in most other phytosaurs. The
1499 descending process of the postorbital in *Coburgosuchus* has a roughly rectangular cross-section, with the
1500 external face relatively thin, but facing anterolaterally. If Spielmann and Lucas (2010) measured this
1501 feature in *Coburgosuchus* diagonally between the anterolateral and posteromedial corners (i.e. the full
1502 width observable in direct lateral view), this could account for the increased width, especially given the
1503 oblique angle of the process in direct lateral view. As this morphology is measured in all other taxa based
1504 on only the flat lateral-most face of the descending process, this procedure should also be applied here to
1505 preserve homology within the character.
1506 *Inflated posterior nasal behind the external narial opening.* Although this entire area of skull is
1507 missing in the type specimen of ‘*Redondasaurus*’ *gregorii* (YPM 3294), it is common to a variable extent
1508 in many other specimens referred to the genus by Spielmann & Lucas (2012). This feature is not,
1509 however, restricted to ‘*Redondasaurus*’, as the morphology of specimens from other taxa frequently
1510 overlap with the range of variation observed in ‘*Redondasaurus*’. Examples include: *Nicrosaurus kapffi*
1511 (SMNS 4379), *Machaeroprosopus mccauleyi* (PEFO 31219) and *Machaeroprosopus lottorum* (TTU-P
1512 10076). It may be valid to say that ‘*Redondasaurus*’ is the only taxon in which this character state
1513 consistently occurs; however, its variability makes the taxonomic utility of this feature unclear. Given the
1514 variable presence of this character in more than one species of *Machaeroprosopus*, this character is likely

to support the hypothesis that '*Redondasaurus*' is nested within *Machaeroprosopus*, though verification would require the inclusion of this character in phylogenetic analyses.

Thickened dorsal osteoderms. The osteoderms of some large phytosaur taxa are also strongly thickened, ~~e.g.~~e.g., *Smilosuchus gregorii* (AMNH 3060); however, we have not carried out any sufficiently detailed study of osteoderms to fully assess this proposed synapomorphy. Until more detailed work emerges on phytosaur osteoderm variation we tentatively accept this character, though emphasize that potential size correlation should be borne in mind.

Synonymy with *Machaeroprosopus*

Hungerbühler *et al*. (2013) presented three lines of reasoning in support of the synonymization of '*Redondasaurus*' into *Machaeroprosopus*. First, they argued that *Machaeroprosopus lottorum* 'bridges the morphological gap' between other members of *Machaeroprosopus* and '*Redondasaurus*' *gregorii* and '*Redondasaurus*' *bermani* in a number of features, and possesses a combination of characters formerly considered exclusive to one or other group. Second, in all trees recovered by Hungerbühler *et al*. (2013), both species of '*Redondasaurus*' were found within the clade of *Machaeroprosopus*; in analyses that were constrained to recover '*Redondasaurus*' as a monophyletic sister group to *Machaeroprosopus*, tree fit lengthened by five extra steps. Third, they did not find '*Redondasaurus*' *gregorii* and '*Redondasaurus*' *bermani* to form a clade to the exclusion of species of *Machaeroprosopus* in any of their trees; instead, the two taxa were interspersed with members of *Machaeroprosopus*, with '*Redondasaurus*' *gregorii* being recovered in a substantially more derived position than '*Redondasaurus*' *bermani* in every tree.

The first two points are consistent with our results; however, with regard to their third point we find the exact opposite - that these taxa are always monophyletic to the exclusion of species of *Machaeroprosopus*. In all trees this clade is supported by two to four synapomorphies, with one

(supratemporal fenestra completely obscured in dorsal view) consistently present in all trees. Despite this, we agree with the suggestions of Long & Murry (1995) and Hungerbühler *et al*. (2013) that '*Redondasaurus*' should be synonymized with *Machaeroprosopus*.

Effects of scoring method

CI and RI. The consistency indices calculated for the four character coding variables (D, DC, DM and DCM) were broadly similar; though as noted above, those which incorporated continuous data produced slightly better scores than the others. Regardless, all CI values displayed a significantly higher consistency than expected of random data (for a dataset of 43 taxa and between 90 and 94 characters), based on comparisons with simulated data in Klassen, Mooi & Locke (1991). Differences in the retention indices (RI) were marginal between all conditions, indicating that despite the increased homoplasy in GM datasets, the same proportion of synapomorphic information was retained as in datasets excluding GM data. As the RIs of the continuous and non-continuous datasets are almost identical, it is unlikely that the difference in homoplasy indicated by CI between the datasets can be ascribed to a greater proportion of uninformative or autapomorphic characters in the continuous dataset.

Tree length. When comparing the tree-length (weighted homoplasy) produced by datasets with equal numbers of characters, trees that incorporate continuous data are consistently shorter than those which exclude it. The D tree (94 characters) produced a tree-length of 31.90, whereas the DC tree (94 characters) produced a length of 27.46. Likewise, the DM tree (90 characters) recovered a length of 30.52, while the DCM (90 characters) tree-length was 25.44.

The effects of including GM data cannot be interpreted in the same way as above; the base D dataset contains more characters than the DM dataset, and we would therefore naturally assume that the

DM tree would be shorter just by virtue of having fewer characters. It is, however, possible to say that the continuous characters in this study do have a shortening effect on tree-length when compared to the standard discrete data tree (D vs DC tree-length). Furthermore, the incorporation of continuous data into the DM dataset (DM vs DCM tree-length) resulted in a greater reduction in tree length than was produced by the combined effect of incorporating GM data into the D dataset and the associated reduction in the number of characters (D vs DM). This may indicate that the continuous characters in this dataset produced a stronger influence on tree length than the GM characters. Additionally, as extended implied weighting was in effect the shorter tree lengths equate to reduced homoplasy. Considering the higher consistency index of the continuous datasets, it is unsurprising that the continuous datasets also produce the shortest tree lengths when compared to D and DM, as under implied weighting, the 'length' of each character is partially calculated using the same technique as the consistency index. The overall tree-length is an ensemble score of estimated homoplasy within the dataset - similarly the CI measures ensemble consistency.

Topological similarity. In analyses of topological similarity (maximum agreement subtrees, SPR distances and Robinson-Foulds distance) the DC tree differed from the base discrete data tree by 37.2%, 32.5% and by 0.45122 in each respective metric, whereas the DM tree only differed from the base tree by 23.3%, 15% and 0.23171 respectively. This suggests that the incorporation of continuous characters into the base dataset altered the topology of the output tree to a greater extent than by incorporating GM characters.

Within our overall dataset, continuous characters appear to exert a stronger influence on tree topology and tree length than GM characters, and the incorporation of continuous rather than GM

characters produces a tree that is found to be slightly less homoplastic by consistency index and implied weighting.

It should be noted that the elevated influence of continuous data may be related to variations in our dataset rather than an inherent property of the scoring method. For example, in the DC condition continuous data accounted for 10.64% of the characters used, but in the DM condition GM data only accounted for 5.56% of the total characters; therefore, continuous data may have more influence as it constituted a greater proportion of the data. Alternatively, it is possible that the characters scored as continuous data may, by chance, have been less homoplastic than those scored using GM techniques. It should also be noted that these two influences are not mutually exclusive.

Support metrics. A slightly different finding to the above was obtained when investigating Bremer and frequency supports. When collapsing nodes with Bremer scores less than that of the average character step length (0.11), the datasets incorporating GM data (DM and DCM) produced consistently poorer total Bremer support for the collapsed tree, and retained less nodes than the non-GM datasets (D and DC). The mean Bremer support values for nodes exceeding the cut-off were almost entirely consistent between all four data treatments, whereas at the lower cut-off (0.08) these means were more variable. This suggests that the cut-off of 0.11 largely retained the nodes for which the Bremer support values were more resistant to the effects of data treatment.

In contrast to Bremer scores, frequency supports performed more consistently between scoring techniques in terms of number of nodes retained; however, similarly to the results of Bremer supports, the DCM treatment produced the worst results. The pattern of summed frequency values matched the general trend of the Bremer supports, i.e. the GM conditions produced lower total support for the collapsed tree; although, the mean frequency supports across the four collapsed trees were again relatively constant.

When the Bremer and frequency support values were averaged in five tree regions and summed within each tree, in both metrics the DC condition produced the best values and the two GM conditions produced the worst.

Conclusions

To broadly summarize our findings - for our dataset it appears that continuous characters consistently exert a greater influence over the results than GM characters, and in comparison to datasets excluding continuous characters, they also appear to reduce homoplasy. GM characters in this study produced trees with generally worse nodal support values, and despite the lack of polytomies within the best-fit trees, when collapsing nodes to adjust for over-resolution of the tree the GM datasets retained fewer nodes at a reasonable cut-off value than the continuous and discrete trees.

A potential drawback of using GM data in particular is the relative difficulty, in comparison to discrete characters, of interpreting morphological changes in a way that is useful for producing written diagnoses. For synapomorphic continuous characters it is possible to express the character 'state' of a taxon or group as a numerical range and transformations as shifts from one range to another; however, describing subtle, but apparently phylogenetically relevant changes in shape according to geometric morphometrics necessitates either multiple diagrams of landmark displacements at supported nodes, or long breakdowns of morphology, and an elevation of analytical complexity for relatively little gain (at least in the case of this dataset). An example of the perplexity caused by GM data may be seen in the nodal synapomorphies in the treatments which incorporate GM data (Appendix 3); in both trees (DM and DCM) almost all GM characters are optimized as synapomorphies for almost every node.

A further obstacle to incorporating substantial amounts of GM data into phylogenetic analyses is that in palaeontological datasets, and especially with phytosaurs, it is relatively uncommon to find the pristine, non-deformed morphologies necessary for geometric morphometric comparisons. Furthermore, GM characters may inherently encompass multiple discrete characters; if one aspect of a morphological feature is deformed (thus rendering the feature unusable for GM), all associated morphological features to be scored by the same configuration of landmarks would also have to be excluded from the analysis. In this sense, the addition of GM characters into a dataset may actually increase the quantity of missing data in a dataset where the characters could be alternatively scored with discrete or continuous methods.

For the various reasons outlined above we prefer the D and DC trees as they either incorporate continuous data, exclude GM data, or both. These trees are also representative of the two conflicting topologies found in this study and are generally consistent with previous analyses of ingroup Phytosauria. Therefore, we recommend use of these datasets and their resultant trees in future phylogenetic analyses of the clade.

Commented [WGP18]: I think the Strict Consensus tree of all four analyses demonstrates the issues we still have with phytosaur taxonomy and phylogeny, especially regarding the non-pseudopalatine leptosuchomorphs which historically have been shuffled between the genera Rutiodon, Leptosuchus, and Smilosuchus. Essentially they could all be redefined as monospecific genera. Could you please briefly address this. Protome batalaria within Machaeroprosopus/Redondasaurus is problematic because that negates to use of isolated phytosaur squamosals in vertebrate biostratigraphy (e.g., Long and Murry, 1995; Irmis & Parker, 2006; Parker, 2006; Parker and Martz, 2011) as P. batalaria has a Leptosuchus/Smilosuchus type squamosal.

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1653

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Appendix 1: Taxonomic list

Institutional abbreviations

AMNH: American Museum of Natural History, New York, USA; **BSPG**: Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **CMNH**: Carnegie Museum of Natural History, Pittsburgh, USA; **FMNH**: Field Museum of Natural History, Chicago, USA; **GPIT**: Institut für Geologie und Paläontologie Tübingen, Tübingen, Germany; **GR**: Ruth Hall Museum of Paleontology, Ghost Ranch, Abiquiu, USA; **ISI**: Indian Statistical Institute, Kolkata, India; **MB**: Museum für Naturkunde, Berlin, Germany; **MBSN**: Museo Civico di Scienze naturali 'E. Caffi', Bergamo, Italy; **MCZ**: Harvard University Museum of Comparative Zoology, Cambridge, USA; **MNA**: Museum of Northern Arizona, Flagstaff, USA; **MNHN**: Muséum National d'Histoire Naturelle, Paris, France; **MSM**: Arizona Museum of Natural History (previously Mesa Southwest Museum), Mesa, USA; **MU**: University of Missouri, Columbia, Missouri, USA; **NHMUK**: Natural History Museum, London, UK; **NHMW**: Naturhistorisches Museum Wien, Vienna, Austria; **NMC**: Naturkundemuseum Coburg, Coburg, Germany; **NMMNHS**: New Mexico Museum of Natural History and Science, Albuquerque, USA; **OMNH**: Oklahoma Museum of Natural History, Norman, USA; **PEFO**: Petrified Forest National Park, Arizona, USA; **PPHM**: Panhandle Plains Historical Museum West Texas A&M University, Canyon, USA; **SMF**: Forschungsinstitut und Natur-Museum Senckenberg, Frankfurt/Main, Germany; **SMNS**: Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; **TMM**: Texas Memorial Museum, Austin, USA; **TTU-P**: Museum of the University of Texas Tech, Lubbock, USA; **UCM**: University of Colorado Museum, Boulder, USA; **UCMP**: University of California Museum of Paleontology, Berkeley, USA; **UMMP**: University of Michigan Museum of Paleontology, Ann Arbor, USA; **USNM**: National Museum of Natural History, Washington D.C., USA; **UW**: University of Wisconsin Geological Museum, Madison,

USA; **YPM**: Yale Peabody Museum, New Haven, USA; **ZMNH**: Zhejiang Museum of Natural History, Hangzhou, China; **ZPAL**: Instytut Paleobiologii PAN, Warsaw, Poland.

Diandongosuchus fuyuanensis Li *et al*., 2012

Age: Ladinian (*c.* 242–237 Mya)

Occurrences: Zhuganpo Member, Falang Formation, southeast Fuyuan County, Yunnan Province, China

Holotype: ZMNH M8770, largely complete skeleton missing many caudal vertebrae

Previously Referred Specimens: Additional specimen under preparation (personal communication with X.-C. Wu cited by Griffin *et al.* [2017])

Specimen(s) Used for Scoring: ZMNH M8770

Key References: Li *et al.* (2012); Stocker *et al.* (2017)

Most Recent Diagnosis:

Stocker *et al.* (2017) distinguished *D. fuyuanensis* from all other phytosaurs using the following characters: 1) Anterodorsal (nasal) process of premaxilla extending well posterior of external naris; 2) Presence of a fossa expanded in anteroventral corner of external naris; 3) Jugal with pronounced longitudinal ridge on lateral surface; 4) Anterior process of jugal much broader than the posterior process underlying anterior process of quadratojugal; 5) Premaxilla with nine teeth; 6) More than one set of paramedian osteoderms dorsal to the cervical series.

Comments: *D. fuyuanensis* was originally described as a rauisuchian archosaur (Li *et al*., 2012), and was subsequently reassessed as the most basal phytosaur (Stocker *et al*., 2017), using the following characters: 1) Posterodorsal process of premaxilla strongly sutured to maxilla; 2) More than six premaxillary teeth; 3) Facial portion of maxilla anterior to anterior edge of antorbital fenestra equal in length or longer than portion posterior to anterior edge of fenestra; 4) Entire anterior margin of scapula straight/convex or

partially concave; 5) Anterior portion of coracoid distinctly hooked; 6) Ectepicondylar flange of humerus present; 7) Obturator foramen of the pubis modified into a notch that opens medioventrally; 8) medial side of distal tarsal 4 with foramen/foramina; 9) Articular surface for the fibula on the calcaneum convex and hemicylindrical shaped; 10) Osteoderms covering the appendages; 11) Retroarticular process of the articular and surangular well ventral to the articulation with the quadrate; 12) Lateral margin of the humerus straight from midshaft to proximal portion. The hypothesis that *D. fuyuanensis* is the most basal known phytosaur was not explicitly tested by Stocker *et al*. (2017); its position within Phytosauria is assessed for the first time in this study.

Wannia scurriensis (Langston, 1949)

Age: late Carnian–early Norian (*c.* 232–225 Mya)

Occurrences: Camp Springs Formation, Dockum Group, Scurry County, Texas, USA

Holotype: TTU-P 00539, partial skull

Previously Referred Specimens: TTU-P 11422 (Stocker 2010)

Specimen(s) Used for Scoring: TTU-P 00539

Key References: Langston (1949); Stocker (2013)

Most Recent Diagnosis: Stocker (2013) diagnosed *Wannia scurriensis* on the basis of the following proposed autapomorphies: 1) Basitubera that are widely separated mediolaterally; 2) Presence of a ridge on the lateral surface of the jugal; 3) Presence of a thickened shelf along the posteroventral edge of an expanded pterygoid-quadrate wing; 4) ‘Septo-maxillae’ that do not contact one another and do not form part of the internarial septum; 5) Presence of a nasal swelling posterior to the posterior border of the nares. In addition to these autapomorphies, Stocker (2013) also provided a differential diagnosis outlining non-autapomorphic characters that distinguish *W. scurriensis* from other phytosaurs.

Modified Diagnosis: Here, we diagnose *Wannia scurriensis* using the following unique combination of characters: 1) Presence of an anteroposteriorly oriented ridge on the lateral surface of the jugal, positioned toward the middle or ventral edge of the jugal posterior process; 2) Presence of a nasal swelling posterior to the posterior border of the nares; 3) Posterior rim of nares smooth (not rugose); 4) Absence of paired depressions posterior to the posterior narial rim.

Comments: Some of the characters (1, 2, 3, 5) used by Stocker (2013) to diagnose *Wannia scurriensis* also occur in species of *Parasuchus* and cannot, therefore, be considered autapomorphic. As noted by Stocker (2013), the separation of the basitubera (character 1) is the same as that in *Parasuchus angustifrons*; however, Stocker suggested that the basitubera in *Parasuchus angustifrons* are not as rounded as those of *W. scurriensis*. Based on our examination of specimens of both taxa, this distinction seems subjective and questionable, particularly given that the holotype of *Parasuchus angustifrons* (BSPG 1931 X 502) has been subjected to dorsoventral compression. Stocker (2013) also noted that the narial swelling (charater 5) is also present in *Parasuchus angustifrons* (and is, therefore, also not autapomorphic), although the latter species can be differentiated from *W. scurriensis* as it possesses paired depressions just posterior to the external nares and a rugose posterior narial rim (BSPG 1931 X 502; Butler *et al*. 2014).

The thickened pterygoid-quadrate shelf (character 3) appears to also be present in TMM 31100-101, a specimen referable to *Parasuchus bransoni* on the basis of its narial morphology (see below). Moreover, the majority of the quadrate is missing in *W. scurriensis*, making character 3 difficult to assess. There are difficulties in scoring character 4 accurately for *W. scurriensis* because interpretative lines have been incorrectly drawn onto the specimen to supposedly mark the positions of the ‘septo-maxillae’, and the dorsal surface of the septum is damaged. On close side-by-side inspection of the holotype and a cast (TTU-P 14911, which lacks the interpretative lines), the septomaxillae do seem to form a midline contact,

and do not therefore differ in any significant regard from those of *Parasuchus hislopi*, *Parasuchus bransoni* and *Parasuchus angustifrons*.

An additional partial skull (TTU-P 11422) was considered referable to *W. scurriensis* by Stocker (2010); however, as noted by Stocker (2013), no characters are preserved that would allow this specimen to be diagnosed, and as such this specimen should be classified as an indeterminate parasuchid excluded from Mystriosuchinae.

