Description and phylogenetic placement of a new marine species of phytosaur (Archosauriformes: Phytosauria) from the Late Triassic of Austria

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DOI:

[10.1093/zoolinnean/zlz014](https://doi.org/10.1093/zoolinnean/zlz014)

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Document Version

Peer reviewed version

Citation for published version (Harvard):

Butler, R, Jones, A, Buffetaut, E, Mandl, G, Scheyer, T & Schultz, O 2019, 'Description and phylogenetic placement of a new marine species of phytosaur (Archosauriformes: Phytosauria) from the Late Triassic of Austria', *Zoological Journal of the Linnean Society*, vol. 187, no. 1, pp. 198-228.
<https://doi.org/10.1093/zoolinnean/zlz014>

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Checked for eligibility 04/02/2019

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**A NEW SPECIES OF MYSTRIOSUCHUS
(ARCHOSAURIFORMES, PHYTOSAURIA) FROM THE LATE
TRIASSIC OF AUSTRIA**

Journal:	<i>Zoological Journal of the Linnean Society</i>
Manuscript ID	ZOJ-09-2018-3439.R1
Manuscript Type:	Original Article
Keywords:	Anatomy, Upper Triassic < Palaeontology, Archosauria < Taxa, Phylogenetics, Taxonomy
Abstract:	Phytosaurs are a group of carnivorous, semi-aquatic archosaurian reptiles that attained an almost global distribution during the Late Triassic. We describe a new species of the phytosaur genus <i>Mystriosuchus</i> from the Norian Dachstein Limestone of Austria, from a marine lagoonal depositional environment. The new Austrian material comprises remains of at least four individuals of similar size (c. 4 metres in total length) found in association but disarticulated, and includes one complete and two partial skulls, as well as postcrania. All of these specimens apparently represent a single taxon, which is distinguished by numerous anatomical features from the two previously named <i>Mystriosuchus</i> species. Maximum parsimony analysis of a comprehensive morphological dataset provides strong statistical support for the phylogenetic position of the new Austrian taxon within <i>Mystriosuchus</i>, as the sister taxon to a clade comprising <i>M. planirostris</i> and <i>M. westphali</i>. Histological analysis suggests that the Austrian phytosaur specimens represent individuals that were at least eight years old at time of death, but which had not yet reached skeletal maturity. Taphonomic and palaeoenvironmental data suggest that these phytosaurs were living within the marine lagoon in which they were preserved, providing the strongest evidence to date of marine adaptations in phytosaurs.

Abstract. Phytosaurs are a group of carnivorous, semi-aquatic archosaurian reptiles that attained an almost global distribution during the Late Triassic. We describe a new species of the phytosaur genus *Mystriosuchus* from the Norian Dachstein Limestone of Austria, from a marine lagoonal depositional environment. The new Austrian material comprises remains of at least four individuals of similar size (c. 4 metres in total length) found in association but disarticulated, and includes one complete and two partial skulls, as well as postcrania. All of these specimens apparently represent a single taxon, which is distinguished by numerous anatomical features from the two previously named *Mystriosuchus* species. Maximum parsimony analysis of a comprehensive morphological dataset provides strong statistical support for the phylogenetic position of the new Austrian taxon within *Mystriosuchus*, as the sister taxon to a clade comprising *M. planirostris* and *M. westphali*. Histological analysis suggests that the Austrian phytosaur specimens represent individuals that were at least eight years old at time of death, but which had not yet reached skeletal maturity. Taphonomic and palaeoenvironmental data suggest that these phytosaurs were living within the marine lagoon in which they were preserved, providing the strongest evidence to date of marine adaptations in phytosaurs.

Key words: Phytosauria, Triassic, Austria, phylogeny, bone histology

INTRODUCTION

Phytosaurs are an important group of early archosauriform reptiles that were nearly globally distributed during the Late Triassic, and which were remarkably morphologically convergent with modern crocodilians (Stocker & Butler, 2013). Phytosaur fossils are most commonly recovered from fluvial and lacustrine depositional environments, and are typically reconstructed as carnivorous and semi-aquatic components of terrestrial ecosystems (Stocker & Butler, 2013). However, a small number of phytosaur specimens have been recovered from Upper Triassic marine deposits in Austria and Italy (Buffetaut, 1993; Renesto & Paganoni, 1998; Gozzi & Renesto, 2003; Renesto, 2008). The majority of these marine specimens have been referred to the genus *Mystriosuchus*, which was first described from the terrestrial deposits of the Löwenstein Formation of southwest Germany (Meyer, 1863; Huene, 1915; Hungerbühler, 1998, 2002; Hungerbühler & Hunt, 2000). However, though the Italian phytosaur material has received detailed study (Renesto & Paganoni, 1998; Gozzi & Renesto, 2003; Renesto, 2008), the Austrian phytosaur material has only been mentioned briefly in the literature (Buffetaut, 1993; Stocker & Butler, 2013).

The Austrian specimens were collected from the Totes Gebirge ('dead mountains'), a group of mountains situated in northwestern Styria (Steiermark) and southern Upper Austria (Oberösterreich), which form part of the Northern Calcareous Alps. In September 1980, a local speleologist, Sepp Steinberger, made a discovery of phytosaur fossils in the Totes Gebirge, close to the mountain Hochweiß. The Department of Geology and Paleontology of the Natural History Museum in Vienna (NHMW) subsequently arranged excavation of the material, which took place July 12th–16th 1982 (Fig. 1). The excavation was completed by Ortwin Schultz, Robert Seemann, Georg Sverak and Walter Prenner of the NHMW, supported by Sepp Steinberger and Johann Segl, members of the local caving club. The

recovered rock and fossils were transported off the mountains by helicopter, with the excavation receiving considerable coverage in the local media.

Subsequent preparation of the fossils took place at NHMW, where several specimens are now on permanent display. Buffetaut (1993) briefly mentioned this material, referring it to *Mystriosuchus planirostris*, and figured a relatively complete skull. However, no subsequent description or detailed taxonomic assessment of this material has been published. Here, we describe this important phytosaur material in detail and assess its phylogenetic position and taxonomic affinities, identifying it as a new species of the genus *Mystriosuchus*.

INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History, New York, USA; GPIT, Palaeontological Collection of the University of Tübingen, Germany; MB, Museum für Naturkunde, Berlin, Germany; MCSNB, Museo Civico di Scienze Naturali “E. Caffi” di Bergamo, Lombardy, Italy; NHMW, Naturhistorisches Museum Wien, Vienna, Austria; NMMNH, New Mexico Museum of Natural History & Science, Albuquerque, USA; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

GEOLOGICAL SETTING

The Totes Gebirge is a large karst plateau covering approximately 1130 square kilometres, with altitudes of between 1400 and 1600 m in the western part and up to 2500 m in the eastern part. The phytosaur remains described here were recovered at an altitude of 1970 m in the southern part of the plateau. Due to the intense karstification and limited vegetation, the plateau is not used for alpine pasture. As a result, only a few trails enable access to the

plateau and only limited geological data are available. Most of the carbonate rocks forming the plateau belong to the Upper Triassic Dachstein Limestone ('Dachsteinkalk') of shallow carbonate platform origin.

The Upper Triassic carbonate platform was situated on the shallow shelf of Pangaea, facing the Tethyan Ocean (e.g. Haas *et al.*, 1995). Parts of this platform are exposed today in the mountains of the Eastern and Southern Alps and the Western Carpathians, and similar platform exposures occur in the Dinaric Alps and further east towards Greece and Turkey (e.g. Flügel, 2002). Due to the strong multiphase deformation that occurred by thrusting (Tollmann, 1976, 1987; Linzer *et al.*, 1995; Mandl, 2000) and strike-slip (Linzer *et al.*, 2002) faulting from the Late Jurassic to Neogene, the original width of the carbonate platform is hard to estimate. Reconstructions of paleogeography suggest an original platform width of more than a hundred kilometres to the shoreline of the Vindelician massif and the siliciclastic/evaporitic German Keuper facies (e.g. Haas *et al.* 1995). Figure 2 shows the phytosaur site and the geographical extent of the Late Triassic platform carbonates in the central part of the Northern Calcareous Alps.

STRATIGRAPHIC POSITION OF THE PHYTOSAUR MATERIAL

The Upper Triassic carbonate platform can be subdivided into several lithological units, with the majority comprising the Dachstein Limestone and the Hauptdolomit (Zankl, 1971; Haas *et al.*, 1995; Mandl, 2000). Unfortunately, these two units lack biostratigraphically useful fossils. Conodonts and ammonoids from intraplatform basins (Seefeld Formation, Kössen Formation) and basinal sediments, which interfinger with the platform margins (Gosausee Limestone, Donnerkogel Limestone, Zlambach Marls), can be used to date the history of growth of the platform indirectly. Figure 3 provides a synopsis of the present knowledge of platform dating, based on lithostratigraphic sequences from several localities (Fig. 2),

described in detail by Golebiowski (1990), Donofrio *et al.* (2003), Roniewicz *et al.* (2007), Krystyn *et al.* (2009), Haas *et al.* (2010) and Martindale *et al.* (2013a, b). Platforms of the Juvavic and Tyrolic Nappe Systems are shown separately, but their development over time seems to be similar. The timescale, ammonoid zones and ranges of conodont species are based on Krystyn *et al.* (2009: fig. 2).

As described in Mandl (2000) and Roniewicz *et al.* (2007), platform growth began following a Carnian phase of regression, which created an erosional relief on top of the Ladinian–Carnian Wetterstein carbonate platform. Latest Carnian flooding of this relief initiated a wide belt of patch reefs and a mixture of lagoonal (oncoids, ooids, calcareous algae) and open marine sediments (planktonic bivalves, conodonts, rare ammonites) in between. This pattern more or less prevailed until the middle Lacinian, when a shift of the reef belt towards the platform margin led to the development of a barrier reef (e.g. Gosaukamm area, Krystyn *et al.* [2009]). In the near reef lagoon, a distinct back-reef belt developed, characterized by massive to indistinctly bedded limestones with lagoonal organisms and only a few patch reefs. Due to the local great thickness of these back-reef sediments (e.g. at Mt. Loser, “massive limestone with patch reefs” in the geological map of Schäffer [1983]), the position of facies belts seems stable through time, with barrier reef growth continuing until the late Alaunian (= middle Norian). The next change in the depositional environment happened in the late Alaunian (Krystyn *et al.*, 2009). The reef front started to prograde towards the open sea, covering the former slope sediments (Gosausee Limestone). This continued until the middle Rhaetian and was terminated by a transgressive pulse of the Donnerkogel Limestone. The latest part of the platform margin development remains uncertain due to erosion.

The phytosaur locality is within the cyclically bedded lagoonal Dachstein Limestone. According to the available maps (Moser, 2014), about 150 metres below this stratigraphically

is the transition to an indistinctly bedded backreef limestone with a minimum thickness of more than 650 meters. This great thickness suggests that the stratigraphic position of this transition is not as early as the middle Lacian, and is more likely to be early Alaunian.

According to the dip of bedding planes and recent topography it is possible to estimate that another lagoonal Dachstein Limestone sequence with a minimum thickness of 600 metres occurs above the phytosaur locality. As such, it seems most likely that the phytosaur material occurs somewhere in the Alaunian (see Fig. 2).

DEPOSITIONAL ENVIRONMENT

The deposition of the lagoonal Dachstein Limestone is characterized by cyclothems, alternating stratigraphic sequences of distinct subunits, described as members “A, B and C” of the Lofer cyclothem by Fischer (1964). According to Fischer, a typical Lofer cyclothem starts with an erosional unconformity at the base. Member A consists of argillaceous brick-red or greenish-gray limestone, filling veins and solution cavities below the unconformity on top of the underlying bed and/or forming the matrix of a “basal conglomerate”. Fossils include thin-shelled ostracods of the genus *Lutkevichinella*, indicative of low salinity or even freshwater (Haas *et al.* 2007). Fischer (1964) interpreted member A as a modified and redeposited soil. As Haas *et al.* (2007, 2009) confirmed, member A is a tidal flat deposit, consisting of a mixture of subtidal carbonate mud, redeposited by storms, and reworked lateritic soil and other material from subaerially exposed parts of the platform. Dark stained litho- and bioclasts (“black pebbles”) are common. Blackening is the result of impregnation by decomposing organic matter under pedogenic, meteoric diagenetic conditions.

A rise in sea level led to the intertidal environment of member B, consisting mainly of dolomitic algal/bacterial mats and crusts and pellet loferites, with mud cracks and desiccation pores (Fischer, 1964). Reworked dolomitic clasts in calcilitic matrix document primary

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2
3 formation of dolomite, or at least a very early Mg/Ca-replacement. Beside the vesicles and
4
5 filaments of the algal/bacterial mats, the biota is restricted to a few foraminifera, ostracods
6
7 and tiny gastropods.
8
9

10 Member C is the main and terminal member of the Lofer cyclothem, ranging in
11
12 thickness from 1–20 metres or more. It consists of well-winnowed calcarenites, arenites in a
13
14 muddy matrix or featureless carbonate mudstones. Components include bioclasts, ooids,
15
16 oncoids, featureless pellets (peloids) and compound lumps. Additional microfacies data are
17
18 given by Haas *et al.* (2007, 2010). The biota is much more diverse than in members A and B.
19
20 The most conspicuous fossils are megalodont pelecypods, which occur occasionally in shell
21
22 beds of scattered valves but more commonly as bivalved specimens in growth position. The
23
24 shells are relatively large (diameters from 10–40 cm or more). Gastropods locally form dense
25
26 accumulations. Calcareous algae, echinoid spines, ostracods, and foraminifera are common,
27
28 whereas brachiopods are rare. Locally bushes of branched corals (“*Thecosmilia*”) grow in the
29
30 lagoon. Detritus of corals and calcareous sponges is restricted to areas near to the reefs.
31
32 Member C represents deposition below low tide, not deeper than a few metres, with normal
33
34 salinity. Water agitation was sufficient for winnowing the arenites and moving ooids and
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36 oncoids but not strong enough for a general and widespread redeposition of the large
37
38 megalodonts.
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44 An idealized cycle from the basal subaerial unconformity to tidal flat conditions of
45
46 members A and B and at last to a subtidal lagoon of member C represents a deepening
47
48 upward sequence. The repetition of such sequences must reflect relative variation in sea level,
49
50 most probably reflecting eustatic sea level changes (Fischer, 1964). Due to a repeated
51
52 variation in the thickness of successive cyclothem, they can be grouped into sets of five.
53
54 These megacycles may correlate with astronomical variations in the Earth’s orbit
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56 (Schwarzacher, 2005).
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The host rock of the phytosaur material is member C of the lagoonal Dachstein Limestone. The bones are embedded in a peloidal packstone (Fig. 4). The featureless peloids are of elongated ovoid form with 40–50 μm diameter and 70–90 μm length, and may represent faecal pellets of molluscs. Locally, they merge to form a pseudomicritic matrix. Millimetre to centimetre sized components include shells and shell fragments of gastropods, echinoid spines and black stained calcareous bio- and lithoclasts. No biostratigraphically useful foraminifera or calcareous algae have been found in the available samples. The bone fragments are in direct contact with the surrounding sediment, and no microbial or other coatings are visible (Fig. 3A). The peloidal sediment infiltrated most of the fine spongy cavities of the bone (Fig. 3B).

MATERIALS AND METHODS

One femur fragment (NHMW 1986/0024/0013) was sectioned to examine the internal histology. Comparison with a more complete femur indicates that the sectioned plane is only slightly proximal to mid-shaft (about 48.2 mm from the distal preserved end of the 162.1 mm long femur fragment). This position was necessary as the distal-most preserved shaft area of NHMW 1986/0024/0013 is damaged and thus lacks most of the external cortical portion. The sectioning of the bone was performed following standard petrographic thin-section procedures as outlined in Chinsamy & Raath (1992). Prior to sectioning and grinding (using a diamond-sintered blade and grinding wheel, as well as manual grinding with SiC powders of 220, 500 and 800 grit), the bone fragment was embedded in removable two component resins (Technovit 5071 and Universal Liquid) to prevent cortical fracturing. The sections were then studied using a Leica composite microscope DM 2500M, equipped with a Leica DFC 420 C digital camera. Images were processed using Adobe Photoshop Creative Suite.

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SYSTEMATIC PALAEONTOLOGY

ARCHOSAURIFORMES Gauthier, 1986

PHYTOSAURIA Jaeger, 1828

PARASUCHIDAE Lydekker, 1885 sensu Kammerer *et al.*, 2015

MYSTRIOSUCHINAE Huene, 1915 sensu Kammerer *et al.*, 2015

LEPTOSUCHOMORPHA Stocker, 2010 sensu Jones & Butler, 2018

MYSTRIOSUCHINI Huene, 1915 sensu Jones & Butler, 2018

Mystriosuchus Fraas, 1896

Type species: Mystriosuchus planirostris (Meyer, 1863).

Referred species: Mystriosuchus westphali Hungerbühler & Hunt, 2000; *Mystriosuchus steinbergeri* n. sp.

Diagnosis: Diagnosed on the basis of the following combination of characters (* indicates characters that can be confirmed as present in *Mystriosuchus steinbergeri* n. sp.):

*interpremaxillary fossa reduced to a slit in the anterior part of the premaxilla; deep sculpture of the skull roof and narial region; *interorbital-narial area dorsally curved in cross-section; *posterior process of the squamosal strongly reduced in anteroposterior length; posttemporal fenestra strongly reduced (modified from Hungerbühler 2002; see ‘Phylogenetic analysis’ section below).

Distribution: Upper Triassic of central Europe. *Mystriosuchus planirostris* and *M. westphali* are known from the middle Stubensandstein, Löwenstein Formation of the Middle Keuper, Baden-Württemberg, southwest Germany. *Mystriosuchus steinbergeri* is known from the Dachsteinkalk of Styria, central Austria. Specimens from the Calcare di Zorzino and Argillite di Rivia di Solto of northern Italy have been referred to *M. planirostris* (Renesto & Paganoni, 1998; Gozzi & Renesto, 2003) and cf. *Mystriosuchus* (Renesto, 2008), but the species-level affinities of this material require reinvestigation in light of the referral of the Austrian *Mystriosuchus* material to a new species. The middle Stubensandstein and Calcare di Zorzino are of middle–late Norian (Alaunian–Sevastian) age (Kozur & Bachmann, 2005; Renesto, 2006), and the age of the Dachsteinkalk material may be broadly similar (middle Norian; see above). *Mystriosuchus* may also be known from a specimen (MB.R. 2747) from the lower Exter Formation near Salzgitter, Niedersachsen, Germany (Huene, 1922; Jones & Butler, 2018; see below), but a redescription and re-examination of the taxonomy of this specimen is needed to confirm this. Kimmig & Arp (2010) referred fragmentary phytosaur material from the Arnstadt Formation near Göttingen, Niedersachsen, Germany, to *Mystriosuchus planirostris*, but provided little evidence to support this hypothesis. The material described by Kimmig & Arp (2010) is here considered Phytosauria indet.

Mystriosuchus steinbergeri n. sp.

“*Mystriosuchus planirostris*”; Buffetaut, 1993: p. 42, fig. 4

“Phytosaur remains (possibly *Mystriosuchus*) in the southern part of the Totes Gebirge”;

Renesto & Paganoni, 1998: p. 119

“*Mystriosuchus* specimens found in the Norian Dachsteinkalk”; Renesto & Lombardo, 1999:

p. 136

“*Mystriosuchus* from the Norian Dachsteinkalk of Austria; Irmis *et al.*, 2010: p. 42

“Dachsteinkalk-Formation...*Mystriosuchus*”; Kimmig & Arp, 2010: p. 222

“Well-preserved material of *Mystriosuchus*...from the Dachsteinkalk of Austria”; Stocker &

Butler, 2013: p. 102

Etymology: The species is named for Sepp Steinberger, who discovered and helped collect the holotype and referred specimens.

Holotype: NHMW 1986/0024/0001, partial skull, missing most of left side.

Paratype: NHMW 1986/0024/0002, articulated mandibles (missing posterior end of right mandible), very likely representing the same individual as NHMW 1986/0024/0001.

Referred specimens: NHMW 1986/0024/0003, left ilium (recovered adjacent to NHMW 1986/0024/0002 and possibly representing the same individual as the holotype and paratype); NHMW 1986/0024/0004, paired anterior portion of articulated premaxillae; NHMW 1986/0024/0005 and NHMW 1986/0024/00016, partial skull and probably associated mandibular remains; NHMW 1986/0024/0006a, b, partial skull (b) and probably associated mandibular remains (a); NHMW 1986/0024/0007, nearly complete left humerus; NHMW 1986/0024/0008, proximal end of left humerus; NHMW 1986/0024/0009, distal end of left humerus; NHMW 1986/0024/0010, left ulna; NHMW 1986/0024/00011, left ulna; NHMW 1986/0024/0012, complete right femur; NHMW 1986/0024/0013, proximal end of right femur; NHMW 1986/0024/0014, left tibia; NHMW 1986/0024/0015, osteoderm; NHMW 1986/0024/0018, fragment of shaft of tibia; NHMW 1986/0024/0019, fragment of distal end of femur; NHMW 1986/0024/0024, jaw fragment. Numerous additional unaccessioned

fragments of cranial and postcranial remains are also present in the NHMW collections, but provide no useful anatomical details in addition to the accessioned specimens listed above.

Locality and horizon: 380 m SSE of the mountain Hochweiß, southern part of the Totes Gebirge mountain range, 7.1 km north of Tauplitz, Liezen district, Styria (Steiermark), central Austria. Coordinates: 47° 37' 30" N, 14° 00' 40" E. The locality has been added to the *Paleobiology Database* and is locality number 97845. Dachstein Limestone (Dachsteinkalk), Upper Triassic (middle Norian: Alaunian).