Parasuchus bransoni (Williston, 1904)

Age: late Carnian–early Norian (*c.* 232–225 Mya)

Occurrences: Popo Agie Formation, Chugwater Group, Wyoming, USA; Colorado City Formation, Dockum Group, Texas, USA

Holotype: FMNH UC 632, skull

Previously Referred Specimens: TTU-P 00539 (holotype of *Wannia scurriensis*); TMM 31025-172; TMM 31100-8; TMM 31100-101; TMM 31100-175; TMM 31100-418; TMM 31100-419; TMM 31100-453; TMM 31185-11; TMM 31185-38 (Long & Murry, 1995)

Specimen(s) Used for Scoring: FMNH UC 632; TMM 31100-101; TMM 31100-418 and 419 (these two specimens likely represent an associated skull and mandible).

Key References: Williston (1904); Lees (1906); Long & Murry (1995); Butler *et al.* (2014); Kammerer *et al.* (2015)

Most Recent Diagnosis: Long & Murry (1995) diagnosed *Parasuchus bransoni* with the following combination of characters: 1) Skull low; 2) Orbit directed dorsolaterally; 3) Rostrum moderately long, prenarial length equals postnarial length; 4) Maxilla with straight ventral margin; 5) Posterior portion of

maxilla not flared laterally; 6) Interpterygoid vacuity small or absent; 7) Homodont dentition; 8) Alveoli circular throughout; 9) Posterior premaxillary alveolae normal; 10) Upper dentition with 36–45 teeth.

Modified Diagnosis: A combination of the three *Parasuchus* characters identified by Butler *et al.* (2014) and Kammerer *et al.* (2015) and one character of Kammerer *et al.* (2015) to distinguish *Parasuchus bransoni* from *Parasuchus hislopi* and *Parasuchus angustifrons*: 1) Presence of an anterior frontal depression; 2) Bifurcated lateral ridge on the squamosal; 3) Row of nodes on the lateral surface of the jugal; 4) Possession of high 'triangular' nares.

Comments: Long & Murry (1995) used a combination of nine characters to diagnose *Parasuchus bransoni*. Characters such as their 1, 2, 5, 7 and 9 have been criticized for being subjective, vague and prone to taphonomic distortion (Hungerbühler, 1998; Stocker, 2010). Character 6 appears to have been generated based on the distorted morphology of the holotype. All non-Mystriosuchinae members of Parasuchidae have an interpterygoid vacuity which extends anteroposteriorly along at least 50% of the palatal vault, and which only becomes restricted in more derived taxa. This proposed diagnostic character is actually therefore plesiomorphic for Mystriosuchinae. Character 7 is problematic as the assessment of dentition used by Long & Murry (1995) was based on empty alveolae and, therefore, may be unreliable. In any case, some degree of heterodonty has now been recognized in all phytosaurs. Character 9 (here inferred to relate to the increase in size of the posterior two or three premaxillary alveolae in many taxa) is also problematic; although the increase in posterior premaxillary alveolar size is subtler in *Parasuchus bransoni* than in many taxa, it does still occur. Several of the characters) are probably plesiomorphic for Phytosauridae (3, 4, 5, 7, 8, and probably 9) and/or are widespread (1, 2, 8, 10) in basal members of the clade.

Parasuchus hislopi Lydekker, 1885

Age: late Carnian–early Norian (*c.* 232–225 Mya)

Occurrences: Lower Maleri Formation, Pranhita Godavari Valley, Telangana, India; Tiki Formation, Madhya Pradesh, India

Holotype: ISI R 42 (neotype), almost complete skeleton including cranium and mandible.

Previously Referred Specimens: ISI R 43; ISI R 44; ISI R 45; ISI R 46; ISI R 47; ISI R 160; ISI R 161 (Chatterjee, 1978)

Specimen(s) Used for Scoring: ISI R 42; ISI R 43

Key References: Lydekker (1885); Chatterjee (1974, 1978); Kammerer *et al.* (2015)

Most Recent Diagnosis: Kammerer *et al*. (2015) diagnosed *Parasuchus hislopi* as follows: a species of *Parasuchus* that is 1) distinguished from *Parasuchus bransoni* by a relatively low narial eminence with a raised, rugose posterior margin of the naris (a 'narial rim'); 2) Distinguished from *Parasuchus angustifrons* by the absence of paired depressions on the anterior portions of the nasals; 3) Tentatively distinguished from '*Pal. ~~Magnoculus'~~ magnoculus'* by the posterior confluence of the raised margins of the nares.

Parasuchus angustifrons (Kuhn, 1936)

Age: late Carnian (*c.* 232–228 Mya)

Occurrences: Blasensandstein (lateral equivalent of Hassberge Formation), Middle Keuper Subgroup, northern Bavaria, Germany; Middle Keuper Subgroup, Opole province, Poland

Holotype: BSPG 1931 X 502, partial skull

Previously Referred Specimens: None, although the phytosaur material from Krasiejów in Opole, southwest Poland, was considered highly similar to *Parasuchus angustifrons* by Butler *et al.* (2014), and

one of these specimens, ZPAL AbIII 200, was noted to be 'probably referable to *Parasuchus Angustifrons*' by Kammerer *et al.* (2015).

Specimen(s) Used for Scoring: BSPG 1931 X 502; ZPAL AbIII 111; ZPAL AbIII 200

Key References: Kuhn (1936); Butler *et al.* (2014); Kammerer *et al.* (2015)

Most Recent Diagnosis: Butler *et al.* (2014) diagnosed *Parasuchus angustifrons* on the basis of the following proposed autapomorphies: 1) Stepped lateral rim of external naris that is strongly swollen and rugose at posterior end; 2) Paired depressions on the anterior portions of the nasals (immediately posterior to the external nares) and anterior portions of the frontals; 3) Foramen in ectopterygoid enlarged and subcircular in outline; 4) Suborbital foramen elongate and boomerang-shaped; 5) Large postparietal foramen at junction of supraoccipital and parietal.

Modified Diagnosis: Species of *Parasuchus* with the following autapomorphies: 1) Paired depressions on the anterior portions of the nasals; 2) Large postparietal foramen at junction of supraoccipital and parietal.

Comments: Of the characters proposed by Butler et al. (2013) as autapomorphic for *Parasuchus angustifrons*, characters 1 and 3 are both present in other members of *Parasuchus*: the laterally stepped and posteriorly rugose nares are also present in *Parasuchus hislopi* (ISI R42), while the enlarged ectopterygoid foramen is visible in the holotype of *Parasuchus bransoni* (FMNH UC 632). Character 4, an elongate and boomerang-shaped suborbital foramen, may be variable within the species, given that it appears to be absent in ZPAL AbIII 200. However, the degree of variability of this character among basal phytosaurs is difficult to assess, given the paucity of well-preserved palates generally within the genus *Parasuchus*. Given this uncertainty, character 4 should not be considered diagnostic until sufficient comparative material is available to assess its usefulness.

‘*Paleorhinus*’ *parvus* Mehl, 1928

Age: late Carnian–early Norian (*c.* 232–225 Mya)

Occurrences: Popo Agie Formation, Fremont County, Wyoming, USA

Holotype: MU 530, rostral/mandibular fragments and partial postcrania

Previously Referred Specimens: None

Specimen(s) Used for Scoring: MU 530

Key References: Mehl (1928); Kammerer *et al.* (2015)

Most Recent Diagnosis: Mehl (1928) did not provide a list of distinct autapomorphies; however, the morphology of ‘*Paleorhinus*’ *parvus* was discussed in relation to other phytosaurs, and a number of distinctive features were highlighted, which are discussed below.

Modified Diagnosis: Diagnosable on the basis of a unique combination of characters: 1) Anterior tip of the rostrum abruptly downturned; 2) Steep anterodorsally concave curve to the nares; 3) Anterior border of nares anterior to the antorbital fenestra; 4) Subnarial facial portion of the maxilla is dorsoventrally extensive.

Comments: ‘*Paleorhinus*’ *parvus* was interpreted by Mehl (1928) to possess a proportionately shorter prenarial rostrum than that of *Parasuchus bransoni*. The postnarial portion of the skull of ‘*Paleorhinus*’ *parvus* is not preserved; therefore, Mehl based his calculations on a partial mandible associated with the cranial remains, which he used to estimate total skull length. Mehl’s measurements suggest that the snout constituted 42.4% of total cranial length, which is indeed proportionately short compared to *Parasuchus bransoni*, for which values are approximately 50% (TMM 31100-101, 31100-418). This character should be treated with caution, however, as Mehl’s calculations of skull length based on the mandible may be somewhat inaccurate. Mehl also suggested that the rostrum of ‘*Paleorhinus*’ *parvus* is more slender than

that of *Parasuchus bransoni*; however, it is uncertain whether this is due to mediolateral compression of the former.

The anterior tip of the rostrum was suggested by Mehl (1928) suggested to be more abruptly downturned than in *Parasuchus bransoni*. We concur with this assessment: the rostrum of '*Paleorhinus*' *parvus* is more abruptly downturned than all species of *Parasuchus*, '*Paleorhinus*' *sawini* and *Ebrachosuchus neukami*, and more closely approximates the rostral morphology of *Brachysuchus* and *Angistorhinus*. Mehl also noted that the nares of '*Paleorhinus*' *parvus* are more steeply curved anterodorsally than *Parasuchus bransoni*, but considered the narial development to be suspect and 'not dependable'. However, we concur with Kammerer *et al.* (2015) that there is no reason to suspect that the morphology of the narial region is not genuine, even considering lateral compression. Kammerer *et al.* (2015) also noted that the 'subnarial facial portion of the maxilla' is well preserved and 'has greater relative height than that of *Parasuchus hislopi*'. We agree with this assessment, and find that this is also true when compared with all other members of *Parasuchus.*

'*Paleorhinus*' *sawini* Long & Murry, 1995

Age: late Carnian–early Norian (*c.* 232–225 Mya)

Occurrences: 'Pre-Tecovas Horizon', Dockum Group, Borden County, Texas, USA

Holotype: TMM 31213-16, skull and possibly associated isolated postcrania

Previously Referred Specimens: None

Specimen(s) Used for Scoring: TMM 31213-16

Key References: Long & Murry (1995); Stocker (2010)

Most Recent Diagnosis: Long & Murry (1995) diagnosed '*Paleorhinus*' *sawini* on the basis of the following combination of characters: 1) Skull high; 2) Rostrum short and robust; 3) Prenarial length less

than postnarial length; 4) Maxilla with strongly convex ventral margin; 5) Posterior portion of maxilla with prominent lateral flare; 6) Probable heterodont dentition; 7) Posterior maxillary alveoli enlarged and transversely rectangular; 8) Posterior premaxillary enlarged; 9) Upper dentition with 38 teeth.

Modified Diagnosis: A non-leptosuchomorph phytosaur with the following unique character complex: 1) Rostrum short and robust; 2) Prenarial length less than postnarial length; 3) Posterior premaxillary alveoli enlarged; 4) Upper dentition with 38 teeth; 5) Parietal/squamosal bars are medially bowed.

Comments: Characters 1, 4 and 5 of Long & Murry (1995) may be related to general large size and robusticity, but this has yet to be tested through ontogenetic studies of early phytosaurs. In particular, the height of the skull in proportion to its width does not appear to differ considerably from other species of early phytosaur such as *Parasuchus bransoni* (TMM 31100-8, 31100-101) or *Parasuchus angustifrons* (ZPAL Ab III 111, Ab III 200). Characters 6 and 7 are based on incomplete or missing morphology. No teeth remain in the skull, thus estimations of heterodonty are based solely on the shapes and relative sizes of empty alveolae. Given that some degree of heterodonty is present in all phytosaurs and the roots of even mediolaterally compressed phytosaur teeth are approximately circular, it is difficult to make meaningful statements about heterodonty without preservation of the actual dentition. Similarly, the posterior maxillary alveolae are heavily reconstructed with plaster, making character 7 questionable. It is unclear how intraspecifically variable tooth counts are in phytosaurs; however, specimens of *Parasuchus bransoni* and *Parasuchus hislopi* consistently have more than 40 teeth in the upper jaw (TMM 31100-101, 31100-239, ISI R42), whereas *Parasuchus angustifrons* appears to possess a similar number to '*Paleorhinus*' *sawini* (ZPAL Ab III 200). This character is therefore retained, as further study may reveal it to contain taxonomic value.

Stocker (2010) noted two further characters that she proposed distinguish '*Paleorhinus*' *sawini* from *Parasuchus*: 1) Shares medially-bowed parietal-squamosal bars with *Angistorhinus*; 2) The

antorbital fossa is highly reduced or absent. It is, however, debatable how reduced in size the antorbital fossa was; upon close examination it appears possible that the fossa may have been broken up to its outer rim, i.e. to the extent of the concavity of the fossa. There is evidence of a thin lamina extending from the interior edge of the purported fenestra in TMM 31213-16, but all of its edges are broken away; this may be the remnants of the original antorbital fossa.

Ebrachosuchus neukami Kuhn, 1936

Age: late Carnian (*c.* 232–228 Mya)

Occurrences: Blasensandstein (lateral equivalent of Hassberge Formation), Middle Keuper Subgroup, northern Bavaria, Germany

Holotype: BSPG 1931 X 501

Previously Referred Specimens: None

Specimen(s) Used for Scoring: BSPG 1931 X 501

Key References: Kuhn (1936); Long & Murry (1995); Butler *et al*. (2014)

Most Recent Diagnosis: Butler *et al.* (2014) diagnosed *E. neukami* based on six autapomorphies: 1) Preorbital length more than 3.8 times that of the orbit + postorbital length; 2) More than 50 teeth in the premaxilla and maxilla combined; 3) Pronounced, sharp flange extending along the lateral surface of the dorsal (postorbital) process of the jugal and the ventral (jugal) process of the postorbital that is continuous posteriorly with the lateral margin of the postorbital-squamosal bar; 4) Infratemporal fenestra is substantially longer anteroposteriorly than deep dorsoventrally, terminates anteriorly beneath the midpoint of the orbit; 5) Quadrate foramen very large, approximately two-thirds of width of foramen magnum; 6) Alveolar ridges absent from the anterior maxilla and only poorly developed on the premaxilla.

Rutiodon carolinensis Emmons, 1856

Age: early Norian (*c.* 228–218 Mya)

Occurrences: Cumnock Formation, Deep River Coal Field, near Gulf, North Carolina, USA; Cumnock Formation, New Egypt coal mine, Chatham County, North Carolina, USA

Neotype: USNM PAL 214513 (formerly 'Williams College unnumbered specimen')

Previously Referred Specimens: Emmons' original material (isolated, assorted postcrania, the location and accession numbers of which are unknown); 17 vertebrae and associated ribs (holotype of '*Clepsysaurus leai*', location and accession numbers unknown); teeth, referred to various taxa by Emmons (1856) (location and accession numbers unknown); USNM 5373 (holotype of '*Rhytidodon rostratus*' Marsh, 1896); AMNH 1 (semi-complete skull plus composite skeleton); AMNH 2 (skull roof); AMNH 3 (right posterior portion of skull roof including squamosal and supratemporal fenestra); AMNH 4 (rostral fragment including partial nares and partial antorbital fenestra); AMNH 5 (Skull roof including left supratemporal region, quadrate and quadratojugal) (Gregory, 1962).

Specimen(s) Used for Scoring: USNM PAL 214513; USNM V 5373; AMNH 1–5

Key References: Emmons (1856; 1860); Marsh (1896); McGregor (1906); Colbert (1947); Gregory (1962); Hunt & Lucas (1989); Stocker (2010)

Most Recent Diagnosis: Stocker (2010) suggested the following diagnostic characters with reference to the neotype specimen: 1) Slender rounded premaxillae that lack a rostral crest; 2) Nares placed posteriorly between the antorbital fenestrae with borders above the level of the skull roof. To enable distinction between *Rutiodon carolinensis* and *Angistorhinus*, Stocker added a further character based on preserved temporal regions referred to *Rutiodon carolinensis* in the AMNH collections (AMNH 1–5): 3) Semi-depressed parietal-squamosal bars.

Comments: Hunt & Lucas (1989) designated a neotype for *Rutiodon carolinensis* and proposed four diagnostic characters that were centred around the temporal region of the skull. Stocker (2010) noted that none of the characters included in the diagnosis of Hunt & Lucas (1989) were observable in their designated neotype due to the temporal region not being preserved. Instead, the diagnostic appear to be based on USNM and AMNH material that was referred to *Rutiodon carolinensis* by Gregory (1962).

Characters 1 and 2 of the diagnosis of Stocker (2010) are observable in the neotype; however, if only these characters are considered it is not possible to differentiate *Rutiodon carolinensis* from *Angistorhinus*. Stocker also therefore used the referred AMNH material to provide a further character and a more robust diagnosis.

It should be noted that the elevation of the nares (character 2 of Stocker, 2010) may not be entirely reliable, as the orbital and narial portions of the neotype do not articulate together meaning there is no way to be certain that the nares would have been elevated above the level of the skull roof. Furthermore, Gregory (1962) noted that in the neotype the nares were inferred to be elevated, while those of AMNH 1 are not, suggesting a degree of variability in this feature.

Angistorhinus talainti Dutuit, 1977

Age: late Carnian–early Norian (*c.* 232–225 Mya)

Occurrences: Timezgadiouine Formation, Western Moroccan Atlas, Morocco

Holotype: MNHN TAL 1–11 (syntypes), three skulls plus four partial mandibles and mandibular fragments

Previously Referred Specimens: None

Specimen(s) Used for Scoring: MNHN TAL 1; MNHN TAL 2

Key References: Mehl (1913); Dutuit (1977); Long & Murry (1995)

Most Recent Diagnosis: Long & Murry (1995) felt the placement of *A. talainti* within the genus *Angistorhinus* was unjustified and therefore considered it as referable to a new and currently unnamed genus within the subfamily 'Angistorhininae' Camp, 1930. They considered it to be diagnosed by the following combination of characters: 1) Supratemporal fenestra extremely elongate and narrow, crescentic in dorsal view and extending to posterolateral corner of squamosal; 2) Postorbital portion of the skull elongate with parietals long, narrow and fused for most of their length; 3) Postfrontal not in contact with supratemporal fenestra; 4) Occiput with shallow posterior emargination; 5) Posterior process of squamosal well developed and terminally convex; 6) Parietal extensions not present; 7) Opisthotic process short and paddle shaped.

Modified Diagnosis: *A. talainti* can be diagnosed from other phytosaurs using a combination of characters that includes generic *Angistorhinus* characters and characters recognized in previous studies (Dutuit, 1977; Long & Murry, 1995): 1) Parietal/squamosal bars equal to, or greater than the thickness of the postorbital/squamosal bars; 2) Parietal/squamosal bars curve medially; 3) Supratemporal fenestrae narrow and short; 4) Postorbital portion of the skull elongate with parietals long, narrow and fused for most of their length; 5) Posterior process of squamosal well developed and terminally convex; 6) Posterolaterally curving groove extends from the supratemporal fenestra to the posterolateral corner of the squamosal; 7) Prominent ridge runs along the anterior dorsolateral edge of the postorbital-squamosal bar; 8) Parietals diverge posterior to the main vacuity of the supratemporal fenestra.