Differential diagnosis: Species of *Mystriosuchus* characterised by the following combination of characters: (1) ratio of length of preorbital region of skull to length of orbital + postorbital length estimated as not exceeding 3.3 (3.9–4.1 in *M. planirostris*) and ratio of prenasal to nasal + postnasal length not exceeding 1.8 (1.8–2.2 in *M. westphali*, 2.6 in *M. planirostris*); (2) fewer than 40 teeth in upper jaws (41–50 in *M. westphali*, 48 in *M. planirostris*); (3) premaxillary crest absent (crest present in *M. westphali*); (4) dorsal margin of internasal bar and dorsal margin of premaxilla merge smoothly into one another (meet at an angle of nearly 90° to one another in *M. planirostris*); (5) anterior part of external naris placed anterior to the antorbital fenestra (naris placed entirely dorsal to antorbital fenestra in *M. westphali*); (6) anteroposterior length of the naris is less than that of the orbit (naris and orbit subequal in anteroposterior length in *M. westphali*); (7) internasal bar not depressed ventrally relative to level of lateral nasal rim and visible in lateral view along entire length (internasal bar depressed ventral to lateral nasal rim and only visible in lateral view at its anterior end in *M. planirostris* and *M. westphali*); (8) posterior rims of nares not distinctly raised into “volcano-like” structure (“volcano-like structure present in *M. westphali*); (9) alveolar margin of maxilla straight to concave in lateral view (alveolar margin convex in lateral view in *M.*

westphali); (10) antorbital fenestra large (maximum dorsoventral height exceeds that of the orbit) and separated from the external naris by a distance equal to or less than the maximum dorsoventral height of the former (antorbital fenestra reduced in size and more broadly separated from the external naris in *M. westphali* and *M. planirostris*); (11) antorbital fenestra expands in dorsoventral height towards its posterior end (antorbital fenestra oval and tapers posterodorsally in *M. westphali* and *M. planirostris*); (12) broad, deep and sharply defined antorbital fossae present on the lacrimal and jugal posterior to the fenestra (fossae absent in *M. westphali*, variably developed and poorly defined in *M. planirostris*); (13) jugal enters posterior rim of antorbital fenestra (excluded from rim by maxilla-lacrimal contact in *M. westphali*); (14) descending process of the postorbital posteriorly expanded at its proximal end (entire process approximately consistent in thickness in *M. westphali* and *M. planirostris*); (15) parietal-squamosal bar depressed approximately 25% of skull height below the posterior portion of the skull table (depressed >30% of skull height in *M. planirostris*); (16) suborbital fenestra anteroposteriorly elongate and wide (reduced to small fenestra in *M. westphali* and *M. planirostris*).

ANATOMICAL DESCRIPTION

General comments: The majority of the material referred to here to *Mystriosuchus steinbergeri* was collected within a single bone accumulation covering approximately 3 m² (quarry map available with the accessioned material at NHMW). There are no indications that more than a single phytosaur species is present, and the only other preserved vertebrate remains were numerous isolated dome-shaped teeth of durophagous fish, some of which are catalogued as NHMW 1986/0024/0017. The holotype skull (NHMW 1986/0024/0001) was found approximately 2 metres distant from this main accumulation, within 20 cm of the nearly complete lower jaws (NHMW 1986/0024/0002), and a left ilium (NHMW

1986/0024/0003). No other bones were recovered from the immediate vicinity of these specimens, and NHMW 1986/0024/0001 and NHMW 1986/0024/0002 are considered highly likely to represent the same individual (the relative sizes of the two specimens are consistent with this hypothesis). NHMW 1986/0024/0004, paired anterior premaxillae, have been mounted together with NHMW 1986/0024/0002 in the NHMW museum display, but there is no evidence from the data available that these specimens were found together or represent a single individual.

Cranial remains accessioned at NHMW indicate a minimum of three individuals, based on the presence of three partial skulls and associated lower jaws; all three of these individuals are of very similar size (based on absolute sizes of cranial openings). Postcranial remains indicate a minimum of two individuals: there are two left ulnae, two right femora, and two left humeri. The large number of unaccessioned jaw fragments suggests that although only three individuals can be recognised with certainty, four or more might be present. This is also supported by recent field photographs provided by the original discoverer, Sepp Steinberger, which show another as-yet-uncollected partial skull at the same site. Skull length is estimated at a maximum of 600 mm (see below). This is relatively small for the genus *Mystriosuchus*, in which skull length typically ranges from 800 mm to more than one metre (Hungerbühler, 2002). Likewise, the femoral length of 235 mm is moderate in size for a phytosaur (61–297 mm in specimens [e.g. NMMNH P-30843, P-37291] of *Machaeroprotopus buceros* from the Synder Quarry, Zeigler *et al.*, 2003; 302 mm in a specimen [AMNH 1] of *Rutiodon carolinensis*, Colbert, 1947; 522 mm in a specimen [AMNH 3060] of *Smilosuchus gregorii*, Colbert, 1947; 270 mm in a specimen [MCSNB 10087] referred to *Mystriosuchus* from Italy, Gozzi & Renesto, 2003). A phytosaur skeleton (MCSNB 10087) from the marine Norian of Italy assigned by Gozzi & Renesto (2003) to *Mystriosuchus* has a skull length of 555 mm and a total body length of 3760 mm. Thus, the

individuals of *Mystriosuchus steinbergeri* described here may have been up to around four metres in length. Measurements of the material are provided in Table 1.

General skull morphology: Except where noted, the description of the skull is based on the holotype NHMW 1986/0024/0001 (Figs 5, 6), which is nearly complete on the right side (as figured by Buffetaut, 1993: fig. 4). However, the left side of the skull was almost entirely eroded away (with the exception of parts of the anterior end of the left premaxilla) prior to discovery and excavation. As a result, a cross section through the midline of the skull is now visible from the left side (Figs 5C, 6C). The anterior tip of the rostrum is missing, and various parts of the preserved portions of the skull (e.g. the right quadratojugal-jugal bar) have suffered damage. Transverse crushing of the skull has occurred, slightly distorting some areas, including the narial region (the right naris faces dorsolaterally rather than dorsally) and the postorbital-squamosal bar. Bone surface preservation is relatively poor, with common fracturing of surface bone, meaning that sutures cannot be identified in most cases and that the depth, nature and distribution of ornamentation cannot be readily established. The skull has an elongated and low rostrum (Figs 5A, 6A), with no development of distinct narial or premaxillary crests. The skull is dorsally inflated relative to the rostrum in the narial, orbital and postorbital regions.

The maximum preserved anteroposterior length of the skull of NHMW 1986/0024/0001, from the preserved tip of the rostrum to the posterior margin of the squamosal, is 540 mm. Based on the length (560 mm) from the anterior rosette to the posterior margin of the glenoid of the associated mandibles (NHMW 1986/0024/0002), and the observation that in *M. planirostris* (SMNS 9134) and other phytosaurs the tip of the premaxilla extends a short distance beyond the tip of the dentary, we estimate the maximum skull length of NHMW 1986/0024/0001 as 580–600 mm. The preserved preorbital length of

the skull is 400 mm and so the complete preorbital length would have been around 440–460 mm. The preserved orbital + postorbital length is 140 mm. As a result, the estimated ratio of preorbital length to orbit + postorbital length is in the region of 3.15–3.3. The prenarial length of the skull as preserved is 325 mm, and so the complete prenarial length would have been 365–385 mm. The narial + postnarial length is 215 mm, and thus the estimated ratio of prenarial to narial + postnarial length is in the region of 1.7–1.8. These ratios are broadly similar to or moderately lower than those in *M. westphali* (3.1–3.3 and 1.8–2.2, respectively; Hungerbühler, 1998: table B1 and ASJ personal observation of AMNH FR 10644), but are strikingly different from those of *M. planirostris* (3.9–4.1 and 2.6; Hungerbühler, 1998: table B1). They are similar to those of other leptosuchomorph phytosaurs such as *Machaeroprotopus pristinus* (3.0–3.2 and 1.6–1.64; Hungerbühler, 1998: table B1) and *Nicrosaurus meyeri* (3.41 and 1.63; Hungerbühler, 1998: table B1), as well as some non-leptosuchomorph phytosaurs such as *Rutiodon carolinensis* (3 and 1.5–1.59; Hungerbühler, 1998: table B1) and *Angistorhinus grandis* (3 and 1.57; Hungerbühler, 1998: table B1). The proportions of the mandible also support the inference of a proportionately shorter skull than that of *M. planirostris* (see below). In order for the preorbital length of the skull to have been as proportionately long as in *M. planirostris*, at least 145 mm of the tip of the rostrum would have to have been lost, and the premaxilla would have extended at least 120 mm anterior to the dentary rosette. We consider such an elongate rostrum in *M. steinbergeri* highly unlikely.

The external naris of *M. steinbergeri* (NHMW 1986/0024/0001) is placed anterior to the orbit (posterior margin of naris separated by 44 mm from the anterior margin of the orbit) but slightly ventral to the frontoparietal skull table (Figs 5A, 6A). The posterior two thirds of the external naris lie dorsal to the antorbital fenestra, whereas the anterior part of the naris lies dorsal to the maxillary antorbital fossa, as in *M. planirostris* (SMNS 9134, 12060). By contrast, in *M. westphali* the external naris is placed entirely dorsal to the antorbital fenestra,

with the anterior rim of the naris being placed slightly posterior to the anterior rim of the fenestra (GPIT 261/001; AMNH FR 10644). In NHMW 1986/0024/0001 only the right naris is well preserved; the lateral margin of the left naris is missing and its medial margin is poorly preserved (Figs 5D, 6D). The naris has a teardrop-shaped outline in dorsal view, and posteriorly it increases in transverse width and extends away from the midline. As in *M. planirostris* (SMNS 9900; Hungerbühler, 2002) and *M. westphali* (AMNH FR 10644), the naris is divided into a short anterior section that opens nearly directly anteriorly, and a posterior section that opens anterodorsally (transverse crushing of the skull means that as preserved the posterior section also opens slightly laterally). In the holotype of *M. westphali* (GPIT 261/001) the naris opens anterodorsally along its entire length; however deformation of the anterior narial region masks the true profile of the external nares (Hungerbühler, 2002).

The external naris of NHMW 1986/0024/0001 has an anteroposterior length of 36 mm and is 9 mm wide at its posterior margin, and its length is therefore only 76% of that of the orbit, similar to the condition in *M. planirostris* (e.g. SMNS 9134, 12060). By contrast, in *M. westphali* (GPIT 261/001) the anteroposterior length of the naris is subequal to that of the orbit, and the posterior margin of the naris is proportionately less broadly separated from the orbit. The medial border of the naris (the internarial bar, formed by the ‘septomaxilla’ and/or the nasal, although sutures cannot be recognised) of NHMW 1986/0024/0001 is raised dorsally above the lateral border of the naris, and is convex in lateral view (Figs 5A, 6A). Although the skull has suffered some distortion in this area it seems unlikely that the internarial bar was set below the lateral margins of the nares. The internarial bar merges smoothly at its anterior margin with the dorsal margin of the rostrum, such that the skull has a smoothly convex dorsal margin anterior to the orbit in lateral view (Figs 5A, 6A). The lateral border of the naris is also gently convex in lateral view. Because the lateral border of the naris is positioned ventral to the medial border, the internarial bar is visible in lateral view

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3 along its entire length (Figs 5A, 6A), although this may have been exaggerated by post-
4 mortem distortion.
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8 The profile of the internarial bar in lateral view in *M. steinbergeri* is substantially
9 different from that of *M. planirostris*. In *M. planirostris* the dorsal margin of the rostrum and
10 the dorsal margin of the internarial bar meet at a very sharp and distinct angle of nearly 90
11 degrees, with the dorsal margin of the rostrum orientated nearly vertically immediately
12 anterior to the external naris (SMNS 9134, 9900, 12060) and the dorsal margin of the
13 internarial bar orientated nearly horizontally. This contrasts with the smooth contour between
14 the dorsal margin of the rostrum and the dorsal margin of the internarial bar in *M.*
15 *steinbergeri*. Although the narial region is slightly distorted in NHMW 1986/0024/0001, it
16 seems highly unlikely that a *M. planirostris*-like condition was present or that the dorsal
17 margin of the rostrum became orientated nearly vertically immediately anterior to the nares.
18
19 The general profile of the skull anterior to the orbits in *M. steinbergeri* is confirmed by a
20 second, poorly preserved skull that is preserved in two pieces (NHMW 1986/0024/0005,
21 1986/0024/0016; Fig. 7). Moreover, in both *M. planirostris* (SMNS 9134, 9900, 12060) and
22 *M. westphali* (GPIT 261/001; Huene, 1911; Hungerbühler, 1998), the internarial bar is
23 strongly depressed below the level of the lateral margins of the naris, and only its most
24 anterior end is visible in lateral view, differing from the condition in *M. steinbergeri* (NHMW
25 1986/0024/0001). In *M. westphali*, the lateral and posterior rims of the nares are raised to
26 form a prominent, volcano-like structure (GPIT 261/001; AMNH FR 10644; Huene, 1911;
27 Hungerbühler, 1998, 2002), again differing from the condition in *M. steinbergeri*.
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51 The large antorbital fenestra of *M. steinbergeri* (NHMW 1986/0024/0001) has an egg-
52 shaped outline, with the long axis of the fenestra extending from anteroventral to
53 posterodorsal (Figs 5A, 6A). It tapers gently towards its anteroventral margin, and is broadly
54 rounded posterodorsally. The posterior border of the fenestra lies slightly anterior to the
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3 anterior margin of the orbit. The antorbital fenestra of NHMW 1986/0024/0001 has a
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5 maximum anteroposterior length of 55 mm, and a maximum dorsoventral depth (close to its
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7 posterior margin) of 37.5 mm. The maximum anteroposterior length of the antorbital fenestra
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9 slightly exceeds that of the orbit, and the maximum dorsoventral height of the antorbital
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11 fenestra is subequal to that of the orbit. By contrast, in *M. planirostris* (SMNS 9134, 9900,
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13 12060, 13420) the antorbital fenestra has a more oval-outline and does not increase in depth
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15 towards its posterior margin; moreover, the maximum dorsoventral height of the antorbital
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17 fenestra is less than that of the orbit. In *M. westphali* (GPIT 261/001; AMNH FR 10644;
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19 Huene 1911) the antorbital fenestra is also broadly oval in shape with a maximum
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21 dorsoventral height that is less than that of the orbit. *Mystriosuchus westphali* (GPIT 261/001,
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23 AMNH FR 10644) also has a projection formed by the maxilla and lacrimal extending into
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25 the posteroventral corner of the antorbital fenestra that is absent in *M. planirostris* and *M.*
26
27 *steinbergeri*. Hungerbühler (2002) considered the outline of the antorbital fenestra of GPIT
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29 261/001 to fall within the range of variation of *M. planirostris*, but this morphology was
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31 considered a diagnostic character of *M. westphali* by Jones & Butler (2018).
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37 In *M. planirostris*, there is a broad area formed by the ascending process of the
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39 maxilla and the nasal that separates the external naris from the dorsal margin of the antorbital
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41 fenestra. This separation between the naris and the antorbital fenestra is more than 150% of
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43 the dorsoventral depth of the antorbital fenestra (SMNS 9134, 9900). In *M. westphali* the
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45 separation between the naris and the antorbital fenestra is moderately lower but still exceeds
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47 the dorsoventral depth of the antorbital fenestra (GPIT 261/001; AMNH FR 10644). By
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49 contrast, in *M. steinbergeri* (NHMW 1986/0024/0001) the antorbital fenestra and the external
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51 naris approach each other proportionately more closely (probably as a result of the
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53 proportionately larger size of the antorbital fenestra), and are separated by a distance that is
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55 only 75% of the maximum dorsoventral depth of the antorbital fenestra (Figs 5A, 6A).
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A well-developed antorbital fossa is present on the maxilla of *M. steinbergeri* (NHMW 1986/0024/0001), adjacent to the anteroventral corner of the antorbital fenestra, and extends onto both the base of the ascending process of the maxilla and onto the horizontal process of the maxilla ventral to the antorbital fenestra (Figs 5A, 6A). The maxillary antorbital fossa is bordered by a sharp rim. A similar maxillary antorbital fossa is present in *M. planirostris*, but is proportionately slightly smaller, and bordered by a less sharply demarcated rim (SMNS 9900). In *M. westphali* a small maxillary antorbital fossa is also present (GPIT 261/001), but does not extend onto the horizontal process of the maxilla and is also only weakly demarcated. At the posterior end of the antorbital fenestra of *M. steinbergeri* (NHMW 1986/0024/0001) there is a well-defined antorbital fossa extending onto the jugal (ventrally) and the lacrimal (dorsally) (Figs 5A, 6A). This fossa is present along the entire dorsoventral height of the posterior border of the antorbital fenestra, and is anteroposteriorly narrow. Although jugal and lacrimal antorbital fossae are present in *M. planirostris* (SMNS 9134, 9900, 12060, 13420), they are variably developed, and tend to be proportionately smaller and less well defined than in *M. steinbergeri*. In *M. westphali* there is a small antorbital fossa present on the lacrimal, restricted to the posterodorsal corner of the antorbital fenestra (AMNH FR 10644).

The border of the antorbital fenestra is well preserved in *M. steinbergeri* (NHMW 1986/0024/0001), although the generally poor preservation of the skull bone surface means that it is difficult to identify contacts between the surrounding elements with certainty. The majority of the ventral border of the antorbital fenestra is formed by the horizontal process or main body of the maxilla (Figs 5A, 6A). The ascending process of the maxilla forms the anterior and anterodorsal borders of the fenestra. The lacrimal forms the posterodorsal border of the fenestra, whereas the jugal forms the posteroventral border. The contribution of the jugal to the posteroventral border of the antorbital fenestra is similar to the condition in *M.*

planirostris (Hungerbühler, 1998, 2002), but differs from the condition in *M. westphali* in which the jugal is excluded from the antorbital fenestra by contact between the maxilla and the lacrimal (Hungerbühler, 1998, 2002; GPIT 261/001). Hungerbühler (2002) suggested that the participation of the jugal in the antorbital fenestra might be subject to intraspecific variation in species of *Mystriosuchus* based on his observations of *Nicrosaurus kapffi*.

The orbit of *M. steinbergeri* (NHMW 1986/0024/0001) is similar in size to the antorbital fenestra, and has a subcircular outline (Figs 5A, 6A), being slightly longer than wide, with a maximum anteroposterior length of 47 mm and a maximum dorsoventral height of 38 mm. It faces laterally and slightly dorsally, and is bordered by the jugal, lacrimal, prefrontal, frontal, postfrontal and postorbital. An unidentified bone fragment is present within the right orbit.

The infratemporal fenestra of *M. steinbergeri* (NHMW 1986/0024/0001) is proportionally large as preserved (Figs 5A, 6A), although its size may be exaggerated by damage to the posteroventral border of the opening. The fenestra has a maximum dorsoventral height of 72 mm, has an anteroposterior length as preserved of 74 mm at its ventral margin (this length is possibly exaggerated by the damage to the posteroventral border) and its dorsal margin is approximately 46 mm in anteroposterior length. The anterodorsal corner of the fenestra is curved to a substantially greater extent than in *M. planirostris* or *M. westphali*. This is due to the posterior expansion of the descending process of the postorbital as it merges with the postorbital-squamosal bar. The anteroventral corner of the fenestra terminates below the midpoint of the orbit. There is a shallow and poorly defined fossa on the lateral surface of the jugal adjacent to the anteroventral corner of the infratemporal fenestra (Fig. 5A), as is common to phytosaurs within *Mystriosuchini* and also present in some non-mystriosuchin phytosaurs. Dorsally, adjacent to the infratemporal fenestra, there is also a fossa along the ventral margin of the postorbital-squamosal bar,

defined dorsally by a sharp ridge on that bar (Figs 5A, 6A). The border of the infratemporal fenestra is formed by the jugal, quadratojugal, postorbital, and squamosal.

The supratemporal fenestra of *M. steinbergeri* (NHMW 1986/0024/0001) is completely preserved on the right side (Figs 5B, D, 6B, D), although its medial margin (formed by the parietal) is damaged and incomplete. The fenestra faces dorsally. The medial margin of the postorbital-squamosal bar would likely have partially overhung the fenestra, but this bar appears to have been deformed and twisted along its anteroposterior axis, and is no longer in its original orientation. The supratemporal fenestra is broadly rounded anteriorly, and tapers to a point posterolaterally. It has a maximum anteroposterior length of 44 mm, and a maximum width of 33 mm. The posterior border of the fenestra (formed by the squamosal process of the parietal and the parietal process of the squamosal) is strongly depressed ventrally below the level of the skull roof (Figs 5B, 6B). The most ventral part of this parietal-squamosal bar is depressed approximately 25% of skull height below the posterior portion of the skull table, similar to the condition in *M. westphali* (Hungerbühler, 2002; GPIT 261/001), but differing from the autapomorphic condition in *M. planirostris* (Hungerbühler, 2002) in which the parieto-squamosal bar is depressed more than 30% of skull height below the posterior skull table. The supratemporal fenestra of *M. steinbergeri* (NHMW 1986/0024/0001) is bordered by the parietal, postorbital and squamosal. Although not well preserved, the anteromedial rim of the fenestra is slightly raised above the surrounding skull roof as in other species of *Mystriosuchus* (Hungerbühler, 2002).