Comments: The interpretation of the supratemporal fenestra of *A. talainti* in character 1 of Long & Murry (1995) contradicts the description of Dutuit (1977), who stated in his diagnosis that the supratemporal fenestrae are narrow and short. The figures in Dutuit (1977) superficially show an elongate fenestra, as suggested by Long & Murry (1995); however, Long & Murry did not distinguish between the dorsal opening of the fenestra and a posterior groove which grades from the posterior corner of the fenestra onto

the posterolateral corner of the squamosal. It is difficult to delimit the fenestra due to the presence of this groove, but we agree with Dutuit (1977), that the actual opening of the fenestra is relatively short. Characters 3 and 4 of Long & Murry (1995) appear to be shared by all members of *Angistorhinus* observed in this study, and character 5 is present in multiple specimens from Texas and New Mexico, such as TMM 31100-1332, TMM 31100-164, TMM 31100-298 and NMMNHS-P 4781. Character 6 is difficult to interpret - the terms 'parietal extensions' and 'horizontal parietal extensions' are used in Long & Murry's revised diagnosis of 'Angistorhininae'; however, no further explanation of these features is given. We assume that this terminology refers to the posterior thickening of the parietal/squamosal bars that is observed throughout *Angistorhinus*. The parietals of *A. talainti* are expanded posteriorly in a horizontal plane to a greater extent than other species and specimens of *Angistorhinus* mentioned by Long & Murry (1995).

Angistorhinus grandis Mehl, 1913

Age: late Carnian–early Norian (*c.* 232–225 Mya)

Occurrences: Popo Agie Formation, between Squaw and Baldwin Creeks, Fremont County, Wyoming, USA

Holotype: FMNH UC 631, Skull and associated partial mandible

Previously Referred Specimens: None

Specimen(s) Used for Scoring: FMNH UC 631

Key References: Mehl (1913); Long & Murry (1995)

Most Recent Diagnosis: Long & Murry (1995) diagnosed *A. grandis* as a species of *Angistorhinus* with the following characters: 1) Posterior process of squamosal very short, but deep with straight posterior

margin; 2) No cleft between posterior process and descending process of the squamosal; 3) Parietal extension ?short; 4) Rostrum delicate; 5) Alveoli circular throughout with posterior premaxillary alveoli not enlarged (this region of snout is not swollen); 6) Ventral margin of maxilla not laterally flared; 7) Orbits directed more dorsally than laterally.

Modified Diagnosis: We diagnose *A. grandis* as a species of *Angistorhinus* with the following unique character combination: 1) Ventral margin of maxilla not laterally flared; 2) Supratemporal fenestrae wide and triangular in shape; 3) Lateral temporal fenestra large and more sub-triangular than rectangular; 4) U-shaped emargination between the supratemporal fenestrae at the posterior border of the parietals in dorsal view.

Comments: We suggest that characters 1 and 2 of Long & Murry (1995) should be treated with caution, or potentially rejected, as the posterior process of the squamosal is not actually preserved in *A. grandis*. The morphology of the posterior process was reconstructed in plaster from a supposed impression of the medial surface of the process preserved in the matrix with the skull; however, no photographs or diagrams exist of this impression, and its described morphology differs from the rounded morphology of the posterior process of the squamosal observed in all other specimens of *Angistorhinus.*

Characters 3 and 4 of Long & Murry (1995) are phrased ambiguously and are therefore difficult to objectively assess. Alongside character 5, these characters are also present in all other specimens of *Angistorhinus* that were examined, and are therefore not useful for a diagnosis at specific level. Character 7 reports the orientation of the orbit; however, phytosaur skulls are often mediolaterally or dorsoventrally compressed meaning that the orientation of the orbits can vary widely both inter- and intraspecifically, and should not be used for diagnostic or phylogenetic purposes (Chatterjee, 1978; Hungerbühler, 1998).

Smilosuchus gregorii (Camp, 1930)

Age: early Norian (*c.* 225–220 Mya)

Occurrences: Blue Mesa Member, Chinle Formation, near Round Rock, Apache County, Arizona, USA

Holotype: UCMP 27200, slightly dorsoventrally compressed skull and mandibles

Previously Referred Specimens: UCMP A270/27192; UCMP A270/27195 (Camp, 1930); AMNH D.VP. 3060 (Colbert, 1947); USNM V 18313; UCMP 63921; UCMP 35737; UMMP 14366; PPHM WT 3217; PPHM WT 3214; PPHM WT 3230 (Long & Murry, 1995).

Specimen(s) Used for Scoring: UCMP 27200; AMNH D.VP. 3060

Key References: Camp (1930); Colbert (1947); Long & Murry (1995)

Most recent diagnosis: Long & Murry (1995) diagnosed the new genus *Smilosuchus* and the sole species that they referred to it, *S. gregorii*, based on the following character combination: 1) Extreme heterodonty; 2) Posterior premaxillary teeth (except last three) abruptly and very greatly enlarged, causing a swelling of the premaxilla in this region; 3) Tooth pattern posteriorly shifted; 4) Ventral margin of the maxilla greatly flared laterally; 5) Rostral crest fully developed; 6) Anterior portion of rostrum very heavy and massive; 7) Posterior portion of the skull considerably wider than in *Leptosuchus*, with lateral temporal fenestra facing dorsolaterally; 8) Orbit directed dorsolaterally.

Modified Diagnosis: *S. gregorii* is diagnosed on the basis of the following unique character combination: 1) Full rostral crest; 2) Greatly dorsoventrally expanded posterior process of the squamosal.

Comments: Characters ~~four~~4, ~~six~~ 6 and ~~seven~~ 7 of Long & Murry (1995) may be size-correlated, which is both undesirable and problematic (Irmis, 2005); ~~seven~~ 7 and ~~eight~~ 8 are highly prone to taphonomic distortion and the phrasing of character ~~three~~ 3 is ambiguous.

Of the remaining characters, ~~two~~ 2 and ~~five~~ 5 are consistently present only in *S. gregorii* rather than '*S*'. *adamanensis* or '*S*'. *lithodendrorum* and may therefore be useful in defining the species. Character one

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(extreme heterodonty) is present in all current species of *Smilosuchus* and is therefore not of diagnostic use for *S. gregorii*.

'*Smilosuchus*' *adamanensis* (Camp, 1930)

Age: early Norian (*c.* 225–220 Mya)

Occurrences: Blue Mesa and lower Sonsela Members, Chinle Formation, ~~near Adamana~~Petrified Forest National Park, Apache County, Arizona, USA

Holotype: UCMP 26699, skull and mandibles

Previously Referred Specimens: All phytosaur material from UCMP/PEFO localities ~~7038~~PFV 122, ~~7039~~PFV 120, ~~7040~~PFV 121, ~~7041~~PFV 142, ~~7046~~ PFV 157 and ~~7047~~ PFV 155 (Camp, 1930; Parker, 2002); (UCMP 26696, 26697, 26698, 26706, 26717, 26718, 26720, 26725, 26727, 26729, 26730, 26731, 26756, 27070, 27093, 27094, 27104 and 27106 referred as paratypes (Camp, 1930)); UCMP 27099, 27006, 27007, 27008, 27010, 27011, 27013, 27014, 27015, 25027, 26026, 27027 (Camp, 1930); UCMP 27446; MNA ~~Pl.~~V-3024; MNA ~~Pl.~~V-3025; MNA ~~Pl.~~V-2675; MNA V3698; UCMP 27444; UCMP 27185; UCMP 27036 (holotype of '*M*'. *zunii*); UCMP 27060; UCMP 126991; USNM 15841; UCMP 124957; USNM (NPS 72-39 in part); AMNH (EHC 1946-23); UCMP 26688 (holotype of '*S*'. *lithodendrorum*); UMMP 7523 (holotype of '*Leptosuchus imperfecta*') (Long & Murry, 1995). PEFO 34852 (Griffin et al., 2017).

Specimen(s) Used for Scoring: UCMP 26699; UCMP 170166

Key References: Camp (1930); Long & Murry (1995); Stocker (2010)

Most Recent Diagnosis: Long & Murry (1995) differentiated '*S'. adamanensis* from other *Leptosuchus*-grade phytosaurs on the basis the following character combination: 1) Posterior process of squamosal is a deep vertical plate with moderate posterior elongation beyond paroccipital process; 2) Post-fenestral

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Commented [WGP5]: Parker, W. G. 2002. Correlation of locality numbers for vertebrate fossil sites in Petrified Forest National Park, Arizona. New Mexico Museum of Natural History and Science Bulletin 21:37-42.

Commented [WGP6]: P1 designation for vertebrates is no longer used.

Commented [WGP7]: Griffin, C.T., Stefanic, C.M., Parker, W.G., Hungerbuhler, A., and M. R. Stocker 2017. Sacral anatomy of the phytosaur Smilosuchus adamanensis, with implications for pelvic girdle evolution among Archosauriformes. Journal of Anatomy 231:886-905.

portion of squamosal wide and abruptly truncated when viewed dorsally, though the extra-fenestral portion of the bar is narrow.

Comments: Both characters of Long & Murry are accurate; however, character 1 is somewhat variable in other early leptosuchomorph taxa e.g. *Leptosuchus crosbiensis* (UMMP 7522, TMM 31173-120), and character 2 is based on heavily distorted morphology in the holotype. The lack of either a rostral or narial crest in '*S.*' *adamanensis* distinguishes it from other putative members of the genus *Smilosuchus* and members of *Leptosuchus*, though it is unclear whether or not this feature is plesiomorphic.

'*S.*' *adamanensis* suffers the same problem as '*S*'. *lithodendrorum* (see below); the majority of material referred to this species by Camp (1930) was referred based on geographical and stratigraphical proximity. As such, previous definitions of the taxon may be chimeric; subsequent analyses should therefore treat referred specimens with caution or rely only on the holotype. A thorough re-examination and redescription of the holotype of '*S'. adamanensis* may bring further diagnostic characters to light; however, such work is beyond the scope of the current study.

'*Smilosuchus*' *lithodendrorum* (Camp, 1930)

Age: Norian (*c.* 219–217 Mya)

Occurrences: Lot's Wife beds ~~Lower Carrizo fossil horizon~~, Sonsela Member, Chinle Formation, ~~near~~ ~~Adamana~~Petrified Forest National Park, Navajo County, Arizona, USA; Tecovas Formation, Dockum Group, Crosby County, Texas, USA

Holotype: UCMP 26688, poorly preserved, fragmentary and compressed left half of skull, and almost complete mandibles.

Previously Referred Specimens: All phytosaur material from UCMP/~~UCMP~~ PEFO localities ~~A 258~~PFV 108, ~~7034~~PFV 096, ~~7037~~PFV 172, ~~7042~~ PFV 146 and ~~7044~~ PFV 161 (Camp, 1930; Parker, 2002);

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(UCMP 26683, 26684, 26719, 27179, 27189, 27181 and 27182 referred as paratypes (Camp, 1930)); UCMP 27151, 26693, 26694, 27017, 27183, 27184, 27149 (Camp, 1930); TMM 31173-121 (Stocker, 2010).

Specimen(s) Used for Scoring: UCMP 26688; TMM 31173-121

Key References: Camp (1930); Long & Murry (1995); Stocker (2010)

Most Recent Diagnosis: Stocker (2010) proposed that '*Smilosuchus*' *lithodendrorum* should be diagnosed as a species of *Smilosuchus* with the following characters: 1) A highly angled rostrum that continues anteroventrally in a smooth descent; 2) The posterior process of the squamosals grade anteroventrally into the opisthotic process; 3) Very slight medial flange on the dorsal edge of the squamosal.

Comments: The validity of '*S*'. *lithodendrorum* has previously been questioned; it was synonymized with *Leptosuchus crosbiensis* by Long & Murry (1995) with no justification given. Stocker (2010) suggested that this may have been due to the narrow postorbital/squamosal bar, which is a prominent feature of *Leptosuchus crosbiensis* and *Leptosuchus studeri.* It is also possible that the synonymization was due to extensive morphological variation exhibited in the specimens referred to '*S*'. *lithodendrorum* by Camp (1930). Camp's assignments of lectotypes and referred specimens were based on geographical and stratigraphical proximity of specimens to the holotype, rather than morphology; as a result, a number of smaller, non-crested skulls (between 678 and 965 mm in length) were assigned to this species as juveniles of '*S.*' *lithodendrorum* (UCMP 26684, 26719, 27179, 27181). These specimens lack the full rostral crest reported in larger individuals of '*S.*' *lithodendrorum*, instead their crests extend anterior of the nares before descending to form tubular rostra close to the most anterior extent of the maxillae. This morphology, combined with the size range of the specimens and aforementioned similarities between *L. crosbiensis* and '*S.*' *lithodendrorum*, seemingly makes them indistinguishable from the holotype of *L.*

crosbiensis. Conversely, the crest morphology in larger specimens of both '*S.*' *lithodendrorum* and *L. crosbiensis* does differ substantially. In larger specimens of '*S*'. *lithodendrorum* (e.g., UCMP 26688; TMM 31173-121) the rostrum is fully crested, with the crest forming a straight diagonal gradient from the nares to the tip of the premaxillae. However, in larger specimens of *L. crosbiensis* (e.g., TMM 43684, 43684-8) the morphology remains unchanged from smaller specimens such as TMM 31173-120, with a partial rostral crest extending from the nares to the most anterior extent of the maxillae, and a separate premaxillary crest at approximately the mid-point of the premaxillae. A more detailed examination of all material potentially referable to these taxa may help to quantify the morphological variation associated with these taxa, and disentangle their diagnoses. Stocker (2010) did tentatively identify some subtle differences between '*S.*' *lithodendrorum* and *L. crosbiensis*, although her diagnosis does not take into account the intermediate morphologies present in some specimens. However, a full redescription and re-evaluation of the species is beyond the remit of this paper. We therefore use the diagnosis of Stocker (2010).

'*Phytosaurus*' *doughty* Case, 1920

Age: early Norian (*c.* 225–220 Mya)

Occurrences: Tecovas Formation, Dockum Group, Texas, USA

Holotype: AMNH FR. 4919, right posterior portion of skull

Previously Referred Specimens: Possibly MSM 92-023.001 (Stocker, 2010).

Specimen(s) Used for Scoring: AMNH FR. 4919

Key References: Case (1920); Stocker (2010)

Most Recent Diagnosis: Case (1920) was able to identify two characters to separate '*Phytosaurus*' *doughtyi* from other *Leptosuchus*-grade phytosaurs: 1) No evidence of the opisthotic process posterior to the quadrate; 2) The nares rise at their posterior rim.

Comments: Character 2 of Case (1920) is present in referred specimens of *Leptosuchus crosbiensis* (TMM 31173-120 and TTU-P 09230); despite this, Stocker (2010) tentatively suggested the referral of MSM 92-023.001 to '*Phytosaurus*' *doughtyi* based in part on the presence of a deep saddle between the orbits and external nares. It may therefore be the case that the differences in this character are more nuanced between *L. crosbiensis* and '*Phytosaurus*' *doughtyi*, rather than being simply present or absent. Character 1 of Case (1920) appears to be an autapomorphy of '*Phytosaurus*' *doughtyi*, and this is supported by our first-hand study of the holotype specimen.

Leptosuchus studeri Case & White, 1934

Age: early Norian (*c.* 225–220 Mya)

Occurrences: Tecovas Formation, Dockum Group, Cerita de la Cruz Creek, Potter County, Texas USA; ~~Lower Petrified Forest~~Blue Mesa Member, Chinle Formation, Arizona, USA

Holotype: UMMP 14267, skull

Previously Referred Specimens: None

Specimen(s) Used for Scoring: UMMP 14267

Key References: Case & White (1934); Stocker (2010)

Most Recent Diagnosis: Stocker (2010) used two characters to diagnose *L. studeri*: 1) Posterior edges of the posterior processes [of the squamosals] curl inwards in *L. studeri*, differing from the straight posterior processes of *L. crosbiensis*; 2) Small dorsally convex area on the dorsal surface of the mid-premaxillae.

Comments: At the time of writing the holotype and referred specimens of *L. studeri* were unavailable to study, so our observations are tentative and brief. It seems possible that character 1 of Stocker (2010) could be due to taphonomic distortion, although the morphology is present on both posterior processes, and to the same degree. Character 2 of Stocker (2010) is also present in *Leptosuchus crosbiensis*, appearing in a line-drawing of the holotype (Case, 1922), and is visible in multiple other specimens (TMM 31173-120, 43684, 43684-8; TTU-P 00902, 09230, 09234, 10001). The shape of the premaxillary crest does, however, appear to be different to that of *L. crosbiensis*. The crest of *L. crosbiensis* is anteroposteriorly symmetrical and forms a smooth 'hump', whereas in *L. studeri* the anterior portion of the crest slopes gently and the posterior slightly more steeply; the apex of the crest is therefore sharper. A partially prepared specimen at Petrified Forest National Park (field no. RLG 11/07-3) also displays this crest morphology, and the posterior process of the squamosal is also identical in lateral view to *L. studeri*.

Leptosuchus crosbiensis Case, 1922

Age: early Norian (*c.* 225–220 Mya)

Occurrences: Tecovas Formation, Dockum Group, Crosby County, Texas, USA

Holotype: UMMP 7522, skull

Previously Referred Specimens: USNM 15481 (Stocker, 2010); PPHM WT 3243; UCMP 27179; UCMP 27181; UCMP 26688 (Holotype of '*S. lithodendrorum*'); UCMP 126992; UCMP 126988; UCMP 126745; UCMP 27195; UCMP 27192; MSM 92-023.001; UMMP 14267 (Holotype of *L. studeri*); UMMP 14366; UMMP 12198; TTU-P '383'; TMM 1010-5; TMM 31173-120; TMM 31173-121 (Long & Murry, 1995).

Specimen(s) Used for Scoring: UMMP 7522; TMM 31173-120; USNM V 15841; TTU-P 09230

Key References: Case (1922); Long & Murry (1995); Stocker (2010)

Most Recent Diagnosis: Stocker (2010) listed diagnostic features of *L. crosbiensis* in comparison to other *Leptosuchus*-grade taxa: 1) An overall slenderness of the skull; 2) Supratemporal fenestrae that are completely visible in dorsal view; 3) Supratemporal fenestrae are bounded anterolaterally by mediolaterally narrow dorsal edges of the squamosals.

Modified Diagnosis: 1) An overall slenderness of the skull; 2) Supratemporal fenestrae that are completely visible in dorsal view; 3) Supratemporal fenestrae are bounded anterolaterally by mediolaterally narrow dorsal edges of the squamosals; 4) Dorsally rounded crest on the anterior portion of the premaxilla; 5) Partial rostral crest extends approximately level from the nares and descends at a point level with the anterior-most extent of the maxillae.

Comments: We suggest two additional characters (4 and 5 in the above modified diagnosis), to reinforce the diagnosis of *L. crosbiensis*. See '*Smilosuchus*' *lithodendrorum* for further discussion of this taxon.

Pravusuchus hortus Stocker, 2010

Age: Norian (*c.* 219–217 Mya)

Occurrences: White 'hoodoo' sandstone, ~~?Jasper Forest Bed/Rainbow Forest Bed~~Kellogg Butte Sandstone, Sonsela Member, Chinle Formation, Devil's Playground, Petrified Forest National Park, Arizona, USA; ?Monitor Butte Member, Chinle Formation, Fry Canyon, Utah, USA

Commented [WGP12]: Parker and Martz, 2011.

Holotype: AMNH FR. 30646, dorsoventrally crushed postnarial portion of skull and separate mediolaterally compressed right half of rostrum

Previously Referred Specimens: PEFO 31218; PEFO 34239 (Stocker, 2010); unnumbered specimen from Utah (McCormack & Parker, 2017).

Commented [WGP13]: This is a Utah Museum of Natural History Specimen. UMNH 28293.

Specimen(s) Used for Scoring: AMNH FR. 30646; PEFO 31218; PEFO 34239

Key References: Stocker (2010); McCormack & Parker (2017)

Most Recent Diagnosis: Stocker (2010) identified one autapomorphy for *Pravusuchus hortus* (the 'septomaxilla' forms part of the lateral rim of the external nares) and a unique character combination: 1) Absence of antorbital fossa; 2) broad and rounded interpremaxillary fossa; 3) Alveolar ridges visible in lateral view; 4) Fully crested rostrum; 5) Long posterior process of squamosal; 6) Posterior process of squamosal is greatly dorsoventrally expanded; 7) Possession of a subsidiary opisthotic process of the squamosal; 8) Supratemporal fenestrae partially depressed; 9) Supratemporal fenestrae that are mostly visible in dorsal view.