The quadrate foramen of *M. steinbergeri* (NHMW 1986/0024/0001) is poorly preserved, but is a subcircular opening (approximately 10 mm in diameter) visible between the quadrate and the quadratojugal in posterior view of the skull (Figs 5B, 6B). This is relatively large as in other species of *Mystriosuchus* (*M. planirostris*, SMNS 9900; *M.*

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2
3 *westphali*, GPIT 261/001), and was suggested as a synapomorphy of the genus by
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5 Hungerbühler (2002).
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8 The subtemporal fenestra of *M. steinbergeri* (NHMW 1986/0024/0001) is a large
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10 opening with an oval outline (Figs 5E, 6E). Its maximum anteroposterior length is 96 mm,
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12 and its maximum width is 54 mm. It is bordered by the quadrate, quadratojugal, jugal,
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14 ectopterygoid, and pterygoid.
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17 The borders of the suborbital fenestra (Figs 5E, 6E) of *M. steinbergeri* (NHMW
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19 1986/0024/0001) are poorly preserved, but it is elongate, with a long axis that extends from
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21 posteromedial to anterolateral, but bends adjacent to the maxilla to give it a somewhat
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23 boomerang-like outline. It is at least 43 mm long along this axis, and is becomes transversely
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25 broader towards its anterolateral termination. The entire posterolateral margin of the opening
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27 is formed by the ectopterygoid, the palatine forms the anteromedial margin, and the pterygoid
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29 is formed by the ectopterygoid, the palatine forms the anteromedial margin, and the pterygoid
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31 and maxilla may form small parts of the posteromedial and anterolateral corners of the
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33 opening, respectively. By contrast, in *M. westphali* (Huene, 1911: pl. 1; Hungerbühler, 1998,
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35 2002) and *M. planirostris* (SMNS 9900; Hungerbühler, 1998, 2002), the suborbital fenestra is
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37 reduced to a small, suboval aperture.
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40 No information is available on the posttemporal fenestra of *M. steinbergeri* (NHMW
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42 1986/0024/0001). Only a small part of the border of the right choana (Figs 5E, 6E) is
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44 preserved in NHMW 1986/0024/0001 (formed by the palatine), and demonstrates only that
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46 the choana was placed directly ventral to the external naris, as occurs commonly in
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48 mystriosuchine phytosaurs (Butler, 2013). The choanae are slightly better preserved in the
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50 skull NHMW 1986/0024/0005/NHMW 1986/0024/0016 (Fig. 7A, C), although their
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52 posterior margins are not preserved, and only the anterior half of the median bar (formed by
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54 the vomers) that separates the choanae is preserved. The choanae are transversely narrow (7
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56 mm in width) and taper anteriorly.
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Skull roof: The premaxillae are both broken anteriorly in NHMW 1986/0024/0001, with the anterior end of the rostrum missing (Figs 5, 6). Of the left premaxilla, only the medial parts are preserved, with a clear median suture separating them from the right premaxilla. The exact positions of sutures between the premaxilla and the maxilla, ‘septomaxilla’, and nasal on the external surface, and the maxilla, vomer, and palatine on the palatal surface, cannot be identified with certainty due to poor preservation. The premaxillae form a tube-like rostrum that is as high dorsoventrally as it is transversely wide. The premaxilla has a consistent dorsoventral height (approximately 20–25 mm) along most of its length, but posteriorly the dorsal border of the premaxilla arches strongly dorsally toward the external nares (Figs 5, 6). In lateral view the premaxilla is curved along its length such that the dorsal surface is anteroposteriorly concave and the ventral surface anteroposteriorly convex. However, this is likely an artefact of post-mortem deformation, and the rostrum was likely straighter in life. Medial to the alveoli there are well-developed alveolar ridges that are visible in lateral view. The interpremaxillary fossa is very narrow anteriorly, forming a very narrow slit; posteriorly the fossa is not preserved because the left premaxilla is missing. The narrow, slit like, interpremaxillary fossa was identified as a generic synapomorphy of *Mystriosuchus* by Hungerbühler (2002). The cross section through NHMW 1986/0024/0001 reveals that an extensive median cavity is present within the rostrum that is positioned anterior to, and continuous with, the airway. This cavity is present in a range of phytosaurs, and represents a pneumatic paranasal sinus that likely housed diverticula of the antorbital air sinuses, possibly as an adaptation to resisting torsion (Witmer, 1997; Butler, 2013).

NHMW 1986/0024/0004 consists of the anterior portions of a pair of premaxillae including the terminal rosette (containing four tooth positions) and the anterior 14 tooth positions (Figure 9). The rosette is slightly anteroposteriorly longer than transversely broad,

and is slightly downturned in lateral view. The anteriormost alveolus of the rosette is apparently enlarged relative to subsequent alveoli. The preserved premaxillary crowns are simple peg-like teeth, which are curved medially and slightly posteriorly. Serrations cannot be identified, possibly due to poor preservation. The premaxillae possess very well developed alveolar ridges that are separated from one another by only a very narrow groove as in NHMW 1986/0024/0001.

No teeth are preserved in NHMW 1986/0024/0001. Thirty-one alveoli, all of which are infilled with sediment, are preserved on the right side, with an additional four alveoli anterior to this on the left side (Figs 5E, 6E); the minimum count in the upper jaws is 35 (but was almost certainly somewhat higher given that the anterior end of the rostrum is missing). Because the contacts between the premaxilla and the maxilla are not clearly distinguishable, it is not possible to determine the tooth counts for individual bones. Alveoli are generally subcircular in outline or slightly longer than wide, with no significant variation in alveolar size occurring along the preserved tooth row.

The maxilla is dorsoventrally narrow below the antorbital fenestra, with a flat external surface (Figs 5A, 6A). The ascending process of the maxilla extends posterodorsally at around 45 degrees to the horizontal, and forms the anterior and anterodorsal margins of the antorbital fenestra. As described above, a small maxillary antorbital fossa is present. Posteriorly, the maxilla contacts the jugal just anterior to the posterior border of the antorbital fenestra. There is no contact between the maxilla and the lacrimal because of the jugal reaching the border of the antorbital fenestra. On the ventral surface of the maxilla there is little development of alveolar ridges medial to the alveoli; at most a slight thickening of the bone is present. A medially extending shelf of the maxilla is present as in other phytosaurs (Figs 5E, 6E), which would have contacted the premaxilla anteriorly (although the position of this contact is unclear) and the palatine posteriorly. The maxilla appears to form the

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3 anterolateral corner of the suborbital fenestra, and is contacted at its posteromedial margin by
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5 the ectopterygoid (Figs 5E, 6E).
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8 The borders of the 'septomaxilla' cannot be clearly identified, although it seems likely
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10 that they form the entire internarial bar, as in *M. planirostris* (Hungerbühler, 1998, 2002).
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12 Both nasals are preserved (although the left nasal is incomplete), and their dorsal surfaces are
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14 acutely convex transversely; however, this likely reflects post-mortem transverse
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16 compression and the convexity would likely have been less exaggerated in life. The sutures
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18 of the nasal with surrounding elements are also not clear (Figs 5A, D, 6A, D), but it is likely
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20 that the nasal forms the posterior and lateral rims of the external naris, much of the lateral
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22 surface of the skull between the antorbital fenestra and the external naris, and the skull roof
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24 between the external naris and the orbit. The maxilla and lacrimal appear to exclude the nasal
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26 from the dorsal border of the antorbital fenestra.
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31 The right prefrontal is damaged along its orbital margin, and contacts with the nasal,
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33 frontal, and lacrimal are unclear (Figs 5A, D, 6A, D). It forms the anterodorsal margin of the
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35 orbit. Part of the left prefrontal is also preserved. The frontals form the majority of the skull
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37 table between the orbits, and contribute to the dorsal margins of the orbits (Figs 5A, D, 6A,
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39 D). The frontal is raised into a low ridge at its orbital margin, and also at the midline, so that
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41 its dorsal surface is gently concave transversely. Posteriorly the frontal contacts the parietal
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43 approximately level with the posterior margin of the orbit. The postfrontal is a small element
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45 forming the posterodorsal margin of the orbit, and contacting the frontal medially, the parietal
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47 posteriorly, and the postorbital laterally (Figs 5A, D, 6A, D).
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52 The lacrimal forms the posterodorsal margin of the antorbital fenestra and the
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54 anteroventral margin of the orbit (Figs 5A, D, 6A, D). It contacts the prefrontal dorsally, the
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56 ascending process of the maxilla anteriorly and the jugal posteriorly and ventrally. It is not
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clear as to whether or not a nasal-lacrimal contact was present. The lacrimal is emarginated anteroventrally by the antorbital fossa. The lacrimal foramen and canal are not visible.

The jugal is a dorsoventrally tall element that forms the posteroventral margin of the antorbital fenestra (where it is emarginated by the antorbital fossa) and contacts the maxilla anteriorly and the lacrimal anterodorsally (Figs 5A, 6A). The jugal contacts the postorbital along the very narrow and anteroposteriorly compressed postorbital-jugal bar, the axis of which extends from posterodorsal to anteroventral, and contributes a small portion to the ventral margin of the orbit. The contact between the postorbital and the jugal is overlapping, with the ventral process of the postorbital extending anterior to the dorsal process of the jugal. The jugal also forms the anteroventral corner of the infratemporal fenestra (adjacent to which a low fossa is present on the lateral surface of the jugal: see above), and contacts the quadratojugal posteriorly. The tip of the anterior process of the quadratojugal appears to fit into a slot on the lateral surface of the posterior process of the jugal. The form of the remainder of the contact between the jugal and the quadratojugal is unclear due to damage to the jugal-quadratojugal bar ventral to the infratemporal fenestra.

The postorbital contacts the parietal and postfrontal dorsomedially, the jugal anteroventrally, and the squamosal posteriorly (Figs 5A, D, 6A, D). It forms the anterolateral corner of the supratemporal fenestra, the ventral half of the posterior margin of the orbit, and the anterodorsal margin of the infratemporal fenestra. It contacts the squamosal at about the midlength of the supratemporal fenestra, with the posterior process of the postorbital fitting into a groove on the dorsal surface of the anterior process of the squamosal. The postorbital has a strong ridge along the lateral surface of its posterior process that extends posteriorly onto the squamosal. This ridge defines the dorsal margin of the infratemporal fenestra, and below this ridge the postorbital-squamosal bar is emarginated, forming a fossa (Figs 5A, 6A). Medially, a flange extending from the postorbital-squamosal bar would have partially

overhung the supratemporal fenestra (see above), but this flange is damaged at its medial margin and the postorbital-squamosal bar has been twisted post-mortem, such that its dorsal surface faces dorsolaterally. Because of the lateral ridge and the medial flange, the postorbital-squamosal bar has a subtriangular cross section with a flat dorsal surface.

The squamosal has a short parietal process medially, which contacts the parietal medially and the paroccipital process ventrally, excluding the paroccipital process from the border of the supratemporal fenestra (Figs 5D, 6D). The anterior process of the squamosal contacts the postorbital, forming the posterior half of the postorbital-squamosal bar, the posterolateral margin of the supratemporal fenestra, and the posterodorsal corner of the infratemporal fenestra (Figs 5A, D, 6A, D). A sharp ridge is present on the lateral surface of the anterior process, and is continuous with a ridge on the postorbital (see above). The anteroventral process of the squamosal extends ventrally along the posterior margin of the infratemporal fenestra, but the length and ventral termination of this process cannot be determined due to damage and attached bone fragments (Figs 5A, 6A). There is no posterior process of the squamosal: i.e. there is no development of a process that extends posteriorly beyond the opisthotic process of the squamosal. This is similar to the condition in *M. westphali* and *M. planirostris*, with strong reduction of the posterior process having been considered a synapomorphy of *Mystriosuchus* by Hungerbühler (2002). A short ventrally directed opisthotic process contacts the paroccipital process and extends ventral and posterior to the head of the quadrate. The posterior margin of the main body of the squamosal is gently concave in lateral view.