Comments: In relation to the 'septomaxillary' autapomorphy of *Pravusuchus hortus* Stocker (2010) stated that 'dorsal examination of the narial region shows a possible dorsolateral process of the 'septomaxilla' on the lateral border of the naris'. Upon first-hand examination of the holotype and other specimens we suggest that a lateral extension of the 'septomaxilla' is unlikely; rather, the suture identified by Stocker may represent the lateral border of the paranasal, as described by Hungerbühler *et al*. (2013). As noted in the holotype by Stocker (2010), 'iron oxide covers potential 'septomaxilla'-premaxilla sutures'; however, amongst the iron oxide a distinct groove extends from the anterior narial border, occupying the same position as the 'septomaxillary' suture in most phytosaurs. Therefore, we suggest that *Pravusuchus hortus* is diagnosed using only the unique character combination proposed by Stocker (2010), until the lateral extent of the 'septomaxillae' can be unambiguously verified in additional specimens.

Nicrosaurus kapffi (Meyer, 1860)

Age: middle–late Norian (*c.* 216–209 Mya)

Occurrences: Löwenstein Formation (middle Stubensandstein), Middle Keuper Subgroup, Baden-Württemburg, Germany

Holotype: SMNS 4060/4060a, poorly preserved rostral fragment and associated symphyseal-postsymphyseal mandibular fragment, and uncat. No. 15, left maxillary and jugal fragment that fits with 4060 (all lectotype); SMNS 54708, anterior fragment of left premaxilla (paralectotype)

Previously Referred Specimens: SMNS 4378; SMNS 4379; SMNS 5725; SMNS 5726, SMNS 5727; SMNS 13078; SMNS 54706; SMNS 56989; SMNS uncat. No. 12; SMNS 4380; SMNS 5730; SMNS uncat. No. 9; SMNS 54708; NHMUK 38036; NHMUK 38043; NHMUK 42743; NHMUK 42744; GPIT 2223.000; GPIT uncat. No. 399 (Hungerbühler, 1998).

Specimen(s) Used for Scoring: SMNS 4378; SMNS 4379; SMNS 5726; SMNS 5727; NHMUK 42743

Key References: Meyer (1860, 1861, 1863, 1865); Hungerbühler (1998); Hungerbühler & Hunt (2000)

Most Recent Diagnosis: Hungerbühler (1998) presented a unique character combination for *N. kapffi* based largely on characters from Long & Murry (1995) and Ballew (1989). The unique combination is composed of the following two characters: 1) Presence of a continuous prenarial crest reaching just behind the downturned tip of the snout; 2) Top of prenarial crest straight or slightly convex.

Nicrosaurus meyeri Hungerbühler & Hunt (2000)

Age: middle–late Norian (*c.* 216–209 Mya)

Occurrences: Löwenstein Formation (middle Stubensandstein), Middle Keuper Subgroup, Baden-Württemburg, Germany

Holotype: SMNS 12593, dorsoventrally compressed skull in two pieces

Previously Referred Specimens: SMNS 4059, 12593/2 & SMNS uncat. No. 11; NHMUK 38038 & 42745; GPIT 261/001 & GPIT 2070.001 (Hungerbühler & Hunt, 2000).

Specimen(s) Used for Scoring: SMNS 12593; SMNS 4059; NHMUK 38038; NHMUK 42745; GPIT 2070.001

Key References: Meyer (1861); Hunt (1994a); Hungerbühler (1998); Hungerbühler & Hunt (2000)

Most Recent Diagnosis: Hungerbühler & Hunt (2000) identified *N. meyeri* as a species of *Nicrosaurus*, differentiated from *N. kapffi* on the basis of the following characters: 1) Rostrum slender and gracile; 2) Prenarial crest absent or over posterior part of the snout only; 3) Septomaxilla terminates at the level of the anterior tip of the nasal; 4) Anterior part of the internasal septum may be prominent and visible in lateral view; 5) Sculpture of the pre-orbital region prominent; 6) Cheek region (quadratojugal + jugal) always with a well developed longitudinal depression; 7) Craniomandibular facet of the quadrate less wide and lateral condyle offset from the cheek; 8) Postorbito-squamosal bar broader; 9) Supratemporal fenestra less wide; 10) In dorsal view the posterior process of the squamosal is continuously broad, the medial rim is angular; 11) Posterior process of the squamosal terminates with a pointed tip; 12) Paroccipital process of the squamosal ('hooklike process') small; 13) Alveolar ridges more prominent, prechoanal part of the vomers mostly slender and tapering; 14) Upper jaw dentition moderately heterodont; 15) Premaxillary teeth set more laterally; 16) Mandibular symphysis equals ~50% of the total mandibular length (rather than 40% as in *Nicrosaurus kapffi*).

Coburgosuchus goeckeli Heller, 1954

Age: middle–late Norian (*c.* 216–209 Mya)

Occurrences: Upper Burgsandstein (lateral equivalent of the Löwenstein Formation), Untersiemau, Baden-Wurttemburg, Germany

Holotype: NMC 15436, postnarial portion of skull

Previously Referred Specimens: None

Specimen(s) Used for Scoring: NMC 15436

Key References: Heller (1954)

Most Recent Diagnosis: Heller (1954) originally described this specimen in German; however, since then this taxon has been largely ignored. Heller (1954) diagnosed the genus as a phytosaur of similar size to *Nicrosaurus kapffi*, though differentiated by an even greater development of the squamosals and more laterally oriented orbits.

Comments: As with many other diagnoses, we doubt the utility of orbital orientation as a reliable diagnostic character; however, the substantially more pronounced lateral curvature of the squamosals does appear to be valid and distinguishes *Coburgosuchus goeckeli* from *Nicrosaurus kapffi*. We are currently preparing a redescription of *Coburgosuchus*, and as such we do not present further diagnostic characters at this time.

'*Machaeroprosopus*' *zunii* Camp, 1930

Age: early Norian (*c.* 225–220 Mya)

Occurrences: ~~Mesa Redondo/~~Blue Mesa Member, Chinle Formation, Arizona, USA

Commented [WGP14]: Not in the Mesa Redondo Member. Lucas et al. 1997 erroneously considered the Placerias Quarry to be low down in the Chinle Formation.

Holotype: UCMP 27036, partial braincase and postcrania

Previously Referred Specimens: All specimens from UCMP localities 7307, 7308, 7309, 7310 & A 255; UCMP 27041, 27044, 27054, 27154, 27155, 27156, 27189, 27158, 27056, 27057, 27159, 27048 & 27189 (Camp, 1930).

Specimen(s) Used for Scoring: UCMP 27159

Key References: Camp (1930); Stocker (2010)

Most Recent Diagnosis: Camp (1930) produced a diagnosis of '*M*'. *zunii* based on various referred specimens. Due to the arbitrary referral of many of the specimens (see below) the characters presented may constitute a mosaic from multiple species: 1) Rostrum very long, slender; 2) Nasals large, extending forward beyond nares and entering dorsal border of antorbital fenestra; 3) Posterior squamosal process

very large, broad, flat, and expanded vertically; 4) Parietals small, anterior suture lies well behind posterior border of orbits; 5) Posterior parietal process Y-shaped; 6) Anterior border of supratemporal fenestra very wide and not excavated forward to or nearly to middle of parietals; 7) Postorbito-squamosal bar narrow.

Comments: Camp (1930) presented the holotype of '*M*'. *zunii* as a partial braincase and postcrania, thus containing little to no material of diagnostic utility. However, a number of specimens containing cranial material, such as UCMP 27048, 27189, 27159 were also referred to '*M*'. *zunii*, of which UCMP 27159 was also used in the matrix of Stocker (2010). As the type material is undiagnostic the rest of the referred specimens are referred on the basis of stratigraphic and geographic proximity to the type and should therefore be treated cautiously or altogether excluded. '*M*'. *zunii* is included here and scored based on only one of Camp's referred specimens. A specimen in the Smithsonian Institute (USNM V17098) is catalogued as '*M*'. *zunii* and appears to share a similar morphology to that of the specimens referred by Camp; we include this specimen as a separate OTU to test the credibility of its referral and this taxon in general, to judge whether it warrants more detailed investigation.

Protome batalaria Stocker, 2012

Age: early Norian (*c.* 220–218 Mya)

Occurrences: Upper Lot's Wife beds, Sonsela Member, Chinle Formation, Petrified Forest National Park, Arizona, USA

Holotype: PEFO 34034, pre-narial rostrum with narial fragments, post-narial skull roof with squamosals, basioccipital and left mandible.

Previously Referred Specimens: None

Specimen(s) Used for Scoring: PEFO 34034

Key References: Stocker (2012)

Most Recent Diagnosis: Stocker (2012) presented three autapomorphies and a unique character combination for *Protome batalaria*. Due to the length of the unique character combination we only present the autapomorphies here: 1) Presence of a flat ventral surface on the basitubera; 2) Posterior prongs from the exoccipitals dorsal to the foramen magnum; 3) Fossa surrounding the anterior corner of the external mandibular fenestra.

Comments: These autapomorphies all appear valid, although the posterior exoccipital prongs mentioned in character 2 may also be present in *Coburgosuchus*, but further study is required to verify this.

'*Machaeroprosopus*' *andersoni* Mehl, 1922

Age: late Norian (*c.* 218–208 Mya)

Occurrences: Bull Canyon Formation, Dockum Group, near Santa Rosa, Guadal~~o~~upe County, New Mexico, USA

Holotype: FMNH UC 396, heavily reconstructed skull

Previously Referred Specimens: None

Specimen(s) Used for Scoring: FMNH UC 396

Key References: Mehl (1922); Long & Murry (1995)

Most Recent Diagnosis: Mehl (1922) suggested that '*M*'. *andersoni* shares a close affinity with '*Machaeroprosopus validus*' and distinguished it using the following characters: 1) Postero-median border of supra-temporal fenestrae not completely depressed; 2) Anterior border of nares not elevated; 3) Terminal expansion of rostrum gradual; 4) Nasals extending some distance in front of anterior border of nares; 5) Greatest length of maxillae at alveolar margin; 6) Approximately ninety-four teeth in upper

dentition; 7) Four large teeth in terminal expansion of rostrum; 8) Alveolae not crowded; 9) Lateral expansion of rostrum at posterior end of premaxillae.

Comments: '*M*'. *andersoni* was synonymized with *Machaeroprosopus buceros* by Long & Murry (1995); however, upon inspection of their diagnosis of *Machaeroprosopus buceros* it is clear that many characters are inappropriate for, or are not preserved in the holotype (and only specimen) of '*M*'. *andersoni*. Two characters pertain to the squamosals, which are not preserved in '*M*'. *andersoni*, three characters are unnecessarily used to describe the same morphology of the pre-narial crest, and the majority of the remaining characters do not distinguish either taxon from many others, even when the characters are taken in combination.

Aside from the problem that the characters of Mehl (1922) may not differentiate '*M*'. *andersoni* from all current species of *Machaeroprosopus*, they are also based on comparison with '*Machaeroprosopus validus*' which has subsequently been lost and also found not to be the type species of *Machaeroprosopus.* This taxon requires reanalysis and thorough comparison to *Machaeroprosopus buceros* (the valid type species) and other members of *Machaeroprosopus*; however, this is beyond the scope of the current study.

Machaeroprosopus jablonskiae Parker & Irmis, 2006

Age: late Norian (*c.* 218–216 Mya)

Occurrences: ~~Basal~~ Jim Camp Wash beds, Sonsela Member, Chinle Formation, Petrified Forest National Park, Arizona, USA

Commented [WGP15]: Found to be in the upper part of the Jim Camp Wash beds. Parker and Martz, 2011.

Holotype: PEFO 31207, skull roof with squamosals

Previously Referred Specimens: None

Specimen(s) Used for Scoring: PEFO 31207

Key References: Parker & Irmis (2006)

Most Recent Diagnosis: Parker & Irmis (2006) noted a single autapomorphy of *Machaeroprosopus jablonskiae*: Distinct smooth bevelled edge on the antero-medial edge of the postorbito-squamosal bar that forms a supratemporal fossa lateral to the supratemporal fenestra. Alongside this they presented a unique character combination as follows: 1) Apomorphic characters for *Pseudopalatus* [*Machaeroprosopus*] clade; 2) Squamosal tips that are not knob-like as in *Machaeroprosopus buceros* + *Machaeroprosopus pristinus*; 3) Thin oar-like paroccipital process of the opisthotic that is fused to the internal squamosal process as in *Machaeroprosopus buceros* + *Machaeroprosopus mccauleyi*; 4) Anterior process of the squamosal enters the lateral wall of the braincase as in *Mystriosuchus westphali* and *S. gregorii*; 5) No lateral groove or ridge on the squamosal; 6) Squamosals are strongly anteroposteriorly shortened.

Commented [WGP16]: This may also be in Machaeroprosopus lottorum.

Machaeroprosopus mccauleyi (Ballew, 1989)

Commented [WGP17]: Should actually be mccauleiorum

Age: late Norian–early Rhaetian (*c.* 213–207 Mya)

Occurrences: ~~Upper Petrified Forest~~Martha's Butte beds, Sonsela Member, Chinle Formation, ~~Billings Gap~~Petrified Forest National Park, Apache County, Arizona, USA

Holotype: UCMP 126999, skull missing anterior rostrum, mandibles present

Previously Referred Specimens: USNM 15839 (Ballew, 1989); PEFO 31219 (Stocker, 2010); NMMNHS-P 4239, 4256; YPM 3293 (Hunt *et al*., 2006).

Specimen(s) Used for Scoring: UCMP 126999; PEFO 31219; PEFO unnumbered

Commented [WGP18]: Probably numbered now.

Key References: Ballew (1989); Hunt *et al*. (2006)

Most Recent Diagnosis: Ballew (1989) diagnosed *Machaeroprosopus mccauleyi* based on the following autapomorphies: 1) Squamosal with distinct triangular outline without knob-like process; 2) Lateral

753 portion of opisthotic thin and elongate; 3) Posttemporal fenestra large because of a medial expansion; 4)
754 Basioccipital head relatively large; 5) Basioccipital neck relatively short.
755 **Modified Diagnosis:** 1) Squamosal with distinct triangular outline without knob-like process; 2) rostrum
756 is completely crested in lateral view; 3) Ventral expansion of the alveolar rim at the border of the
757 premaxillae and maxillae 4) Pre-infratemporal shelf does not extend under the posterior corner of the
758 antorbital fenestra; 5) Anteroposterior corners of the antorbital fenestra rounded; 6) Anteromedial portion
759 of the supratemporal fenestrae remain visible in dorsal view.
760 **Comments:** Characters 2, 3, 4 and 5 of Ballew (1989) do not appear to be different to those in other
761 specimens of *Machaeroprosopus*. Character 1 does appear to be valid, but may be subject to intraspecific
762 variability; PEFO 31219 (referred by Stocker, 2010) does possess a short, robust terminal knob on the
763 posterior process of the squamosal, though in all other respects greatly resembles UCMP 126999 (the
764 holotype).
765 Hunt *et al*. (2006) referred three specimens from Bull Canyon, New Mexico to *Machaeroprosopus*
766 *mccauleyi* and cited three characters which link them to the holotype. The first character is the same as
767 character 1 of Ballew (1989), the others are: 2) In posterior view, the lateral margins of the skull flare at
768 about 60°; 3) In lateral view, the rostrum is completely crested (inferred from the gradient of the holotype
769 of *Machaeroprosopus mccauleyi* which lacks the distal rostrum). Character 2 of Hunt *et al*. (2006) is not
770 diagnostic, being present in all robust species of *Machaeroprosopus* and may be prone to taphonomic
771 distortion, and/or ontogenetic changes. Character 3 is useful as no other current species of
772 *Machaeroprosopus* share this character. Neither character 1 of Ballew (1989), nor character 3 of Hunt *et*
773 *al.* (2006) allow distinction of *Machaeroprosopus mccauleyi* from '*Redondasaurus*' *bermani*; therefore,
774 we suggest four further characters (our characters 3–6) to allow this differentiation.
775

Commented [WGP19]: Do you agree with this assignment?

Machaeroprosopus buceros (Cope, 1881)

Age: late Norian–early Rhaetian (*c.* 213–207 Mya)

Occurrences: Petrified Forest Member, Chinle Formation, Orphan Mesa, New Mexico, USA; ~~Upper~~ Petrified Forest Member, Chinle Formation, Canjilon Quarry, New Mexico, USA; ~~Upper~~ Petrified Forest Member, Chinle Formation, Snyder Quarry, New Mexico, USA

Holotype: AMNH FR. 2318, poorly preserved skull missing anterior end of rostrum

Previously Referred Specimens: UCMP 27228, 34246 & 34258; MNA V3478, CMNH 69727 (holotype of '*Redondasaurus*' *bermani*) (Ballew, 1989); UCMP 27149 & 34250; UW 3807; MNA ~~Pl.~~V-25; NMMNHS-P 18191, 31292, 33662, 33667, 33846, 33849, 33935, 35366, 35444, 35982, 36000, 36051, 36829, 37283, 37894 & 39700; FMNH UC 396 (holotype of '*Machaeroprosopus*' *andersoni*); YPM 3293; TTU-P 09234 (Long & Murry, 1995); UCMP 27231, 27234, 34245 & 34249; GR 147 (Zeigler *et al.*, 2003a).

Specimen(s) Used for Scoring: AMNH FR. 2318; TTU-P 11423; UCMP 34250; NMMNHS-P 39700

Key References: Cope (1881); Ballew (1989); Long & Murry (1995); Lucas *et al.* (2002); Zeigler *et al.* (2003a, b)

Most Recent Diagnosis: Long & Murry (1995) diagnosed *Machaeroprosopus buceros* as a 'heavy-skulled' 'pseudopalatine' with the following combination of characters: 1) Squamosal with posterior process elongated, but deeper and shorter than that of *Pseudopalatus* [*Machaeroprosopus pristinus*], tapering into a blunt apex; 2) Descending process of squamosal large; 3) Rostrum partially crested; 4) Length shorter than posterior portion of skull; 5) Snout does not descend abruptly immediately anterior to external nares; 6) The latter are raised above the level of the skull roof as in *Pseudopalatus* [*Machaeroprosopus pristinus*]; 7) Crest sharp-edged with no sculpturing; 8) Dentition heterodont; 9)

798 Alveoli closely spaced; 10) Enlarged anteriormost teeth and with dagger-like teeth at mid-length of
799 premaxilla; 11) Crest deepest posteriorly.
800 **Modified Diagnosis:** In this study, we diagnose *Machaeroprosopus buceros* on the basis of the following
801 unique character combination: 1) Posterior process of the squamosal is elongate and knob-like; 2) Tubular
802 anterior portion of the rostrum has a triangular, rather than semi-circular, cross-section (amended from
803 Ballew [1989] character 56); 3) Rostrum partially crested; 4) Snout does not descend abruptly
804 immediately anterior to external nares.
805 **Comments:** Characters 1, 2, 4, 6, 8 and 9 of Long & Murry (1995) present problems; characters 1 and 2
806 describe morphologies that vary between specimens of *Machaeroprosopus buceros* (AMNH FR. 2318,
807 TTU-P 11423, UCMP 34250). The morphologies described by characters 4 and 6 disagree with the first-
808 hand observations made in this study; with the rostrum measured from the most anterior point of the snout
809 to the anterior border of the nares, no specimens observed here possessed a rostrum shorter in length than
810 the narial + postnarial region of the skull - including even the holotype in which the most anterior section
811 of the snout is lost. As in other species of *Machaeroprosopus* such as *Machaeroprosopus pristinus* and
812 *Machaeroprosopus mccauleyi*, we found no evidence for the nares exceeding the height of the skull roof.
813 Characters 8 and 9 describe features that are common to some extent in many, if not most,
814 leptosuchomorph phytosaurs, and within *Machaeroprosopus* they are shared with *Machaeroprosopus*
815 *mccauleyi*.
816 In their revision of North American phytosaurs, Long & Murry (1995) erected the new genus
817 '*Arribasuchus*', referring to it both *Machaeroprosopus buceros* and *Machaeroprosopus mccauleyi*. In a
818 similar manner to their diagnosis of *Smilosuchus* the diagnostic character combination for the genus
819 '*Arribasuchus*' is the same as that for the type species, in this case *Machaeroprosopus buceros*.
820 *Machaeroprosopus mccauleyi* was tentatively retained in '*Arribasuchus*' by Long & Murry (1995),

despite characters such as ‘rostrum partially crested’ being directly inconsistent with the species diagnosis of *Machaeroprosopus mccauleyi* given by Ballew (1989) (also used by Long & Murry to diagnose *Machaeroprosopus mccauleyi*).