The parietals form part of the median skull roof anterior to the supratemporal fenestra, suturing with the frontals, postfrontals and postorbital (Figs 5D, 6D). Only the right parietal is complete anteriorly; the left is almost entirely missing. The dorsal surface of the parietal is gently concave both anteroposteriorly and transversely. The parietal forms most of the

1
2
3 anterior, the entire medial, and most of the posterior margins of the supratemporal fenestra,
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5 although most of the medial and posterior margins are damaged or missing. The parietal is
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7 raised into a low rim at the anteromedial corner of the supratemporal fenestra (see above).
8
9
10 The squamosal process of the parietal is strongly depressed ventrally relative to the level of
11
12 the skull roof, and contacts the paroccipital process along its ventral margin.
13

14
15 The quadratojugal is badly damaged, but is a triangular element with a tapering,
16
17 elongate anterior process that forms the posteroventral corner of the infratemporal fenestra
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19 (Figs 5A, 6A). Dorsally, the contact between the quadratojugal and the squamosal is not well
20
21 preserved. Medially, the quadratojugal contacts the quadrate and forms the lateral border of
22
23 the quadrate foramen.
24

25
26 The quadrate is also damaged but was probably nearly vertically oriented in life, with
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28 the posterior border of the bone concave in lateral view (Figs 5A, 6A). The condyles are
29
30 transversely expanded relative to the rest of the element in posterior view (Figs 5B, 6B) and
31
32 strongly compressed anteroposteriorly in ventral view (Figs 5E, 6E). The main body of the
33
34 element articulates laterally with the squamosal and quadratojugal, and forms the medial
35
36 margin of the quadrate foramen. The head of the quadrate articulates tightly with the
37
38 squamosal and also forms a contact with the distal end of the paroccipital process (Figs 5B,
39
40 6B). Medially, the quadrate is drawn out into an extensive pterygoid flange that extends
41
42 anteromedially to contact the pterygoid. This flange of the quadrate is drawn out posteriorly
43
44 at its ventral margin, and its posterior surface is concave dorsoventrally.
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50

51 *Braincase:* Very little information on the braincase is preserved in NHMW 1986/0024/0001.
52
53 The distal part of the right paroccipital process of the opisthotic is partially preserved (Figs
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55 5B, 6B), and contacts the squamosal process of the parietal and the parietal process of the
56
57 squamosal dorsally, the opisthotic process of the squamosal distally, and the head of the
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59
60

quadrate anteriorly. Parts of the right wall of the braincase, likely including parts of the prootic, basioccipital and basisphenoid are visible in cross section (Figs 5C, 6C), but yield few anatomical details. A cross section through the right basal tuber reveals that it is ventrally directed (Figs 5C, 6C).

Palate: Fragments of the right pterygoid, ectopterygoid, palatine and possibly vomer are present in NHMW 1986/0024/0001 (Figs 5C, E, 6C, E). The pterygoid articulates posteriorly with the pterygoid wing of the quadrate and anterolaterally with the palatine and ectopterygoid, probably forming the posteromedial corner of the suborbital fenestra. The ectopterygoid articulates medially with the pterygoid and extends laterally and dorsally as an arched rod of bone. At its distal end it articulates with the posteromedial corner of the maxilla and the anteromedial corner of the jugal immediately posterior to the termination of the maxillary tooth row (Figs 5E, 6E). A foramen or fossa in the ectopterygoid is not visible, although this may reflect poor preservation. Only the horizontal lateral flange of the palatine is preserved (Figs 5E, 6E). This flange articulates laterally with the maxilla and forms the anteromedial border of the suborbital fenestra. Anteriorly it narrows in transverse width, forming the lateral margin of the choana and articulating with a medial shelf of the maxilla.

Mandible: NHMW 1986/0024/0002 is a block that contains articulated but badly damaged lower jaws (Figure 10). The mandible was found within 20 cm of the holotype skull (NHMW 1986/0024/0001) and without any other bones being found in the immediate area and we consider it very likely that they belong to the same individual. Although some small areas of the mandible have been reconstructed, the original quarry map at NHMW demonstrates that the total length of the mandible as currently preserved in the block is accurate.

The dentary is poorly preserved on both sides (Figure 10). Teeth are absent, and an accurate tooth count based on alveoli is difficult, but they contain at least 49 alveoli, including four within a terminal rosette. This rosette is expanded transversely relative to the succeeding section of the dentary, and is longer than wide. The first three alveoli within this symphysis are enlarged (around 6 mm in diameter), and they are followed by smaller alveoli (3–4 mm in diameter). Alveolar size increases again toward the end of the tooth row, reaching a maximum of 10 mm in anteroposterior length. Alveoli are subcircular along most of the tooth row, but become slightly transversely compressed at the distal end of the tooth row. There is an elongate dentary symphysis, extending for approximately 40 tooth positions. The dentaries are transversely slender and there is a flat dorsal surface between the tooth rows. The mandibular rami diverge from one another posteriorly. Due to preservation, sutures between the dentaries and post-dentary bones cannot be recognised. The anterior part of the external mandibular fenestra is visible on the right mandible (the external mandibular fenestra and surrounding bone has been lost on the left side): the fenestra is dorsoventrally deep and it expands dorsally and ventrally at its preserved posterior end (Figure 10D). The glenoid region is only retained on the left side and is very poorly preserved: all that can be determined is that there is a ventromedial process medial to the glenoid and a short retroarticular process (Figure 10B).

The length from the anterior rosette to the termination of the symphysis is 305 mm, so that the symphyseal region consists of 52.5% of the total mandibular length. By contrast, in *M. planirostris* (SMNS 9134) the symphyseal region consists of approximately 60% of total mandibular length. This confirms the inference based on the skull (see above) that *M. steinbergeri* had a relatively short rostrum in comparison with *M. planirostris*.

Postcranium: The humerus is represented by three examples, including a relatively complete left humerus (NHMW 1986/0024/0007; Fig. 11A–D) that is damaged and incomplete at proximal and distal ends, the proximal end of a left humerus (NHMW 1986/0024/0008; Fig. 11E, F) that is broken just distal to the termination of the deltopectoral crest, and the distal end of a left humerus (NHMW 1986/0024/0009; Fig. 11G, H). It is possible that NHMW 1986/0024/0008 and NHMW 1986/0024/0009 represent the same element, but this cannot be ascertained.

The humerus is strongly transversely expanded at its proximal end (NHMW 1986/0024/0008; Fig. 11E, F), with the greatest expansion relative to the shaft occurring medially. The proximal and medial margins of the humerus meet at an acute angle. Anterolaterally, there is a low, symmetrical and rounded deltopectoral crest. Proximal and medial to this crest the anterior surface of the humerus is depressed and gently concave transversely. Medially, there is a short, proximodistally extending ridge on the anterior surface of the proximal end (NHMW 1986/0024/0008; Fig. 11E). The posterior surface of the proximal end is gently convex transversely, but there is no distinct development of a head. A low proximodistally extending muscle scar is present adjacent to the deltopectoral crest on the posterior surface of the proximal end (NHMW 1986/0024/0007, NHMW 1986/0024/0008; Fig. 11F).

The shaft of the humerus is preserved in NHMW 1986/0024/0007 (Fig. 11A–D). It is damaged and possibly deformed, but is slender and twisted along its length, with the maximum expansion of the distal end oriented at around 40° to the maximum expansion of the proximal end. In dorsal or ventral view the shaft is bowed outwards (laterally) along its length. At midshaft, the shaft has a subcircular cross section, being slightly wider transversely than dorsoventrally.

The distal end of the humerus is best preserved in NHMW 1986/0024/0009 (Fig. 11G, H), which however lacks the distal articular surface. The distal end of the humerus is expanded transversely and compressed anteroposteriorly. The anterior surface of the distal end has a subcircular depression, the depth of which may have been exaggerated by post-mortem deformation. The posterior surface of the distal end is flat to gently convex transversely. An ectepicondylar groove is present laterally (Fig. 11H), and extends from the posterior surface (proximally) onto the lateral margin of the anterior surface (distally). A broken supinator process is present posterior and lateral to this groove. In overall morphology, the humerus is more slender and more strongly laterally bowed than in other described phytosaur species (Chatterjee, 1978; Zeigler *et al.*, 2003; Kimmig, 2013).

The ulna is represented by two left examples (NHMW 1986/0024/0010, NHMW 1986/0024/0011; Fig. 12), of nearly identical size. The ulna is slender and slightly curved along its length. The element is strongly compressed transversely (although this may have been exaggerated by post-mortem compression), and expanded anteroposteriorly. The proximal end is damaged in both elements (Fig. 12), but has a well-developed olecranon process and lacks any development of a lateral tuber (Nesbitt, 2011: character 237). The medial surface of the shaft is flattened to gently concave anteroposteriorly, whereas the lateral surface is convex. The distal end is not preserved in either element, but was transversely compressed judging from the morphology of the most distal preserved parts. The tibia closely resembles the same element in other phytosaurs (e.g. Zeigler *et al.*, 2003).

The ilium is represented by a single left element (NHMW 1986/0024/0003; Fig. 13) that is preserved adjacent to the mandible (NHMW 1986/0024/0002; Fig. 10B) and that is visible in lateral view only. There is only a very short and blunt anterior or preacetabular process, and an elongate, tapering posterior or postacetabular process. There is no ridge on the lateral surface of the ilium above the acetabulum. A very narrow supraacetabular flange is

present above the acetabulum (Fig. 13). The border of the acetabulum that articulated with the ischium is concave in lateral view, whereas the border that articulated with the pubis is convex. The elongate postacetabular process of *Mystriosuchus steinbergeri* is similar to that present in specimens referred to *Leptosuchus crosbiensis*, *Machaeroprotopus buceros*, *Redondasaurus gregorii* and *Nicrosaurus kapffi* by Kimmig (2013:fig. 3), but proportionately longer than in the early phytosaur *Parasuchus* (Chatterjee, 1978). The preacetabular process is proportionately shorter than in other phytosaur species for which the element has been described (Camp, 1930; Chatterjee, 1978; Kimmig, 2013).

The femur is represented by a nearly complete right element (NHMW 1986/0024/0012; Fig. 14A–F) and the proximal end of a right element (NHMW 1986/0024/0013; Fig. 14G–I). The femur is twisted along its length such that the maximum expansion of the proximal end is at nearly 90° to the maximum expansion of distal end (thus, the proximal end is expanded transversely and the distal end is expanded anteroposteriorly). The femur is sigmoidal in lateral and anterior views (Fig. 14A, F), and is slender relative to its length. The proximal end is medially inturned, and has a well-developed posteromedial tuber on its posterior surface (Fig. 14C). The region in which the anterolateral tuber should be preserved is reconstructed in both elements. The proximal end narrows anteroposteriorly towards the lateral margin. There is a raised, proximodistally extending ridge for the attachment of the caudofemoralis musculature on the posterior surface of the femur (Fig. 14E). Distally, the femur is divided into paired condyles with shallow fossae separating them anteriorly and posteriorly. The femur is generally very similar in morphology to other phytosaurs for which the element has been described (Camp, 1930; Chatterjee, 1978; Zeigler *et al.*, 2003; Kimmig, 2013).

A single left tibia (NHMW 1986/0024/0014; Fig. 15A–D) is preserved. The tibia is relatively slender and has a straight shaft. In medial or lateral view the posterior margin of the

shaft is gently concave, whereas the anterior margin is nearly straight (Fig. 15A, D). The lateral surface of the proximal end is damaged. The element is expanded both anteroposteriorly and mediolaterally at its proximal end. The lateral surface of the shaft is damaged; the medial surface is strongly convex dorsoventrally. Distally the shaft is expanded slightly anteroposteriorly and transversely and has a subquadrate outline (Fig. 15C). The tibia closely resembles the same element in other phytosaurs (e.g. Zeigler *et al.*, 2003).