Subsequent analyses have suggested that ‘*Arribasuchus*’ is paraphyletic (Hungerbühler, 2002; Hungerbühler *et al*., 2013; Parker & Irmis, 2006), and should be considered a junior synonym of *Machaeroprosopus* (Hungerbühler *et al*., 2013).

Macheroprosopus pristinus (Mehl, 1928)

Age: late Norian–early Rhaetian (*c.* 213–207 Mya)

Occurrences: Chinle Formation, Petrified Forest National Park, Apache County, Arizona, USA; ~~Upper~~ Petrified Forest Member, Chinle Formation, Canjilon Quarry, New Mexico, USA; ~~Upper~~ Petrified Forest Member, Chinle Formation, Snyder Quarry, New Mexico, USA

Holotype: MU 525, skull with many areas of plaster restoration

Previously Referred Specimens: UCMP 27018, 27235, 34245, 34249, 34251, 119436 & 131331; AMNH FR. 7222; MNA V3495 (Ballew, 1989); NMMNHS-P 31292; AMNH/GR 1027; UCM 55163; PEFO 4852; UCMP 27159 (referred to ‘*M*’. *zunii* by Camp [1930] and used for scoring ‘*M*’. *zunii* by Stocker [2010]; however, in the latter study this specimen is also referred to *Machaeroprosopus pristinus*, being mistakenly presented as the holotype of ‘*Machaeroprosopus tenuis*’. The correct specimen would be UCMP 27018), UCMP 27231, UCMP 27234; YPM 3294 (holotype of ‘*Redondasaurus*’ *gregorii*) (Long & Murry, 1995).

Specimen(s) Used for Scoring: MU 525; AMNH FR. 7222; NMMNHS-P 50040; PEFO 382; UCMP 137319; UCMP 27018 (‘*Machaeroprosopus tenuis*’ holotype)

Key References: Mehl (1928); Long & Murry (1995); Zeigler *et al.* (2002, 2003a, b)

Most Recent Diagnosis: Stocker (2010) used the following characters to diagnose *Machaeroprosopus pristinus*: 1) Supratemporal fenestrae nearly completely closed in dorsal view by medially expanded postorbital-squamosal bars, and the fenestrae are completely depressed below the level of the skull roof; 2) Squamosal process of the parietals immediately posterior to the main body of the parietals drop ventrally before continuing on to articulate with the parietal processes of the squamosals; 3) The posterior processes of the squamosals are expanded posteriorly as in *Leptosuchus*; however, there is no dorsoventral expansion of this posterior process, which is usually described as 'knob-like' in this taxon.

Modified Diagnosis: We use a combination of characters from Stocker (2010), one modified from Ballew (1989), and other novel characters: 1) Proportionally long rostrum (ratio of pre-narial to narial + post-narial length [measured to the posterior extremity of the parietals] greater than or equal to 2.2); 2) Subtriangular antorbital fenestra; anterior corner is pointed/acutely rounded and posterior border is taller and straight/gently rounded; 3) Rostrum descends immediately anterior to external nares and remains low and tubular for the majority of its length; 4) Tubular portion of rostrum is semi-circular in cross-section; 5) Weak heterodonty.

Comments: In her phylogenetic analysis, Stocker (2010) did not score *Machaeroprosopus pristinus* using the holotype, and instead used UCMP 27159 and NMMNHS-P 31292. UCMP 27159 is a referred specimen of '*M*'. *zunii* (Camp, 1930) and was used as a referred specimen to phylogenetically score '*M*'. *zunii* in Stocker's analysis; however, Stocker reported the same specimen number as the holotype of *Machaeroprosopus tenuis*, which was referred to, and used to score *Machaeroprosopus pristinus*. We assume this was a typographical error, and that Stocker actually scored and referred UCMP 27018 (actual holotype of '*Machaeroprosopus tenuis'*) to *Machaeroprosopus pristinus*, as UCMP 27159 is clearly different from *Machaeroprosopus pristinus* and UCMP 27018, based both on morphology and preservation. The choice to refer, and use NMMNHS-P 31292 for scoring is puzzling; the skull displays a

partial rostral crest which rises above the level of the nares and abruptly descends approximately at the midpoint of the external nares. No other referred specimen of *Machaeroprosopus pristinus* has a rostral crest, and the crest morphology is unknown in any other species of phytosaur. The specimen has previously been referred to *Machaeroprosopus buceros* (Zeigler *et al*., 2002), to which *Machaeroprosopus pristinus* was also referred as a junior synonym and may explain the use of NMMNHS-P 31292 to define *Machaeroprosopus pristinus* by Stocker. However, Stocker clearly stated that her analysis would not investigate the synonymy of these species, and in accordance used the proposed junior synonym '*Machaeroprosopus pristinus*' in her analysis, demonstrating that no synonymy was assumed. Furthermore, Zeigler *et al*. (2002) attributed the unusual crest of NMMNHS-P 31292 to post-mortem deformation; however, upon close study we believe the morphology to be genuine, which if true, casts uncertainty over the referral of this specimen to any currently known species.

The diagnosis of Stocker (2010) does not allow differentiation of *Machaeroprosopus pristinus* and *Machaeroprosopus buceros*; in our revised diagnosis we therefore highlight that *Machaeroprosopus pristinus* possesses only weak heterodonty, whereas *Machaeroprosopus buceros* is strongly heterodont.

Commented [WGP20]: Hungerbuhler et al 2013 agreed with Zeigler's assessment that they are sexual dimorphs; however, this is difficult to support.

Machaeroprosopus lottorum Hungerbühler *et al*., 2013

Age: late Norian (*c*. 218–208 Mya)

Occurrences: Upper Cooper Canyon Formation, Dockum Group, Texas, USA

Holotype: TTU-P 10076, skull

Previously Referred Specimens: TTU-P 10077 (Hungerbühler *et al*., 2013).

Specimen(s) Used for Scoring: TTU-P 10076; TTU-P 10077

Key References: Hungerbühler *et al*. (2013)

Most Recent Diagnosis: Hungerbühler *et al*. (2013) diagnosed *Machaeroprosopus lottorum* with the following characters: 1) Lateral rim of the naris broad, flat and rugose; 2) Supratemporal fenestra fully closed in dorsal aspect, forming a shallow semi-circular indentation into the skull roof, with a strongly bevelled rim that continues onto the parietal; 3) Free section of the postorbital/squamosal bar short; 4) Strongly developed horizontal medial laminae of palatines, that almost close the posterior section of the palatal vault in ventral view.

Modified Diagnosis: 1) Lateral rim of the naris broad, flat and rugose; 2) Supratemporal fenestra fully closed in dorsal aspect, forming a shallow semi-circular indentation into the skull roof, with a strongly bevelled rim that continues onto the parietal; 3) Strongly developed horizontal medial laminae of palatines, that almost close the posterior section of the palatal vault in ventral view.

Comments: We generally agree with the characters proposed by Hungerbühler *et al*. (2013), with the exception of their character 3. In TTU-P 10076 character 3 holds true i.e. the free section of postorbital/squamosal bar is proportionately shorter than in almost all other phytosaur specimens studied. However, in TTU-P 10077 the length of the free section of postorbital/squamosal bar is greater than in some specimens of *Machaeroprosopus pristinus* (UCMP 34249, 27231, 34228) including the holotype (MU 525), but shorter than other referred specimens (NMMNHS P-50040; PEFO 382; AMNH FR 7222); this character is also shorter in the majority of specimens of *Mystriosuchus planirostris*. This suggests the feature may be more variable than previously realized in *Machaeroprosopus lottorum* and is therefore removed from the diagnosis.

'*Redondasaurus*' *gregorii* Hunt & Lucas, 1993

Age: Rhaetian (*c.* 208.5–201.3 Mya)

Occurrences: Redonda Formation, Dockum Group, Shark Tooth Hill, Quay County, New Mexico, USA

Holotype: YPM 3294, poorly preserved and compressed skull missing left quadrate area, dorsal narial area and tip of rostrum

Previously Referred Specimens: OMNH 1250 (Hunt & Lucas, 1993).

Specimen(s) Used for Scoring: YPM 3294

Key References: Gregory (1972); Hunt & Lucas (1993); Hungerbühler *et al*. (2013)

Most Recent Diagnosis: Spielmann & Lucas (2012) built on the original diagnosis of Hunt & Lucas (1993) and diagnosed *Redondasaurus gregorii* using the following character combination: 1) Supratemporal fenestrae concealed in dorsal view; 2) Reduced antorbital fenestrae; 3) A prominent pre-infratemporal shelf at the anteroventral margin of the lateral temporal fenestra; 4) Septomaxillae that wrap around the outer margin of the external narial opening; 5) A thickened orbital margin; 6) An inflated posterior nasal behind the external narial opening; 7) Thickened dorsal osteoderms.

Modified Diagnosis: We retain most of the characters proposed by Spielmann & Lucas (2012) but reword them for more precise interpretation: 1) Supratemporal fenestrae concealed in dorsal view; 2) Antorbital fenestra with a distinct sharp corner at the anterior-most and posterior-most extremities; 3) Pre-infratemporal shelf projects anteriorly as a lobe reaching beneath the posterior corner of the antorbital fenestra, and dorsally joins with a ventrally descending flange of the postorbital; 4) Posterior border of the orbit equal to- or thicker than the dorsoventrally thinnest part of the posterior process of the jugal; 5) An inflated posterior nasal behind the external narial opening; 6) Postorbital/squamosal bars wide; 7) Thickened dorsal osteoderms.

Comments: We find issues with characters 2 and 4 of the diagnosis of Spielmann & Lucas (2012). The reduction of the antorbital fenestra in '*Redondasaurus*' appears to be subjective based on the relative size of the antorbital fenestra when compared to the robusticity and size of the skull. In large specimens such as NMMNHS P-4256 and NMMNH P-31094 that have previously been referred to '*Redondasaurus*', the

antorbital fenestra appears small; however, in the holotype of '*Redondasaurus*' *gregorii* (YPM 3294) the antorbital fenestra appears of similar proportions relative to the skull as in other phytosaurs such as *Mystriosuchus planirostris* or *Machaeroprosopus pristinus*. We suggest instead that the shape of the antorbital fenestra is unique in '*Redondasaurus*' as both its anterior and posterior apices are sharp, rather than rounded; the antorbital fenestra only appears to be relatively small in specimens of '*Redondasaurus*' *bermani* and is therefore used as a character for that species only. Although this is a generic feature of '*Redondasaurus*' it is retained in this species diagnosis in case '*Redondasaurus*' is synonymized with *Machaeroprosopus.* In such a scenario this character would be useful as part of a character combination to differentiate the species from almost all other members of the genus. We find no evidence for 'septomaxillae' that wrap around to the lateral side of the nares; Stocker (2010) found this feature to be present in both '*Redondasaurus*' and *Pravusuchus hortus*; however, in the holotype of the latter this area is covered with iron oxide and may actually be the paranasal suture, which was identified in *Machaeroprosopus lottorum* by Hungerbühler *et al.* (2013). Given the phylogenetic proximity of *Machaeroprosopus lottorum* and '*Redondasaurus*' it is likely that the feature described in '*Redondasaurus*' may also be the paranasal; as the feature is currently ambiguous it is excluded from the diagnosis given here.

'*Redondasaurus*' *bermani* Hunt & Lucas, 1993

Age: Rhaetian (*c.* 208.5–201.3 Mya)

Occurrences: 'siltstone member', Chinle Formation, ~~*Bull Canyon, Quay*~~*Coelophysis* Quarry ~~County~~, New Mexico, USA

Holotype: CMNH 69727, skull

Commented [WGP21]: Holotype is from the Coelophysis Quarry at Ghost Ranch New Mexico.

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Previously Referred Specimens: Hungerbühler (2002) used a silhouette of NMMNHS-P 4256 in their phylogeny to denote '*Redondasaurus*' *bermani*, but referred to as 'NMMNHS-P 5246'. This appears to be a typographical mistake. NMMNHS-P 4256 is included as a separate OTU to '*Redondasaurus*' in this study so its affinities can be tested.

Specimen(s) Used for Scoring: NMMNHS-P 4983

Key References: Hunt & Lucas (1993); Hunt *et al.* (2006); Hungerbühler (2002); Hungerbühler *et al.* (2013)

Most Recent Diagnosis: Hunt & Lucas (1993) diagnosed '*Redondasaurus*' *bermani* as a '*Redondasaurus* species that differs from others in possessing a rostrum with a partial crest'.

Modified Diagnosis: A species of '*Redondasaurus*' with the following characters: 1) Full rostral crest extending from nares to the terminal rosette of the premaxilla; 2) Antorbital fenestra reduced in size relative to other taxa of similar size and robuusticity; 3) Length of the symphyseal portion of the mandible approximately half that of the post-symphyseal region.

Comments: '*Redondasaurus*' *bermani* was synonymized with *Machaeroprosopus buceros* by Long & Murry (1995) as mentioned above, and was also synonymized with '*Redondasaurus*' *gregorii* by Spielmann & Lucas (2012) who concluded that it was the male sexual dimorph. Due to the lack of evidence for synonymy we tentatively retain '*Redondasaurus*' *bermani* as a distinct species, but a thorough re-description of the species would be of great benefit.

Mystriosuchus westphali (Hungerbühler & Hunt 2000)

Age: middle–late Norian (*c.* 216–209 Mya)

Occurrences: Löwenstein Formation (middle Stubensandstein), Middle Keuper Subgroup, Baden-Württemburg, Germany

Holotype: GPIT 261/001, skull with left side slightly distorted

Previously Referred Specimens: GPIT 261/17/7 (Hungerbühler & Hunt, 2000); GPIT 2145.000, 2146.000 & 2156.000 (provisionally included) (Hungerbühler, 2002).

Specimen(s) Used for Scoring: GPIT 261/001; AMNH 10644

Key References: Huene (1909; 1911); Hungerbühler (1998; 2002); Hungerbühler & Hunt (2000)

Most Recent Diagnosis: Hungerbühler (2002) listed eight autapomorphies for *Mystriosuchus westphali* as follows: 1) Discrete snout crest at midlength of the premaxillae; 2) Semicylindrical alveolar ridges; 3) Posterior process of the squamosal absent; 4) Squamosal contacts the prootic anteriorly; 5) Supraoccipital reaches the post-temporal fenestra and borders its dorsomedial half; 6) Lobate extension of the vertically descending squamosal process of the parietal; 7) Post-temporal fenestra is reduced to a narrow slit; 8) Presence of a discrete ossification (orbitosphenoid) anterior to the laterosphenoid.

Modified Diagnosis: 1) Discrete snout crest at midlength of the premaxillae; 2) Squamosal contacts the prootic anteriorly; 3) Supraoccipital reaches the post-temporal fenestra and borders its dorsomedial half; 4) Post-temporal fenestra is reduced to a narrow slit; 5) Presence of a discrete ossification (orbitosphenoid) anterior to the laterosphenoid; 6) A sharp corner of bone extends into the antorbital fenestra at approximately the midpoint of the posterior border, giving the posterior border a ‘stepped’ appearance.

Comments: Based on subsequent analyses and first-hand examination of specimens, we exclude characters 2, 3 and 6 of Hungerbühler (2002) from this diagnosis. Character 2 is present in almost all phytosaurs; characters 3 and 6 are both observed in the holotype of *Mystriosuchus westphali*. However, a specimen found in the collections of the AMNH (AMNH 10644), which is referable to *Mystriosuchus westphali* (as a species of *Mystriosuchus* that possesses a distinct sharp crest at the midlength of the premaxilla and lacks the abrupt concave rise of the rostrum into a narial crest), differs in displaying

neither of these states. In AMNH 10644 the posterior process of the squamosal shares the same morphology as *Mystriosuchus planirostris* and the 'lobate extensions' on the squamosal process of the parietal are absent. Furthermore, these lobate extensions have been found in an indeterminate specimen of *Machaeroprosopus* (either *Machaeroprosopus pristinus*, *Machaeroprosopus buceros* or *Machaeroprosopus lottorum*) by Hungerbühler *et al*. (2013), but not in any others, suggesting this state is likely intraspecifically variable in multiple taxa. A further character, relating to the antorbital fenestra, is added which is found in both the holotype and AMNH 10644 but in no specimens of *Mystriosuchus planirostris*.

Mystriosuchus planirostris (Meyer, 1863)

Age: middle–late Norian (*c.* 216–209 Mya)

Occurrences: Löwenstein Formation (middle Stubensandstein), Middle Keuper Subgroup, Baden-Württemburg, Germany; Zorzino Limestone, Lombardy, Italy

Holotype: MCZ 1018, fragment of right pre-orbital (lectotype); MCZ 1019A, 1019B, 1019C; MCZ 1022A, 1022B, rostral and skull fragments, partial caudal centrum (paralectotypes)

Previously Referred Specimens: SMNS 9134 (Fraas, 1896); SMNS 10260 (McGregor, 1906); SMNS 11126(1) (Huene, 1911); GPIT 249/002 (Huene, 1909); AMNH 10644 (Witmer, 1997); SMF uncat (Drevermann, 1918); MBSN 2 (Pinna, 1987); NHMW 1986 0024 0001 (Buffetaut, 1993); SMNS 13007, 13240, uncat 180, uncat 183, uncat 184 (possibly SMNS 9900); SMNS uncat 397, uncat 205;, 2074.000, 2149.002, 2149.003, 2150.000; MB.I.008.05 (Hungerbühler, 1998).

Specimen(s) Used for Scoring: SMNS 10260; SMNS 9900; SMNS 9134; SMNS 13240; SMNS 91574

Key References: Meyer (1863); Fraas (1896); Hungerbühler (1998; 2002); Hungerbühler & Hunt (2000)

Most Recent Diagnosis: Hungerbühler (2002) listed six autapomorphic characters to distinguish *Mystriosuchus westphali* from *Mystriosuchus planirostris*: 1) The rostrum is extremely elongated; 2) A subvertical slope results in a concave profile of the prenarial area from side to side; 3) The external nasal opening is subdivided into a posterior section facing dorsally, and a strongly inclined anterior section that opens anteriorly; 4) The raised anterior border of the supratemporal fenestra extends along the medial rim of the squamosal; 5) The parieto-squamosal bar is depressed by more than 30 per cent of the skull height; 6) A larger quadrate foramen is present in a round recess formed by quadratojugal and quadrate.