A single presacral dorsal osteoderm (NHMW 1986/0024/0015; Fig. 15E, F) is preserved. The osteoderm is subquadrate in outline, although several of its margins are damaged, and is curved along its axis transversely, such that the ornamented dorsal or external surface is convex and the internal or ventral surface concave. The ventral surface is relatively smooth whereas the dorsal surface is ornamented by pits.

Histology: The thin-section of the shaft of femur fragment NHMW 1986/0024/0013 (Fig. 16) revealed an ovoid cross-section (31.1 mm x 21.7 mm) with an overall compact cortex surrounding a medullary cavity (ca. 16.5 mm x 7.2 mm) that is free of trabeculae. The bone tissue has been strongly altered by diagenetic processes, thus histological details can be seen only in better preserved patches. In addition, most of the cortex has experienced fracturing and subsequent mineral infillings. Surrounding the medulla (also completely infilled by minerals), there are remnants of an endosteally deposited thin layer of lamellar bone (Fig. 16A), followed by a transitional zone where the cortical bone was being remodelled, as indicated by the presence of larger erosion cavities and scattered secondary osteons. Locally the remodelling is more extensive, as in the lateral bone quadrant (Fig. 16B), compared to the other quadrants.

The periosteally deposited cortex has a lamellar-zonal composition, consisting of growth zones of parallel-fibred bone separated by lines of arrested growth (LAGs). The

vascularisation (Fig. 16C) of the cortical tissue is composed of scattered, longitudinally arranged primary osteons, as well as of reticular arrangement of simple vascular canals. The growth record of the bone fragment is best visible in the anterior and medial quadrants (Fig. 16A). Here, a minimum of eight growth cycles could be identified based on LAGs count. The growth zones are reduced in thickness in the anterior to lateral quadrant, but expanded, for example, anteromedially. There is no evidence for a closer spacing of LAGs in the superficial parts of the cortex, and thus for the development of an outer circumferential layer sensu Ponton *et al.* (2004).

The lamellar-zonal bone with a parallel-fibred bone matrix separated by LAGs and overall low levels of vascularisation of the femur shaft of NHMW 1986/0024/0013 are indicative of low bone deposition rates. This is in support of previous palaeohistological analyses including phytosaur long bones, which also hypothesised low growth in these animals (Ricqlès *et al.*, 2003; Werning, 2011), although at least some phytosaurs might have had also raised growth rates based on osteoderm histological data (Scheyer *et al.*, 2014). The number of eight LAGs in the cortex (although a few growth cycles might have been lost due to expansion of the medullary cavity) and the continuous, wide spacing of LAGs up to the external bone, together indicate that the animal was still actively growing and had not yet reached skeletal maturity.

PHYLOGENETIC ANALYSIS

NHMW 1986/0024/0001, the holotype of *M. steinbergeri*, was included in the phylogenetic analysis of Jones & Butler (2018). That analysis is described in detail in Jones & Butler (2018) and a brief summary of their results is provided here. Jones & Butler (2018) conducted four separate analyses using distinct character-coding treatments, including combinations of discrete, continuous and landmark character data. Eight equally

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2
3 parsimonious trees were found across the four different analyses conducted, and in all of
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5 them *M. steinbergeri* was consistently recovered in a sister group relationship with the clade
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7 formed by *M. planirostris* and *M. westphali*. Figure 17 shows a strict consensus of the eight
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9 trees recovered by Jones & Butler (2018). The clade comprising the three named species of
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11 *Mystriosuchus* and MB.R. 2747 (which likely represents a further unnamed species of
12
13 *Mystriosuchus*, but is in need of redescription) was consistently present in all trees to the
14
15 exclusion of any other taxon; however, due to the present uncertain taxonomic status of
16
17 MB.R. 2747 we here define the genus *Mystriosuchus* at the node that includes only *M.*
18
19 *planirostris*, *M. westphali* and *M. steinbergeri* (Fig. 17).
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23

24 The phylogenetic analysis of Jones & Butler (2018) found one unambiguous
25
26 synapomorphy in support of *Mystriosuchus*: ‘interpremaxillary fossa reduced to a slit in the
27
28 anterior part of the premaxilla’ [character 2: 1→2]. A further synapomorphy was found in
29
30 seven out of eight most parsimonious trees: ‘interorbital-narial area dorsally curved in cross-
31
32 section’ [character 20: 0→1]. In the remaining tree this character was not found to be
33
34 synapomorphic due to the recovery of the preceding node as polymorphic. The remaining
35
36 characters used here in the differential diagnosis of *Mystriosuchus* are not unambiguous
37
38 synapomorphies in the phylogenetic results due to missing data and recovery of polymorphic
39
40 states at preceding nodes. ‘Deep sculpture of the skull roof and narial region’ is recovered as
41
42 polymorphic at the *Mystriosuchus* node due to missing data in NHMW 1986/0024/0001. The
43
44 character state ‘posterior process of the squamosal strongly reduced’ is found in all three
45
46 species of *Mystriosuchus*; however, the character state is not synapomorphic due to missing
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48 information in MB.R. 2747. A different state is however present at the next most basal node
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50 in all trees, suggesting that, in the absence of MB.R. 2747, the reduction of the posterior
51
52 process of the squamosal would be unambiguously synapomorphic of *Mystriosuchus*.
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58 ‘Posttemporal fenestra strongly reduced’ is consistently recovered as synapomorphic for *M.*
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3 *planirostris* and *M. westphali*; however, data is missing for both NHMW 1986/0024/0001
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5 and MB.R. 2747, as well as for many of the terminals most closely related to this clade in all
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7 trees.
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12 DISCUSSION

15 TAPHONOMY

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17 The taphonomy of the phytosaur specimens from the Totes Gebirge has significant
18
19 implications for our understanding of the life environment of *Mystriosuchus steinbergeri*. The
20
21 depositional environment is reconstructed as shallow subtidal and fully marine, and
22
23 palaeogeographical reconstructions suggest that the shoreline may have been tens of
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25 kilometres to the north (Haas *et al.*, 1995). Remains of at least four individuals were present
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27 at the locality, scattered over a limited area of a few square metres, and no fossils of certainly
28
29 terrestrial groups are preserved in the same deposit. Although the various skeletal elements
30
31 were no longer articulated, suggesting some kind of disturbance of the carcasses (possibly by
32
33 scavengers) before burial, this taphonomic pattern suggests that little post-mortem transport
34
35 took place. Once they become bloated by putrefaction gases, tetrapod carcasses can float for a
36
37 long time and over great distances (Schäfer, 1962) before they become stranded or drop to the
38
39 bottom, which explains the not uncommon occurrence of dinosaur remains in marine
40
41 sediments (see Buffetaut, 1994 for examples from the French fossil record). However, this
42
43 kind of process cannot explain the occurrence of multiple individuals of *Mystriosuchus*
44
45 *steinbergeri*, represented by a large number of bones, over a small area of a former sea floor,
46
47 as there is no reason why floating carcasses should have accumulated in such a way as a
48
49 result of a random process of drift. This makes it unlikely that the remains are those of
50
51 freshwater phytosaurs that were somehow transported kilometres out from land and deposited
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53 together within very close proximity to one another. We consider the most likely explanation
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therefore to be that *Mystriosuchus steinbergeri* habitually lived in a marine environment. The occurrence of skeletal elements from several individuals of similar ontogenetic stages suggests an episode of mass mortality, the reasons of which cannot be ascertained. Future work on functional morphology and geochemistry may be useful to test these hypotheses.

PHYTOSAURS IN MARINE ENVIRONMENTS

The vast majority of known phytosaur fossils have been collected from terrestrial deposits, usually representing fluvial or lacustrine environments, including the type and referred specimens of *Mystriosuchus planirostris* and *Mystriosuchus westphali* from southwest Germany (Kimmig & Arp, 2010; Stocker & Butler, 2013). However, a small number of phytosaur specimens have been recovered from marine deposits, leading to speculation on the ability of the clade to occupy or pass through saltwater environments. These specimens include a complete skeleton and an isolated skull, both referred to *Mystriosuchus planirostris*, from the Calcare di Zorzino of northern Italy (Renesto & Paganoni, 1998; Gozzi & Renesto, 2003), as well as a series of caudal vertebrae referred to cf. *Mystriosuchus* (Renesto, 2008) from the Argillite di Rivia di Solto of the same region. The specimens described here represent another marine occurrence of the genus *Mystriosuchus*. The stratigraphically oldest and phylogenetically most basal known phytosaur, *Diandongosuchus fuyuanensis* (originally identified as a poposauroid pseudosuchian: Li *et al.*, 2012) from the Middle Triassic of China, is also known from marine deposits (Stocker *et al.*, 2017). A lower jaw fragment that may belong to a phytosaur was described by Maisch & Kapitzke (2010) from earliest Jurassic marine deposits in England, and identified as aff. *Mystriosuchus*. Other occurrences of isolated teeth in latest Triassic–earliest Jurassic marine deposits in Europe have also been identified as phytosaurian (Huene & Maubeuge, 1954; Kimmig & Arp, 2010; Maisch & Kapitzke, 2010), although none of these are definitive. A supposed marine occurrence of the

1
2
3 phytosaur *Parasuchus* (Huene, 1939; Hunt & Lucas, 1991) has been shown to not represent
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5 this genus, and possibly not be phytosaurian (Butler, 2013).
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8   These occurrences of phytosaur specimens in marine deposits have been used as
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10 evidence of the ability of at least some phytosaur species to live in shallow marine
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12 environments (Buffetaut, 1993; Renesto & Paganoni, 1998; Gozzi & Renesto, 2003; Stocker
13
14 *et al.*, 2017). As noted by Buffetaut (1993) and above, the Dachstein Limestone material of
15
16 *Mystriosuchus steinbergeri* provides some of the best evidence in support of this hypothesis
17
18 (Figure 18). Renesto & Paganoni (1998) and Gozzi & Renesto (2003) presented evidence for
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20 marine adaptations in the postcranial skeleton of a complete *Mystriosuchus* skeleton from the
21
22 Calcare di Zorzino. Clear skeletal adaptations to a marine habitat are not evident in
23
24 *Mystriosuchus steinbergeri*, but that may simply reflect the highly limited available
25
26 postcranial material.
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33 ACKNOWLEDGEMENTS 34 35 36 37

38 We thank Ursula Göhlich (NHMW) for access to the specimens of *Mystriosuchus*
39
40 *steinbergeri*, and providing us with reports, photographs, drawings and rock samples from the
41
42 fieldwork in July 1982. Philippe Havlik (University of Tübingen) and Rainer Schoch (SMNS)
43
44 provided access to key comparative material. Christian Kolb and Marta Ladeira (both
45
46 PIMUZ) are thanked for help in preparing the thin sections. GWM thanks Leo Krystyn from
47
48 Vienna University for additional biostratigraphic data and discussion of the carbonate
49
50 platform development. Mark Witton is thanked for creating the life restoration in Figure 18.
51
52 RJB was supported by a DFG Emmy Noether Programme award (BU 2587/3-1),
53
54 SYNTHESYS funding to visit Vienna, and a Marie Curie Career Integration Grant (grant
55
56 number 630123). ASJ was supported by a NERC Training Grant (grant number
57
58
59
60

NE|L002493|1). TMS acknowledges funding by the Swiss National Science Foundation (No. 205321_162775). EB's visit to Vienna in 2013 was made possible by a SYNTHESYS grant. We thank reviewers Michelle Stocker and Axel Hungerbühler and the editor Louise Allcock for helpful comments.