Comments: Hungerbühler (2002) provided a detailed and useful discussion of characters previously used to diagnose *Mystriosuchus planirostris*, giving reasons why they should now be excluded.

Specimen-level OTUs

NMMNHS-P 4781

Age: early Norian (*c.* 225–218 Mya)

Occurrence: Los Esteros Member, Santa Rosa Formation, Santa Fe County, New Mexico, USA

Notes: This specimen consists of the right orbital plus postorbital region of a skull, though lacking any of the interior or posterior elements such as the braincase, occipitals or palatines. Hunt *et al.* (1993) assigned this specimen to *Angistorhinus* sp. based on a combination of features: 1) Supratemporal fenestrae at the level of the skull roof; 2) Squamosals project posteriorly; 3) Squamosal process (parietal/squamosal bar) is rounded.

TMM 31100-1332

Age: late Carnian–early Norian (*c.* 232–225 Mya)

Occurrence: 'Otis Chalk Quarry 3', Colorado City Formation, Dockum Group, Howard County, Texas, USA

Notes: Stocker (2013) mentioned this specimen in reference to '*Angistorhinus*-like specimens from the Otis Chalk localities'. The specimen consists of a complete cranium, infilled with sediment, though lacking an associated mandible. Although the surface preservation is relatively good, there are many cracks through the skull, which cause slight displacements in areas such as the rostrum. The temporal region of the skull is slightly compressed dorsoventrally, causing the squamosal posterior processes and parietal/squamosal bars to curve posteroventrally.

USNM v 21376

Age: late Carnian–early Norian (*c.* 232–225 Mya)

Occurrence: Base of the Dockum Group, three miles North of Otis Chalk, Howard County, Texas, USA

Notes: This specimen was figured in lateral view by Stocker & Butler (2013) (Figure 5d), as an example of the genus *Angistorhinus*. The preorbital portion of the specimen is preserved, as is an area of skull roof including the prefrontals, frontals and the anterior parts of the postfrontals and parietals. The posterior processes of the squamosals are also preserved, as is the occipital condyle and ventral parts of the quadrates; however almost all of the postorbitals, jugals, quadratojugals and anterior and ventral parts of the squamosals are modelled with plaster. Due to the plaster reconstruction, the orientation of the supratemporal fenestrae is incorrect; the proximal remnants of the parietal/squamosal bars preserved on the squamosals have been aligned with the reconstructed postorbital/squamosal bars, whilst the parietal/squamosal bars are reconstructed entirely from plaster mimicking the depressed temporal morphology of *Mystriosuchus* or *Machaeroprosopus*. The specimen also preserves the symphysial region of the mandible, the anterior portions of the two rami including approximately the anterior third of the

mandibular fenestra, and part of the left articular and retroarticular process. The nares appear to be elevated well above the level of the skull roof, although their posterior extremity appears to be damaged and the skull roof may be slightly crushed. The specimen may also be slightly mediolaterally compressed.

PEFO 34852

Age: early Norian (*c.* 225–220 Mya)

Occurrence: Blue Mesa Member, Chinle Formation, Petrified Forest National Park, Arizona, USA

Notes: This specimen consists of a complete cranium which has been crushed laterally at an oblique angle such that the external elements of the left half of the skull retain their original morphology, whereas the right half is strongly dorsoventrally compressed.

Griffin *et al*. (2017) referred this specimen to *Smilosuchus adamanensis* based on the following characters from the matrix of Kammerer *et al*. (2015): 1) An antorbital fossa is absent (3-3); 2) A rostral crest is present but not continuous (18-1); 3) The interorbital-nasal area is concave (21-1); 4) There is a moderate posterior process of the squamosal (24-1); 5) The posterior process of the squamosal is expanded in lateral view, but not rounded (25-1); 6) The squamosal fossa extends to the posterior edge of the squamosal (30-0); 7) The supratemporal fenestrae are partially depressed (32-1); 8) The supratemporal fenestrae are mostly visible in dorsal view (33-1).

However, upon first-hand comparison of these character scorings with the holotype of *S. adamanensis* and specimens of other non-mystriosuchin leptosuchomorph taxa, we find that all the above character scorings, aside from number 5, may equally refer to *Leptosuchus crosbiensis.* Furthermore, we find that the score for character 2 does not reflect the rostral morphology of either the holotype of *S. adamanensis* or our referred specimen UCMP 170166; in both specimens there is no evidence of any rostral crest, i.e. the rostrum forms an unbroken, straight slope from the posterior border of the nares to the

premaxillae, whereupon the rostrum becomes tubular. However, in PEFO 34852, previously referred specimens of *L. crosbiensis* (USNM 15481, TMM 31173-120, TTU-P 09230), the holotype of *L. crosbiensis* (subtly) and the holotype of *Leptosuchus studeri* (the sister taxon to *L. crosbiensis* in the analysis of Stocker (2010)), the narial openings extend horizontally from their posterior border, and directly anterior to the nares the rostrum either continues horizontally or slopes slightly ventrally, before dipping more strongly ventrally and levelling out to form a tubular rostrum. Therefore, from the characters presented it is unclear whether this specimen actually represents *S. adamanensis*; for this reason we include the specimen here as a separate OTU so its affinities can be tested phylogenetically.

NMMNHS-P 4256

Age: late Norian (*c.* 218–208 Mya)

Occurrence: lower Bull Canyon Formation, ~~Chinle~~ Dockum Group, Barranca Badlands, Quay County, New Mexico, USA

Notes: This specimen consists of a large skull, missing the majority of its right postnarial region, the entire palate and the posterior section of the right mandibular ramus. Similarly to PEFO 34852, the skull has been compressed at an oblique dorsolateral angle leaving the left half relatively free from deformation, whilst the right half is strongly compressed and sheared dorsally.

According to Heckert *et al.* (2001) this specimen was originally referenced in the PhD thesis of Hunt (1994b) as a 'robust morph' of '*Redondasaurus*' *gregorii*. Subsequently it was used in the phylogeny of Hungerbühler (2002) to exemplify '*Redondasaurus*' *bermani*, rather than the unnumbered Carnegie Museum specimen assigned as the holotype of '*Redondasaurus*' *bermani* by Hunt & Lucas (1993). Hunt *et al.* (2006) then referred this specimen to *Machaeroprosopus mccauleyi*, as a male sexual dimorph of the species due to the difference in skull size and rostral robusticity between this specimen and

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the holotype of *Machaeroprosopus mccauleyi*. Their species referral was based on three characters: 1) Posterior squamosal process is sub-triangular and lacks a knob-like termination; 2) In posterior view, the lateral margins of the skull flare at about 60 degrees; 3) In lateral view the rostrum is completely crested. All of these characters (regardless of their legitimacy or usefulness) can also be found in '*Redondasaurus*' *bermani*; however, Hunt *et al.* also based their identification on an assumption that two species of 'brachyrostral' phytosaurs were unlikely to have occurred simultaneously geographically and temporally. As detailed earlier, the genus '*Redondasaurus*' was redefined by Spielmann & Lucas (2012), and more diagnostic characters were added; again, disregarding the legitimacy of these characters, many of them are applicable to NMMNHS-P 4256, suggesting the need for the placement of this specimen to be tested more thoroughly.

USNM v 17098

Age: early Norian (*c.* 221–219 Mya)

Occurrence: ?Bluewater Creek Member, Chinle Formation, Apache County, Arizona, USA

Commented [WGP22]: Possibly. Hard to get into David Ranch these days, but it is pretty low in the Chinle.

Notes: USNM v 17098 is a poorly preserved partial skull and mandible that are dorsoventrally compressed. The skull lacks most of the left lateral postnarial elements, though preserves much of the right half, the palate and braincase. The mandible is largely complete, though aspects are fragmentary and lacks the anterior-most portion of the terminal rosette.

This specimen was referred to *Leptosuchus* sp. by Long & Murry (1995) and again by Heckert & Lucas (2003); however, the label with the specimen identifies it as *Machaeroprosopus zunii*, though no justification has been provided for any of these three identifications. By scoring this specimen phylogenetically it may be possible to more definitively constrain its position.

NMMNHS-P 31094

Age: Rhaetian (*c.* 208.5–201.3 Mya)

Occurrence: Redonda Formation, Dockum Group, Apache Canyon, Quay County, New Mexico, USA

Notes: This specimen consists of an extremely robust cranium, missing the majority of the premaxillae and the anterior extremities of the maxillae. The skull is slightly dorsoventrally crushed and slightly sheared. Heckert *et al.* (2001) provided a short description of the skull, referring the specimen to '*Redondasaurus*' sp. on the basis of comparisons with other taxa, which we summarize as four characters: 1) Supratemporal fenestrae that are depressed and concealed in dorsal view; 2) Antorbital fenestra 'tiny' relative to narial length; 3) Postorbital/squamosal bars are anteroposteriorly short; 4) Postorbital/squamosal bars are broad.

MB.R. 2747

Age: Rhaetian (*c.* 208.5–201.3 Mya)

Occurrence: lower Exter Formation, near Salzgitter, Lower Saxony, Germany

Notes: MB.R. 2747 represents the largest phytosaur specimen found in Europe, and consists of a strongly deformed skull preserved in 11 articulating and non-articulating fragments, a partial mandible preserved in four articulating fragments, multiple vertebrae and centra, partial scapulae and coracoids, a humerus, and a set of articulated osteoderms. The skull retains the majority of the rostrum up to the anterior corner of the antorbital fenestrae, the posterior process of the right maxilla and the main bodies of the left and right jugals with the anterior corners of the lateral temporal fenestrae, a postnarial portion of the skull roof including a section of the posterior narial border and a dorsal part of the right orbital rim, a relatively complete, but crushed, braincase with dorsal portions of the parietals preserved and a fragment of the left postorbital/squamosal bar. The mandible consists of a short posterior section of the symphysis, from

which the two rami bifurcate; the left ramus extends posteriorly such that part of the mandibular fenestra is preserved, whilst the right ramus does not extend as far as the beginning of the fenestra. The surface preservation of the material is generally good, but is extensively fractured making sutures difficult to discern.

This specimen was originally described by von Huene (1922) and was referred to the species '*Angistorhinopsis ruetimeyeri*'. This referral was based entirely on stratigraphic age and the size of the specimen, as the holotype of '*A. ruetimeyeri*' consists of a partial phytosaur basioccipital, mandibular and postcranial fragments from a bonebed in Switzerland - none of which are diagnostic. The taxon '*A. ruetimeyeri*' is therefore a nomen dubium; furthermore, MB.R. 2747 has never before been included in a phylogenetic analysis of phytosaurs. Its inclusion here will therefore provide a phylogenetic placement that may be useful in any future redescription of the specimen.

NHMW 1986 0024 0001

Age: middle–late Norian (*c.* 216–209 Mya)

Occurrence: Dachsteinkalk, Totes Gebirge, Styria, Austria

Notes: This specimen is an undescribed right half of a phytosaur skull from Austria, with a possibly associated partial mandible and ilium, that was referred to *Mystriosuchus planirostris* by Buffetaut (1993). Aside from the anterior tip of the snout and the quadratojugal, the half skull is relatively complete and well preserved with some sutures discernible; however, it may be somewhat mediolaterally compressed. The mandible is more poorly preserved; its dorsal surface is heavily weathered and the posterior half of the left ramus is missing, although the ventral surface is retained, allowing a more accurate estimate of skull length. Approximately the posterior quarter of the right ramus is missing. Similarly to MB.R. 2747,

this specimen has never before been analysed phylogenetically, and its inclusion may assist future descriptive work.

Appendix 2: Character list

It is important to note here that when incorporating continuous and geometric morphometric character scorings for analysis, the format of the TNT data file requires these characters to be presented first in the file. This differs from how the characters are ordered in the character list below. Our character list presents characters in the order in which they occur for the base discrete matrix; where a character possesses a continuous or GM variant this is flagged next to that character, as indicated below. It should also be noted that characters in a TNT file begin at zero, whereas we shift our characters such that the list begins at one.

*** Character possesses a corresponding continuous variant**

† Character possesses a corresponding/partially corresponding GM variant

1) Anterior end of premaxillae [from Stocker 2010, character 7]

0: In anteroposterior plane of posterior rostrum

1: downturned

Although the distal terminus of the rostrum is downturned in all phytosaurs, in some such as *Parasuchus* and some specimens of *Machaeroprosopus pristinus*, there is dorsoventral constriction of the rostrum just posterior to the terminal rosette subsequent to which the rostrum deepens again such that the ventral edge is approximately level with the downturned anterior tip.

2) Interpremaxillary fossa [Hungerbühler 2002, character 43; Stocker 2010, character 8]

0: Absent

1: Present, broad and rounded

2: Present, narrow slit

Only species of *Mystriosuchus* display a narrow, slit-like fossa between the alveolar ridges; all other phytosaurs possess a broadly rounded fossa.

3) Alveolar ridges [modified from Stocker 2010, character 9]

0: Continuously visible in lateral view

1: Inconsistently visible, or entirely hidden in lateral view

Modified such that the state differences reflect the development of any kind of ventral overhang of the ventral rostral margin, rather than separating only those taxa in which such a ventral overhang is complete from those that display either an intermediate state or no overhang.

4) Ventral alveolar bulge between premaxilla and maxilla [modified from Hungerbühler *et al.* 2013, character 2]

0: Absent

1: Present

Wording modified for clarity. This ventral bulge of the tooth-row is consistently visible in *Smilosuchus gregorii* and most robust members of *Machaeroprosopus*. In some other taxa such as *Smilosuchus lithodendrorum*, *Pravusuchus hortus* and '*Redondasaurus*' *gregorii* the bulge is not present in all specimens.

5) Alveolar rim of maxilla [modified from Hungerbühler 2002, character 3; Stocker 2010, character 10]

0: Horizontal or subconvex

1: Strongly ventrally convex

Wording altered slightly for clarity.

6) Premaxillary crest [modified from Hungerbühler 2002, character 48]

0: Absent

1: Present, rounded

2: Present, sharp

In the majority of phytosaurs an isolated premaxillary crest is absent, however *Mystriosuchus westphali* possesses a premaxillary crest with a sharp dorsal edge, giving the rostrum a more triangular coronal cross-section through the crest. *Leptosuchus studeri* and *crosbiensis* both also display an isolated premaxillary crest, however the dorsal edge is rounded, maintaining a curved dorsal profile in cross-section. This character is modified here to account for the different crest morphologies.

7) Rostral crest [modified from Stocker 2010, characters 17, 18, 19]

0: Absent

1: Narial crest a relatively abrupt rise to the nares interrupting a straight profile from rostrum to orbit

2: A straight steep slope from the nares to the premaxilla

3: Extends horizontally level from the nares for the majority of the crest with a terminal anterior slope

4: Extends horizontally level from nares for less than half the rostral length then descends and becomes tubular

This character was previously three separate characters, the first of which pertained to the morphology of the premaxilla, while the subsequent two scored the presence or absence of a 'rostral crest' and its morphology. Putting aside disputes over the cladistic usefulness of crest characters, these characters appear to overlap, risking artificial inflation of the influence of some traits. From the character state descriptions in the second and third characters, the 'rostral crest' appears to refer to the crest across both the premaxilla and maxilla. State zero of the first character (premaxilla dorsoventrally taller than mediolaterally wide) therefore directly overlaps with the second state of the next character (presence of a rostral crest). State one of the first character (tube-like morphology of the premaxilla) does not completely correlate with state zero of the next character (absence of rostral crest - rostrum tube-like for entire length) as morphologies exist (e.g., *Leptosuchus crosbiensis* and *Leptosuchus studeri*) where the premaxilla is slender, but rises into a crest posterior to its contact with the maxilla; this would be described by a combination of state one in the first character, and state zero in the second. This morphology is, however, given a distinct state of its own in the third character: state zero (rostral crest partial or undulating from nares to terminal rosette); this state correlates exactly with a combination of states of the previous two characters. Furthermore, the third character is only applicable to taxa with rostral crests; un-crested taxa must therefore be scored as inapplicable which is treated as uncertainties during character optimization, resulting in their morphologies being 'estimated' for a trait they do not possess. Here we present a multi-state combination of the previously used characters, in which states are mutually exclusive and that is applicable to all taxa. An example of character state one is the abrupt rise to the nares in *Mystriosuchus planirostris*; state two is exemplified by *Smilosuchus gregorii*; state three is autapomorphic for *Nicrosaurus kapffi* and state four applies to taxa such as *Leptosuchus crosbiensis* and *studeri*.

*** [ORDERED] 8) Transverse width of the rostrum between the antorbital fenestrae in dorsal view [modified from Butler *et al.* 2014, character 46]**

0: Less than or equal to 1.20

1: 1.21 to 1.59

2: Greater than or equal to 1.60

States are here modified to represent the greater range of morphologies measured in this study. Measured as the ratio of the width of the rostrum between the antorbital fenestrae at their midpoint, and the interorbital distance at its shortest point. State zero corresponds to a narrow width, state one to moderate, and state two to a large width.

9) Suture between maxilla, premaxilla and nasal [from Hungerbühler 2002, character 2]

0: Slopes anteroventrally

1: Dorsally convex lobe

10) Posterior portion of maxilla lateral outline in dorsal view [from Hungerbühler 2002, character 4]

0: Straight/subconcave

1: Convex

*** [ORDERED] 11) Ratio of rostral to narial plus post narial length [modified from Hungerbühler 2002, character 1; Stocker 2010, character 14]**

0: Less than or equal to 1.50

1: 1.51 to 1.99

2: Greater than or equal to 2.00

In previous analyses this character used the pre-orbital and orbital + post-orbital lengths; however, orbital + post-orbital length was measured to the posterior process of the squamosal - the morphology of which is highly variable,

and the subject of a number of other characters in their matrices. To avoid mixing the signal of this character with those of characters pertaining to the squamosal, we use the posterior extremity of the parietals as our posterior measuring point. The nares are used here rather than the orbits as phylogenetic signal is either unclear or lost when pre-orbital length is compared to the orbital + postorbital length to the posterior tip of the parietals. This suggests that much of the signal previously found in this character may be linked to variation in the squamosals, combined with rostral variation. The position of the nares does shift between phytosaurs belonging to, and excluded from Mystriosuchinae and thus presents a partial correlation with one other character pertaining to this change in position. However this is here judged to be a more favourable option than correlation with the squamosals, which are far more variable than the position of the nares, are the subject of more characters and have traditionally been used as one of the main diagnostic features for different groups of phytosaurs.

12) Narial openings [from Hungerbühler 2002, character 50]

0: Dorsally or anterodorsally

1: Anterior section opens forward, posterior upward

13) Narial openings B [from Sereno 1991, character P; Stocker 2010, character 1]

0: Directed laterally

1: Directed dorsally

[ORDERED] 14) Position of nares [from Hungerbühler 2002, character 10; Stocker 2010, character 2]

0: Terminal

1: Non-terminal, posterior rim of nares in front of anterior rim of antorbital fenestra

2: Non-terminal, posterior rim of nares behind anterior rim of antorbital fenestra

15) Anterior extent of septomaxillae [from Stocker 2010, character 12]

0: Anterior to anterior tip of nasal

1: Posterior to or at level with anterior tip of nasal

16) Narial outlets [from Hungerbühler *et al.* 2013, character 10]

0: Absent

1: Present

This character refers to grooves exiting the anterior extremity of the external nares, often resulting from the anterior convergence of the lateral narial borders. Narial outlets are almost entirely pervasive throughout non-leptosuchomorph phytosaurs, but only occur in a handful of more derived taxa; specifically in *Machaeroprosopus lottorum* and some specimens of *Nicrosaurus meyeri*, *Mystriosuchus planirostris* and *westphali* and *Machaeroprosopus pristinus*.

17) Dorsal rim of nares [from Hungerbühler 2002, character 9; Stocker 2010, character 20]

0: At or below level of skull roof

1: Above level of skull roof

18) Narial wing [from Hungerbühler *et al.* 2013, character 11]

0: Present

1: Absent, narial opening closed anteriorly

State zero refers to a raised lateral rim of the external nares, which descends prior to the anterior border of the nares, often abruptly, leaving a roughly 90 degree corner at the anterodorsal oint of the lateral narial rim, exemplified in *Mystriosuchus planirostris*.

19) Interorbital nasal area lateral view [modified from Hungerbühler 2002, character 14; Stocker 2010, character 21]

0: Flat from orbit to nares

1: Posterior border of nares and anterior border of orbits dip down into a concavity

This character and the subsequent one were previously a single character, describing the morphology of the interorbital-nasal area. However the original description of the character and its states are confusing: 'Interorbitonasal area: flat (0); convex (1). The area between the nares and the orbits is primitively flat and broad. In derived phytosaurs, the area is narrower, transversely round, and saddle-shaped because of the elevation of the nares and the orbital rims.' Hungerbühler (2002). The character initially appears to be describing only the transverse profile of the interorbital-narial area, however at the end the phrase 'saddle-shaped' is used in relation to the concavity seen in some phytosaurs in lateral view caused by the raised posterior border of the nares and anterior border of the orbits. This suggests the character should be aimed at describing the full three-dimensional morphology of the area, however this laterally visible morphology is not represented in the character states. The character is split here, in order to allow representation of both the laterally visible profile (character 19) and transverse morphology (character 20).

Additionally, whilst the states of character 20 are roughly similar to their original wording, their applicability to some taxa is different. Previously all derived taxa were stated to possess an interorbital-nasal area that 'is narrower, transversely round'; however all members of Mystriosuchini excluding *Mystriosuchus* (and *Nicrosaurus* if included within Mystriosuchini) possess a much broader area between the nares and orbits than the

more basal taxa, which is transversely flat, prior to its lateral descent. The cross section of this morphology is roughly rectangular in dorsal profile, rather than the inverted U-shape present in *Leptosuchus*-like phytosaurs, *Rutiodon* and *Angistorhinus*. In *Parasuchus*-grade phytosaurs, the large anteroposterior extent of the interorbital-nasal area results in a varied transverse morphology depending on the position at which it is sampled. We therefore tentatively exclude *Parasuchus*-grade phytosaurs from this character

20) Interorbital nasal area cross section [modified from Hungerbühler 2002, character 14; Stocker 2010, character 21]

0: Flat and broad

1: Dorsally curved in cross section

[See notes for character 19]

21) Infranasal recess [from Hungerbühler 2002, character 11]

0: Absent

1: Present

[ORDERED] 22) Antorbital fossa [from Hungerbühler 2002, character 12; Stocker 2010: character 3; Butler *et al.* 2014, character 3]

0: Present lacrimal jugal and maxillary fossae touching

1: Present but reduced lacrimal jugal and maxillary fossae in contact dorsally but not ventrally

2: Present but reduced lacrimal jugal and maxillary fossae not touching

3: Absent

23) Discrete row of anteroposteriorly extending nodes on the lateral surface of the jugal [from Butler *et al.* 2014, character 44]

0: Absent

1: Present

24) Jugal and antorbital fenestra [from Stocker 2010, character 4]

0: Excluded from antorbital fenestra

1: Contributing to antorbital fenestra

*** [ORDERED] 25) Length of antorbital fenestra [modified from Hungerbühler *et al.* 2013, character 13]**

0: Less than 1.9 times naris length

1: Greater than or equal to 1.9 times naris length

Modified to reflect the range of morphology sampled in this study. Measured as the ratio between the length of the antorbital fenestra and the length of the external nares. State zero scores a relatively shorter antorbital fenestra, while state one scores a relatively longer antorbital fenestra.

26) Broad median depression on dorsal surface of frontals near border with nasals [from Kammerer *et al.* 2015, character 47]

0: Absent

1405 1: Present

1406

1407 **27) Posterolateral margins of nares [modified from Kammerer *et al.* 2015, character 48]**

1408 0: Relatively low without ornamentation or derived features

1409 1: Swollen and rugose creating a distinct narial rim

1410 2: Distinctly raised in lateral view forming a sharp triangular peak well above the surrounding skull roof

1411 State two is added here to reflect the morphology of *Parasuchus bransoni*, which deviates from the previous two
1412 states with the dorsally pronounced morphology of its posterior narial rim.

1413

1414 **28) Pre-orbital depression [from Hungerbühler 2002, character 15]**

1415 0: Absent

1416 1: Present

1417

1418 **29) Depression and flange in postorbital bar [from Hungerbühler *et al.* 2013, character 14]**

1419 0: Absent

1420 1: Small elongate depression posterior rim of postorbital may create a small flange behind orbit

1421 2: Strong elongate depression posterior rim of postorbital bar forms a distinct flange merging with po/sq bar

1422

1423 **30) Jugal and orbit [from Stocker 2010, character 5]**

1424 0: Excluded from orbit

1425 1: Contributing to orbit

1426 In *Nicrosaurus kapffi*, both states of this character are present, with both states represented in individual specimens
1427 in some cases **(Hungerbühler, 1998)**.

1428

1429 **31) Medial margins of orbits [from Stocker 2010, character 6]**

1430 0: Flat with skull roof

1431 1: Raised into orbital ridges

1432

1433 **32) Deep sculpture of the skull roof [from Hungerbühler 2002, character 17]**

1434 0: Absent

1435 1: Present

1436

1437 **33) Sutural articulation of squamosal and postorbital in dorsal view [from stocker 2010, character 22]**

1438 0: Slot like, posterior process of po fits into slot in sq

1439 1: Diagonal, sq forms anteromedial portion of po/sq bar and po forms posterolateral portion

1440 2: Approximately transverse

1441

1442 **[ORDERED] 34) Most anterior extent of infra-temporal fenestra [from Butler *et al.* 2014, character 45]**

1443 0: Beneath the posterior corner of the orbit

1444 1: Extended anteriorly, reaches below the middle or anterior half of the orbit

2: Anteroventral corner distinctly in front of anterior rim of orbit

35) Pre-infratemporal shelf [from Hungerbühler 2002, character 18]

0: Absent

1: Present

The ‘pre-infratemporal shelf’ is an anteriorly convex, crescent-shaped ridge slightly anterior of the anterior border of the antero-ventral corner of the infratemporal fenestra. This morphology is present in all members of *Mystriosuchus*, *Machaeroprosopus* and ‘*Redondasaurus*’ to some degree, and also in some specimens of *Nicrosaurus*.

36) Lateral ridge from post-orbital/squamosal bar [modified from Stocker 2010, character 23; Butler *et al.* 2014, character 23]

0: Absent

1: Continues posteriorly onto squamosal as a horizontal ridge forming a shelf overhanging the infratemporal fenestra

2: Bifurcates into two small ridges on lateral surface of squamosal

The morphology of any ridge on the lateral surface of the postorbital/squamosal bar has previously been scored with considerable subjectivity. The original character on which this is based possesses a number of states which may be equally applicable to multiple taxa depending on interpretation. Here, the character is simplified to reflect the morphologies that were recognized in this study, including the absence of a ridge.

37) Lateral ridge of postorbital squamosal bar continues as ridge onto posterior process of squamosal [from Hungerbühler *et al.* 2013, character 19]

0: Absent

1: Present

*** [ORDERED] 38) Length of posterior process of squamosal in relation to postorbital length [modified from Hungerbühler 2002, character 31; Stocker 2010, character 24]**

0: Absent or extremely short, posterior edge of squamosal does not extend or barely extends posteriorly beyond the distal end of the paroccipital process of the opisthotic

1: Less than 3.60

2: 3.60 to 4.99

3: Greater than, or equal to 5.00

Modified to reflect the measurements made for the greater range of taxa included in this study. The character is measured as the ratio of the distance from the posterior border of the orbit to the posteriormost point of the squamosal, and the distance from the posterior border of the paroccipital process to the tip of the squamosal. State one scores a long posterior process, state two a moderate process, and state three a short process.

† 39) Posterior process of squamosal [modified from Hungerbühler 2002, character 32; Stocker 2010, character 25]

0: Greatly dorsoventrally expanded

1: Moderately dorsoventrally expanded

2: Terminal knob

Ballew (1989), character 50 references the presence of a ‘knob-like’ posterior process of the squamosal in *Machaeroprosopus pristinus* and *buceros*; this then became the ‘terminal knob’ of Hungerbühler (2002) and was subsequently used to describe this morphology. This character is modified to use this terminology, which is assumedly referenced by the ‘dorsally compressed’ state, used in previous versions of this character. Using this terminology makes the character less ambiguous.

† 40) Terminal knob [modified from Hungerbühler 2002, character 32; Hungerbühler *et al.* 2013, character 24]

0: Terminal knob raised distally above po/sq bar

1: Terminal knob in plane of po/sq bar

In some specimens the distal region of the terminal knob-like process of the squamosal is inflexed dorsally. The previous version of this character mentioned the posterior raising of the posterior process of the squamosal in reference to a greatly dorsoventrally expanded posterior process. This morphology was not recognized in any specimens in this study, whereas it was noted to be relatively common among individuals possessing a terminal knob.

41) Dorsal edge of squamosal [from Hungerbühler 2002, character 33; Stocker 2010, character 26]

0: Straight and narrow, no medial expansion

1: Expanded medially

This character essentially scores the presence or absence of any size of medial flange of the postorbital/squamosal bar.

42) Dorsal edge of squamosal B [from Stocker 2010, character 27]

0: Mediolaterally flat

1: Ventral depression between medial and lateral edges of the dorsal edge of the squamosal

*** [ORDERED] 43) Length of free postorbital/squamosal bar [modified from Hungerbühler *et al.* 2013, character 17]**

0: Less than 2.90

1: 2.90 to 3.39

2: Greater than or equal to 3.40

Modified to reflect the measurements made for the greater range of morphologies in this study. The character is measured as the ratio between the distance from the most anterior point of the supratemporal fenestra and the posteriormost point of the squamosal, to the shortest distance between the posterior border of the orbit and the most anterior point of the supratemporal fenestra. State zero corresponds to 'short', one corresponds to 'moderate' and two to 'long'.

44) Medial extent of squamosal [modified from Hungerbühler 2002, character 30]

0: To mid length of parieto squamosal bar

1: Enters base of supraoccipital shelf wedged between parietal and supraoccipital

The character state 'Enters rim of supraoccipital shelf dorsal to parietal' has been removed as it was not recognized in any of the specimens examined in this study.

45) Cross section of posterior half of postorbito squamosal bar [from Hungerbühler 2002, character 22]

0: Low, dorsoventrally compressed

1: High, triangular

† 46) Ventral margin of squamosal [from Stocker 2010, character 28]

0: Gently sloping anteroventrally from posterior edge of posterior process to opisthotic process

1: Distinct horizontal ventral edge between posterior edge of posterior process and opisthotic process

47) Subsidiary opisthotic process of squamosal [from Hungerbühler 2002, character 35; Stocker 2010, character 29]

0: Absent

1: Present

48) Extent of squamosal fossa [from Stocker 2010, character 30]

0: Extends to posterior edge of sq

1: Does not reach posterior edge of sq

[ORDERED] 49) Orientation of supratemporal fenestra [from Stocker 2010, character 32]

0: Dorsally expressed parietal squamosal bar at level with skull roof

1: Partially depressed parietal process of squamosal below level of skull roof

2: Fully depressed posterior process of parietal and entire parietal squamosal bar below level of skull roof

† 50) Mediolateral expansion of posterior process of squamosal [modified from Hungerbühler *et al*. 2013, character 25]

0: Tip of squamosal tapers strongly posteriorly

1: Tip of squamosal tapers with a smooth lateral deflection distally

51) Face of medial rim of squamosal along supratemporal fenestra and posterior process [modified from Hungerbühler *et al*. 2013, character 23]

0: Entire rim rounded or sharp

1: Rim entirely or in part squared

52) Extent of squaring of the squamosal rim [modified from Hungerbühler *et al*. 2013, character 23]

0: Squared in posterior section

1: Entire rim squared

53) Ridge around anterior and or medial edge of supratemporal fenestra [modified from Hungerbühler 2002, character 20]

0: Absent

1: Present, medial only

2: Present, anterior and medial

The terminology used in the original character is quite vague ‘Anterior border of supratemporal fenestra… raised above skull roof’. This character is a reinterpretation of the original, with more specific terms. In state one, the ridge would only be present on the parietal ledge, whereas in state two the ridge may extend to the anterior border of the supratemporal fenestra.

*** † [ORDERED] 54) Width of squamosal [modified from Hungerbühler *et al.* 2013, character 18]**

0: Less than or equal to 3.80

1: Greater than 3.80

Modified to reflect the greater range of morphologies measured in this study. Scored as the ratio between the length of the squamosal from the anteriormost point of the supratemporal fenestra to the posterior-most extent of the posterior process, and the width of the postorbital/squamosal bar at its approximate mid-point, or the point most representative of its general width. State zero corresponds to a wide postorbital/squamosal bar, state one denotes a relatively less wide bar.

† 55) Outline of medial rim of squamosal along supratemporal fenestra and posterior process [modified from Hungerbühler 2002, character 29]

0: Sinuous

1: Angular

2: Straight

3: Curved

Character state three has here been added to represent the morphologies found in *Nicrosaurus* and *Coburgosuchus*, which we feel were not adequately described by the previous character states.

56) Path of parietal/squamosal bars [from Stocker 2010, character 34]

0: Trending straight posteriorly to attachment on squamosals

1: Curved medially convex before attaching on squamosals

[ORDERED] 57) Visibility of supratemporal fenestrae in dorsal view [modified from Hungerbühler 2002, character 19; Stocker 2010, character 33]

0: Visible, STF completely open dorsally

1: Mostly visible, posterolateral portions of STF covered in dorsal view

2: Mostly covered dorsally, at most only anteromedial corners or medial slit of STF visible in dorsal view

3: Lamella merges with parietal, STF obliterated in dorsal view

This character combines those of Hungerbühler and Stocker. The wording used by Stocker is more inherently understandable, as Hungerbühler describes the visibility of the fenestra via the expansion of the squamosal, which is technically correct, but less intuitive. The final state of Hungerbühler's character is, however, missing from Stocker's and is useful in describing the morphology found in some extremely robust members of *Machaeroprosopus* and most specimens of '*Redondasaurus*'.

58) Parietal/squamosal bars [from Stocker 2010, character 35]

0: Slender, narrower than the width of po/sq bars

1: Wide, approximately the same mediolateral width as po/sq bars

[ORDERED] 59) Dorsal edge of parietal/squamosal bar [from Hungerbühler 2002, character 26]

0: Horizontal

1: Gently sloping

2: Steeply sloping

3: Either entirely, or in parts vertical

*** [ORDERED] 60) Parietal ledge, ratio of width to length [modified from Hungerbühler *et al.* 2013, character 30]**

0: Less than 1.30

1: 1.30 to 2.10

2: Greater than 2.10

Modified to reflect the greater range of morphologies sampled in this study. Width is measured either at the mid-point of the ledge, or the point that is most representative of its general width. Length is measured from the posterior-most extent of the ledge to the anterior-most point of the supratemporal fenestra (in phytosaurs where the parietal/squamosal bars are at the level of the skull roof, the posterior-most point of the ledge is measured at the midline of the parietals). State zero corresponds to a parietal ledge that is generally more anteroposteriorly prominent, whereas state two is very wide and hardly projects posteriorly.

61) Medial half of parieto squamosal bar lateral wall of supraoccipital shelf [from Hungerbühler 2002, character 37]

0: High and thin

1: Low, continuously thin

2: Low, basally thickened

62) Lobate extension on the vertical rim of the squamosal processes of the parietal [from Hungerbühler 2002, character 53]

0: Absent

1: Present

63) Depth and shape of supraoccipital shelf [from Hungerbühler 2002, character 36]

0: Shallow, longitudinal axis of shelf vertical

1: Deep, axis of shelf straight and horizontal

2: Deep axis of shelf with steep slope anteriorly and terminal horizontal deflection of shelf

64) Top of parieto supraoccipital complex formed by squamosal processes of parietals [from Ballew 1989, character 19; Hungerbühler 2002, character 24]

0: Angular, inverted V shape

1: Rounded, inverted U shape

2: Rectangular

65) Parietal prongs [from Hungerbühler 2002, character 25]

0: Absent

1: Present

66) Posttemporal fenestra [from Hungerbühler 2002, character 41]

0: Moderately wide and tall

1: Moderately wide and compressed

2: Extremely reduced in width and height to a slit

67) Lateral border of posttemporal fenestra [Hungerbühler 2002, character 38; Stocker 2010, character 37]

0: Formed by contact of the parietal process of the squamosal and the paroccipital process of the opisthotic

1: Formed laterally only by the paroccipital process

2: Formed laterally and slightly ventrally by process of squamosal that extends onto paroccipital process

68) Shape of quadratojugal [modified from Sereno 1991, character Q; Stocker 2010, character 31]

0: L shaped, anterior suture trends anteroventrally

1: Subtriangular

2: L shaped, anterior suture trends anterodorsally

69) Anterior border of parabasisphenoid contribution to basitubera [from Stocker 2010, character 39]

0: Basitubera separated widely

1: Basitubera separated narrowly with a ridge along their anterior border

2: Basitubera connected tubera form a sharp ridge along their anterior border

70) Morphology of basioccipital between tubera [from Stocker 2010, character 40]

0: Concave depression

1: Anteroposteriorly oriented ridge on the midline

71) Lateral extent of basitubera compared to basipterygoid processes in ventral view [from Stocker 2010, character 41]

0: Lateral extent of basitubera even with lateral extent of basipterygoid processes

1: Lateral extent of basitubera more laterally expanded compared to basipterygoid processes

72) Length of interpterygoid vacuity [from Chatterjee 1978, phenetic feature 7; Hungerbühler 2002, character 47]

0: Long, more than 50 per cent of length of palatal vault

1: Tiny oval indentation at posterior rim of conjoined pterygoids

73) Suborbital foramen [from Hungerbühler 2002, character 46; Stocker 2010, character 43]

0: Elongated, wide

1: Elongated, slit-like

2: Reduced to a single oval fenestra or subdivided into two or more small openings

74) Anterior extent of the palatine [from Hungerbühler 2002, character 44]

0: Tip located behind the posterior rim of choana

1: Tip extends forward beyond the posterior rim of choana

2: Tip extends forward beyond the anterior rim of choana

75) Palatal ridge [from Hungerbühler *et al.* 2013, character 40]

0: Low, rounded longitudinal elevation

1: Prominent, sharp ventrally to ventromedially directed crest

76) Medial edge of palatine below posterior part of palatal vault [from Hungerbühler *et al.* 2013, character 41]

0: Sloping or vertical

1: Horizontal flange may restrict the opening of the palatal vault significantly

77) Dorsal surface of surangular [from Mateus *et al.* 2014]

0: Gently convex

1: Gently concave rising to apex just posterior to dentary contact

78) Shape of retroarticular process in lateral view [from Mateus *et al.* 2014]

0: Distally sharply pointed or curved into a posterodorsally oriented hook

1: Distally rounded or blunt

79) Snout dorsal surface cross sectional shape

0: Rounded, dorsal surface of snout is curved from side to side

1: Triangular, sides of the snout are straight and slope up to the midline

80) Anterior separation of the septomaxillae

0: Septomaxillae separate posterior to level with the anterior narial border

1: Septomaxillae separate distinctly anterior of the anterior narial border

† 81) Shape of antorbital fenestra

0: oval

1: Sausage-shaped

2: Approximately triangular

3: Approximately triangular - point posteriormost

Commented [WGP23]: What kind of sausage? This is not an adequate descriptive term.

82) Lateral surface of maxilla and jugal ventral/posteroventral to AOF

0: Flat/laterally convex

1: Concavity running along the length of the element

83) Lateral surface of main body of jugal

0: Generally flat, element forms one dorsolaterally facing plane between its ventral and dorsal extremities

1: Anteroposteriorly directed ridge running from below AOF towards ventral border of subTF splits jugal into a dorsolaterally facing facet and a laterally facing facet

2: Anteroposterior ridge running along the centre of the jugal posterior process

3: Anteroposterior ridge running toward ventral border of jugal posterior process

84) Anterior extension of the sub temporal shelf

0: Anteriormost border of shelf is posterior to the posteriormost border of the antorbital fenestra

1: Anteriormost border of shelf terminates anterior of the posteriormost corner of the antorbital fenestra

85) Dorsal extension of sub temporal shelf

0: Merges dorsally into lateral surface of jugal

1: Continues dorsally contributing to the posterior edge of the postorbital descending process

86) Jugal foramen in anteroventral corner of the sub temporal fenestra

0: Visible only in medial view, not visible in lateral view

1: Visible in lateral view

*** [ORDERED] 87) Relative robusticity of the jugal**

0: Less than 7.30

1: 7.30-8.40

2: Greater than 8.40

88) Proximal section of postorbital descending process where posterior border of orbit meets skull roof

0: Flares anteroposteriorly creating a wide triangular connection

1: Posterior border of orbit remains thin until it reaches skull roof

*** † [ORDERED] 89) Sub temporal fenestra diagonal aspect ratio**

0: Less than or equal to 2.30

1: Greater than 2.30

90) Additional ridge on lateral surface of posterior process of squamosal below ridge or rugosity from po/sq bar

0: Absent

1: Present

† **91) Posterior border of quadrate in lateral view**

0: Straight anterodorsal line for majority of element

1: Ventral section of border is anteroposteriorly concave

92) Internarial septum

0: Restricted to between, or extends slightly anterior of the external nares

1: Extends anterior of the nares by approximately the narial length

93) Triangular projection ventral to articular condyle

0: Anterior border is straight, trending posteroventrally

1: Ventral half of anterior border possesses an anteriorly projecting process

*** [ORDERED] 94) Relative length of mandibular symphysis**

0: Less than 1.00

1: Greater than or equal to 1.00

Appendix 3: Nodal synapomorphies

This list presents all synapomorphic character changes at every node of each of the four data treatments: discrete, discrete + continuous, discrete + GM, and discrete + continuous + GM.

Discrete tree

1) No synapomorphies

2) 13: 0→1
   22: 0→1

3) 36: 0→1
   69: 0→1

4) 23: 0→1
   26: 0→1
   50: 0→1

5) 82: 0→1
   91: 0→1

6) 1: 0→1
   22: 1→2

73: 0→1

83: 1→0

7) 9: 0→1

14: 1→2

19: 0→1

29: 0→1

36: 1→0

38: 0→2

69: 1→2

72: 0→1

74: 1→2

80: 0→1

81: 0→2

8) 22: 2→1

60: 1→0

92: 0→1

9) 56: 0→1

58: 0→1

10) 42: 0→1

51: 0→1

11) 12: 0→1

17: 0→1

66: 0→1

70: 0→1

12) 69: 2→1

13) 8: 0→2

16: 1→0

25: 0→1

41: 0→1

44: 0→1

49: 0→1

57: 0→1

59: 0→1

88: 1→0

14) 81: 2→1

15) 90: 0→1

16) 19: 1→0

20: 0→1

39: 0→1

17) 7: 0→4

18) 48: 0→1

19) 3: 0→1

7: 4→2

33: 0→2

20) 21: 0→1

29: 1→0

21) 49: 1→2

53: 2→0

54: 1→0

57: 1→2

67: 0→2

22) 38: 2→3

23) 49: 1→2

24) 35: 0→1
43: 2→0
54: 1→0
75: 0→1
87: 0→1, 2

25) 59: 1, 2→3
84: 0→1
85: 1→0

26) 2: 1→2
20: 0→1

27) 88: 0→1

28) 65: 0→1

29) 3: 0→1
4: 0→1
7: 1→4
46: 1→0

47: 0→1

30) 25: 1→0

48: 0→1

31) 30: 1→0

36: 0→1

51: 0→1

60: 1→2

32) 3: 1→0

4: 1→0

48: 0→1

90: 0→1

33) 7: 4→1

8: 2→1

89: 0→1

34) 7: 4→2

22: 2→3

35) 11: 1→0

36) 48: 1→0

53: 1→0

37) 19: 1→0

57: 2→3

59: 2→3

63: 1→0

38) 89: 0→1

Discrete + continuous tree

1) No synapomorphies

2) 13: 0→1

22: 0→1

3) 36: 0→1

69: 0→1

4) 23: 0→1

26: 0→1

50: 0→1

54: 0.525-0.545 → 0.353-0.420

5) 25: 0.452-0.470 → 0.409-0.446

82: 0→1

91: 0→1

6) 1: 0→1

11: 0.459-0.484 → 0.490-0.686

22: 1→2

25: 0.452-0.470 → 0.514

73: 0→1

83: 1→0

89: 0.244-0.272 → 0.457-0.520

7) 9: 0→1

14: 1→2

29: 0→1

36: 1→0

60: 0.060-0.090 → 0.036-0.038

69: 1→2

72: 0→1

74: 1→2

80: 0→1

8) 19: 0→1

22: 2→1

25: 0.514 → 0.503

92: 0→1

9) 56: 0→1

58: 0→1

87: 0.106-0.110 → 0.103

10) 42: 0→1

51: 0→1

11) 8: 0.240-0.253 → 0.274

12: 0→1

17: 0→1

66: 0→1

70: 0→1

12) 69: 2→1

13) 5: 0→1

16: 1→0

25: 0.514 → 0.684-0.718

41:0→1

88: 1→0

90: 0→1

14) 57: 0→1

87: 0.106-0.110 → 0.117-0.132

15) 10: 0→1

79: 0→1

16) 11: 0.678-0.686 → 0.729

54: 0.525-0.545 → 0.395-0.406

17) 48: 0→1

89: 0.457 → 0.462

18) 21: 0→1

29: 1→0

19) 49: 1→2

54: 0.395-0.406 → 0.270

57: 1→2

67: 0→2

20) 54: 0.270 → 0.159

89: 0.457 → 0.615-0.833

21) 19: 0→1

20: 1→0

22) 33: 0→1

38: 0.281 → 0.457

54: 0.525-0.545 → 0.494

67: 0→2

90: 1→0

23) 49: 1→2

54: 0.494 → 0.383-0.399

24) 43: 0.106-0.118 → 0.070

53: 2→1

54: 0.383-0.399 → 0.213

61: 0→2

65: 0→1

25) 59: 1→2

60: 0.098-0.102 → 0.125

26) 60: 0.125 → 0.236-0.267

27) 48: 0→1

28) 35: 0→1
38: 0.457-0.751 → 0.325-0.442
89: 0.507 → 0.550-0.582

29) 22: 3→2
75: 0→1

30) 39: 1→0
53: 1→2

31) 3: 1→0
4: 1→0

32) 39: 1→2
90: 0→1

33) 43: 0.070 → 0.034-0.043
48: 1→0

59: 2→3

86: 0→1

34) 25: 0.439-0.514 → 0.113

34: 1→2

53: 1→0

54: 0.180-0.197 → 0.039-0.095

89: 0.550-0.620 → 0.710

35) 84: 0→1

87: 0.338-0.401 → 0.574-0.577

36) 7: 1→2

53: 1→2

57: 2→3

37) 57: 2→1

61: 2→1

85: 1→0

38) 2: 1→2

20: 0→1

39) 19: 0→1

88: 0→1

Discrete + GM tree (excluding landmark 'state changes')

1) [39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

91: LANDMARK

2) 13: 0→1

22: 0→1

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

91: LANDMARK

3) 36: 0→1

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

69: 0→1

81: LANDMARK

89: LANDMARK

91: LANDMARK

4) 23: 0→1

26: 0→1

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

91: LANDMARK

5) [39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

82: 0→1

89: LANDMARK

91: LANDMARK

6) 1: 0→1

22: 1→2

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

83: 1→0

89: LANDMARK

91: LANDMARK

7) 11: 0→1,2

34: 0→1

42: 1→0

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

91: LANDMARK

8) [39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

91: LANDMARK

9) 9: 0→1

14: 1→2

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

80: 0→1

81: LANDMARK

89: LANDMARK

91: LANDMARK

10) 19: 0→1

22: 2→1

[39, 40, 46]: LANDMARK

81: LANDMARK

89: LANDMARK

91: LANDMARK

92: 0→1

11) [39, 40, 46]: LANDMARK

56: 0→1

58: 0→1

81: LANDMARK

89: LANDMARK

91: LANDMARK

12) 42: 0→1

[39, 40, 46]: LANDMARK

51: 0→1

81: LANDMARK

89: LANDMARK

91: LANDMARK

13) 12: 0→1

17: 0→1

66: 0→1

70: 0→1

81: LANDMARK

14) 69: 2→1

81: LANDMARK

15) 5: 0→1

16: 1→0

25: 0→1

[39, 40, 46]: LANDMARK

49: 0→1

[50, 54, 55]: LANDMARK

57: 0→1

59: 0→1

81: LANDMARK

89: LANDMARK

91: LANDMARK

16) 41: 0→1
[39, 40, 46]: LANDMARK
[50, 54, 55]: LANDMARK
81: LANDMARK
89: LANDMARK
91: LANDMARK

17) [39, 40, 46]: LANDMARK
48: 0→1
[50, 54, 55]: LANDMARK
81: LANDMARK
89: LANDMARK
90: 0→1
91: LANDMARK

18) [39, 40, 46]: LANDMARK
[50, 54, 55]: LANDMARK
81: LANDMARK
89: LANDMARK
91: LANDMARK

19) 3: 0→1
33: 0→2
[39, 40, 46]: LANDMARK
[50, 54, 55]: LANDMARK
81: LANDMARK
89: LANDMARK
91: LANDMARK

20) 29: 1→0
33: 0→1
[39, 40, 46]: LANDMARK
[50, 54, 55]: LANDMARK
81: LANDMARK
89: LANDMARK
91: LANDMARK

21) 38: 2→3
[39, 40, 46]: LANDMARK
[50, 54, 55]: LANDMARK
60: 0→1
67: 0→2
81: LANDMARK
89: LANDMARK

91: LANDMARK

22) [39, 40, 46]: LANDMARK
49: 1→2
[50, 54, 55]: LANDMARK
81: LANDMARK
89: LANDMARK
91: LANDMARK

23) 9: 1→0
33: 1→2
[39, 40, 46]: LANDMARK
53: 2→1
[50, 54, 55]: LANDMARK
75: 0→1
81: LANDMARK
89: LANDMARK
91: LANDMARK

24) [39, 40, 46]: LANDMARK
[50, 54, 55]: LANDMARK
57: 1→2
81: LANDMARK

89: LANDMARK

90: 0→1

91: LANDMARK

25) 33: 2→0

[39, 40, 46]: LANDMARK

53: 1→0

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

91: LANDMARK

26) 38: 3→2

43: 2→0

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

64: 0→1

81: LANDMARK

87: 0→1, 2

89: LANDMARK

91: LANDMARK

27) [39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

59: 1, 2→3

81: LANDMARK

84: 0→1

85: 1→0

89: LANDMARK

91: LANDMARK

28) 2: 1→2

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

91: LANDMARK

29) 19: 0→1

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

88: 0→1

89: LANDMARK

91: LANDMARK

30) 29: 0→1
[39, 40, 46]: LANDMARK
[50, 54, 55]: LANDMARK
65: 0→1
81: LANDMARK
89: LANDMARK
91: LANDMARK

31) 3: 0→1
4: 0→1
7: 1→4
[39, 40, 46]: LANDMARK
47: 0→1
[50, 54, 55]: LANDMARK
81: LANDMARK
89: LANDMARK
91: LANDMARK

32) [39, 40, 46]: LANDMARK
48: 0→1
[50, 54, 55]: LANDMARK
81: LANDMARK
89: LANDMARK

91: LANDMARK

33) 19: 0→1

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

91: LANDMARK

34) 30: 1→0

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

60: 1→2

81: LANDMARK

89: LANDMARK

91: LANDMARK

35) 3: 1→0

4: 1→0

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

90: 0→1

91: LANDMARK

36) 7: 4→1

8: 2→1

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

91: LANDMARK

37) 7: 4→2

22: 2→3

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

91: LANDMARK

38) 11: 1→0

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

91: LANDMARK

39) [39, 40, 46]: LANDMARK

48: 1→0

53: 1→0

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

91: LANDMARK

40) 19: 1→0

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

57: 2→3

59: 2→3

63: 1→0

81: LANDMARK

89: LANDMARK

91: LANDMARK

41) [39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

91: LANDMARK

Discrete + Continuous + GM tree (excluding landmark ‘state changes’)

1) [39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

91: LANDMARK

2) 13: 0→1

22: 0→1

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

91: LANDMARK

3) 36: 0→1

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

69: 0→1

81: LANDMARK

89: LANDMARK

91: LANDMARK

4) 23: 0→1

26: 0→1

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

91: LANDMARK

5) 25: 0.452-0.470 → 0.409-0.446

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

82: 0→1

89: LANDMARK

91: LANDMARK

6) 1: 0→1

11: 0.459-0.484 → 0.490

22: 1→2

25: 0.452-0.470 → 0.514

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

83: 1→0

89: LANDMARK

91: LANDMARK

7) 8: 0.178-0.219 → 0.253-0.616

11: 0.490 → 0.686-0.800

34: 0→1

42: 1→0

43: 0.126-0.150 → 0.104-0.106

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

91: LANDMARK

8) [39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

91: LANDMARK

9) 9: 0→1

14: 1→2

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

80: 0→1

81: LANDMARK

89: LANDMARK

91: LANDMARK

10) 19: 0→1

22: 2→1

25: 0.514 → 0.503

[39, 40, 46]: LANDMARK

81: LANDMARK

89: LANDMARK

91: LANDMARK

92: 0→1

11) [39, 40, 46]: LANDMARK

58: 0→1

81: LANDMARK

87: 0.106-0.132 → 0.103

89: LANDMARK

91: LANDMARK

12) 42: 0→1

[39, 40, 46]: LANDMARK

51: 0→1

81: LANDMARK

89: LANDMARK

91: LANDMARK

13) 12: 0→1

17: 0→1

66: 0→1

70: 0→1

81: LANDMARK

14) 69: 2→1

81: LANDMARK

15) 5: 0→1

16: 1→0

25: 0.514 → 0.684-0.718

41: 0→1

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

90: 0→1

91: LANDMARK

16) [39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

57: 0→1

81: LANDMARK

89: LANDMARK

91: LANDMARK

17) 10: 0→1

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

79: 0→1

81: LANDMARK

87: 0.117-0.132 → 0.145

89: LANDMARK

91: LANDMARK

18) 11:0.686-0.690 → 0.729
43: 0.104-0.106 → 0.103
[39, 40, 46]: LANDMARK
[50, 54, 55]: LANDMARK
81: LANDMARK
89: LANDMARK
91: LANDMARK

19) [39, 40, 46]: LANDMARK
48: 0→1
[50, 54, 55]: LANDMARK
81: LANDMARK
89: LANDMARK
91: LANDMARK

20) 21: 0→1
29: 1→0
[39, 40, 46]: LANDMARK
[50, 54, 55]: LANDMARK
81: LANDMARK
89: LANDMARK
91: LANDMARK

21) [39, 40, 46]: LANDMARK
49: 1→2
53: 2→0
[50, 54, 55]: LANDMARK
57: 1→2
67: 0→2
81: LANDMARK
89: LANDMARK
91: LANDMARK

22) 38: 0.251 → 0.521
[39, 40, 46]: LANDMARK
[50, 54, 55]: LANDMARK
81: LANDMARK
89: LANDMARK
91: LANDMARK

23) 19: 0→1
20: 1→0
[39, 40, 46]: LANDMARK
[50, 54, 55]: LANDMARK
81: LANDMARK

89: LANDMARK

91: LANDMARK

24) 33: 0→1

38: 0.218 → 0.442-0.457

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

67: 0→2

81: LANDMARK

89: LANDMARK

90: 1→0

91: LANDMARK

25) 3: 0→1

4: 0→1

[39, 40, 46]: LANDMARK

49: 1→2

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

91: LANDMARK

26) 43: 0.106-0.118 → 0.070

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

73: 1→2

76: 0→1

81: LANDMARK

89: LANDMARK

91: LANDMARK

27) [39, 40, 46]: LANDMARK

53: 2→1

[50, 54, 55]: LANDMARK

70: 0→1

81: LANDMARK

89: LANDMARK

91: LANDMARK

28) [39, 40,46]:

[50, 54, 55]: LANDMARK

59: 1→2

60: 0.098-0.102 → 0.125

81: LANDMARK

89: LANDMARK

91: LANDMARK

29) [39, 40, 46]: LANDMARK
[50, 54, 55]: LANDMARK
60: 0.124 → 0.236-0.267
81: LANDMARK
89: LANDMARK
91: LANDMARK

30) [39, 40, 46]: LANDMARK
48: 0→1
[50, 54, 55]: LANDMARK
81: LANDMARK
89: LANDMARK
91: LANDMARK

31) 35: 0→1
[39, 40, 46]: LANDMARK
[50, 54, 55]: LANDMARK
81: LANDMARK
89: LANDMARK
91: LANDMARK

32) 3: 1→0

4: 1→0

7: 2→1

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

75: 0→1

81: LANDMARK

89: LANDMARK

91: LANDMARK

33) 38: 0.442-0.457 → 0.077-0.319

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

90: 0→1

91: LANDMARK

34) 19: 1→0

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

91: LANDMARK

35) [39, 40, 46]: LANDMARK
48: 1→0
[50, 54, 55]: LANDMARK
81: LANDMARK
86: 0→1
89: LANDMARK
91: LANDMARK

36) 25: 0.325-0.439 → 0.113
34: 1→2
[39, 40, 46]: LANDMARK
53: 1, 2→0
[50, 54, 55]: LANDMARK
81: LANDMARK
89: LANDMARK
91: LANDMARK

37) [39, 40, 46]: LANDMARK
[50, 54, 55]: LANDMARK
81: LANDMARK
84: 0→1
87: 0.338-0.401 → 0.574-0.577

89: LANDMARK

38) 7: 1→2

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

57: 2→3

81: LANDMARK

89: LANDMARK

91: LANDMARK

39) [39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

57: 2→1

61: 2→1

81: LANDMARK

85: 1→0

89: LANDMARK

91: LANDMARK

40) 2: 1→2

20: 0→1

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

89: LANDMARK

91: LANDMARK

41) 19: 0→1

[39, 40, 46]: LANDMARK

[50, 54, 55]: LANDMARK

81: LANDMARK

88: 0→1

89: LANDMARK

91: LANDMARK

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