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FIGURE LEGENDS

42 **Figure 1.** Photographs taken in 1982 during the collection of the type and referred material of
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44 *Mystriosuchus steinbergeri* sp. nov. A, the type locality. The five figures in the centre of the
45
46 photograph are clustered around the excavation site. B, the excavation team, including from
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48 left-to-right, Johann Segl, Sepp Steinberger, Georg Sverak and Walter Prenner. Georg Sverak
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50 is using the pneumatic hammer to drill a hole for a wedge used to split the blocks of
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52 limestone for removal. C, Georg Sverak and Walter Prenner in front of their tent. D,
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54 photograph of the block, as originally excavated, including the holotype skull (NHMW
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3 1986/0024/0001; bottom right of photograph) and paratype mandible (NHMW
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5 1986/0024/0002; top middle of photograph) in close association.
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10 **Figure 2.** Extent of Late Triassic platform carbonates in the central part of the Northern
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12 Calcareous Alps (Austria), with the type locality of *Mystriosuchus steinbergeri* sp. nov. Note
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14 the tectonic deformation by thrusts and faults. Based on the geological map of Upper Austria
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16 1:200.000 (Krenmayr and Schnabel 2006).
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21 **Figure 3.** Stratigraphic framework of the Late Triassic carbonate platforms of the Northern
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23 Calcareous Alps (Austria). A, Juvavic Nappe System, B, Tyrolic Nappe System.
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25 Based on Golebiowski (1990), Mandl (2000), Donofrio *et al.* (2003), Maslo (2008), Krystyn
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27 *et al.* (2009), Haas *et al.* (2010), Martindale *et al.* (2013a, b) and Krystyn (pers. comm. 2017).
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33 **Figure 4.** Microfacies of the Dachstein Limestone in which *Mystriosuchus steinbergeri* sp.
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35 nov. is embedded. A, bone fragment without any microbial encrustation, in direct contact
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37 with peloidal carbonate sediment, fragments of gastropod shell, sparitic cementation (sample
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39 NHMW1986/0024/0026). B, bone fragment with infillings of the surrounding peloidal
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41 sediment (sample NHMW 1986/0024/0026). C, common facies type with shell fragments in a
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43 peloidal matrix, sparitic cementation (sample NHMW 1986/0024/0027). D, gastropod shell
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45 showing geopetal infilling (sample NHMW 1986/0024/0025). E, echinoid spine,
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47 documenting a marine environment (sample NHMW 1986/0024/0025). F, G, “black
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49 pebbles”, dark-brown stained carbonate extraclasts, fossil in F is *Cayeuxia* sp. (sample
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52 NHMW 1986/0024/0028).
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Figure 5. Holotype skull of *Mystriosuchus steinbergeri* sp. nov. (NHMW 1986/0024/0001) in right lateral (A), posterior (B), medial cross-sectional (C), dorsal (D) and ventral (E) views.

Figure 6. Holotype skull of *Mystriosuchus steinbergeri* sp. nov. (NHMW 1986/0024/0001), line drawings in right lateral (A), posterior (B), medial cross-sectional (C), dorsal (D) and ventral (E) views. Abbreviations: ant.fen, antorbital fenestra; bsptg, basiptyergoid process; ch, choana; ect, ectopterygoid; exn, external naris; f, frontal; jg, jugal; lc, lacrimal; lpmx, left premaxilla; ltf, laterotemporal fenestra; max, maxilla; n, nasal; pa, parietal; op.sq, opisthotic process of the squamosal; pal, palatine; pf, postfrontal; po, postorbital; pop, paraoccipital process; ppsq, parietal process of the squamosal; prf, prefrontal; ptg, pterygoid; ptoc.fen, pteroccipital fenestra; qd, quadrate; qdf, quadrate foramen; qdj, quadratojugal; rpmx, right premaxilla; smx, septomaxilla; sns, sinus; so.fen, suborbital fenestra; sq, squamosal; stf, supratemporal fenestra; sut.fen, subtemporal fenestra.

Figure 7. Referred partial skull and probably associated partial mandible (NHMW 1986/0024/0005, NHMW 1986/0024/00016) of *Mystriosuchus steinbergeri* sp. nov. The specimen is preserved in two blocks, which are shown in articulation in A, whereas in B and C the smaller of the blocks (containing the post-premaxilla part of the skull) is shown separately. A, skull in ventral view, with probably associated partial mandible. B, right lateral view of preserved post-premaxilla part of the skull. This surface articulates with the other block that forms this specimen (see A). C, ventral view of preserved post-premaxilla part of the skull. Abbreviations: ant.fen, antorbital fenestra; cho, choana; ect, ectopterygoid; exn, external naris; imp.pmx, impression of the premaxillae; lect, left ectopterygoid; lmax, left maxilla; lpmx, left premaxilla; ltf, laterotemporal fenestra; mnd, mandible; orb, orbit; pal,

palatine; pmx, premaxillae; ptg, pterygoid; rmax, right maxilla; so.fen, suborbital fenestra; v, vomers.

Figure 8. Referred partial skull and probably associated mandibular remains (NHMW 1986/0024/0006a, b) of *Mystriosuchus steinbergeri* sp. nov. A, partial skull (NHMW 1986/0024/0006b) in ventral view. B, mandibular material (NHMW 1986/0024/0006a). Abbreviations: alv, alveoli; ch, choana; ect, ectopterygoid; jg-qdj, jugal-quadratojugal bar; l.alv, last alveolus; pal, palatine; pmx, premaxillae; ptg, pterygoid; qd, quadrate; so.fen, suborbital fenestra; sut.fen, subtemporal fenestra.

Figure 9. Paired anterior premaxillae (NHMW 1986/0024/0004) of *Mystriosuchus steinbergeri* sp. nov. in ventral (A), left lateral (B), right lateral (C) and dorsal (D) views.

Figure 10. Articulated mandibles (NHMW 1986/0024/0002), missing posterior end of right mandible, of *Mystriosuchus steinbergeri* sp. nov. A, dorsal view. B, left dorsolateral view. C, dorsal view of the symphyseal region. D, lateral view of the right external mandibular fenestra. Abbreviations: emf, external mandibular fenestra; gl, glenoid; il, ilium; ret, retroarticular process.

Figure 11. Humeri of *Mystriosuchus steinbergeri* sp. nov. NHMW 1986/0024/0007, nearly complete left humerus, in anterior (A), lateral (B), posterior (C), and medial (D) views. NHMW 1986/0024/0008, proximal end of a left humerus, in anterior (E) and posterior (F) views. NHMW 1986/0024/0009, distal end of a left humerus, in posterior (G) and anterior (H) views. Abbreviations: dpc, deltopectoral crest; ectg, ectepicondylar groove; msc, muscle scar; sup, supinator process.

Figure 12. Left ulnae of *Mystriosuchus steinbergeri* sp. nov. NHMW 1986/0024/0010 in lateral (A) and medial (B) views. NHMW 1986/0024/0011 in lateral (C) and medial (D) views.

Figure 13. Left ilium (NHMW 1986/0024/0003) of *Mystriosuchus steinbergeri* sp. nov. in lateral view. Abbreviation: saf, supraacetabular flange.

Figure 14. Femora of *Mystriosuchus steinbergeri* sp. nov. NHMW 1986/0024/0012, complete right femur, in anterolateral (A), medial (B), proximal (C), distal (D), posteromedial (E) and lateral (F) views. NHMW 1986/0024/0013, proximal right femur, in posteromedial (G), anterolateral (H) and proximal (I) views. Asterisks in G and H mark the plane of the histological cross section shown in Figure 17. Abbreviations: cf, attachment site for the caudofemoralis musculature; pmt, posteromedial tuber.

Figure 15. Left tibia (NHMW 1986/0024/0014) and osteoderm (NHMW 1986/0024/0015) of *Mystriosuchus steinbergeri* sp. nov. Left tibia in medial (A), proximal (B), distal (C) and lateral (D) views. Osteoderm in dorsal (E) and ventral (F) views.

Figure 16. Thin-section images of femur shaft (NHMW 1986/0024/0013) in normal transmitted light. A, thick and well-preserved part of the cortex composed of parallel-fibred bone tissue in the anterior (up) and medial (left) quadrants. Note that lines of arrested growth (LAGs) are marked with white arrow heads and numbers. B, Close-up of thick transitional zone in lateral quadrant showing numerous erosion cavities and secondary osteons. C, close-up of the longitudinal and reticular vascularisation of the parallel-fibred bone tissue.

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Abbreviations: eb, endosteal bone; ec, erosion cavity; mc, medullary cavity; pfb, parallel-fibred bone; po, primary osteon; so, secondary osteon; svc, simple vascular canal.

Figure 17. Strict consensus of eight most parsimonious trees from Jones & Butler (2018). Positions of *Mystriosuchus steinbergeri* sp. nov. and the genus *Mystriosuchus* are indicated.

Figure 18. Life reconstruction of *Mystriosuchus steinbergeri* sp. nov. in the Dachstein Limestone depositional environment. Copyright Mark Witton.

For Review Only

Figure 1. Photographs taken in 1982 during the collection of the type and referred material of *Mystriosuchus steinbergeri* sp. nov. A, the type locality. The five figures in the centre of the photograph are clustered around the excavation site. B, the excavation team, including from left-to-right, Johann Segl, Sepp Steinberger, Georg Sverak and Walter Prenner. Georg Sverak is using the pneumatic hammer to drill a hole for a wedge used to split the blocks of limestone for removal. C, Georg Sverak and Walter Prenner in front of their tent. D, photograph of the block, as originally excavated, including the holotype skull (NHMW 1986/0024/0001; bottom right of photograph) and paratype mandible (NHMW 1986/0024/0002; top middle of photograph) in close association.

165x110mm (300 x 300 DPI)

Figure 2. Extent of Late Triassic platform carbonates in the central part of the Northern Calcareous Alps (Austria), with the type locality of *Mystriosuchus steinbergeri* sp. nov. Note the tectonic deformation by thrusts and faults. Based on the geological map of Upper Austria 1:200.000 (Krenmayr and Schnabel 2006).

166x111mm (300 x 300 DPI)

226x166mm (300 x 300 DPI)

Figure 4. Microfacies of the Dachstein Limestone in which *Mystriosuchus steinbergeri* sp. nov. is embedded. A, bone fragment without any microbial encrustation, in direct contact with peloidal carbonate sediment, fragments of gastropod shell, sparitic cementation (sample NHMW1986/0024/0026). B, bone fragment with infillings of the surrounding peloidal sediment (sample NHMW 1986/0024/0026). C, common facies type with shell fragments in a peloidal matrix, sparitic cementation (sample NHMW 1986/0024/0027). D, gastropod shell showing geopetal infilling (sample NHMW 1986/0024/0025). E, echinoid spine, documenting a marine environment (sample NHMW 1986/0024/0025). F, G, "black pebbles", dark-brown stained carbonate extraclasts, fossil in F is *Cayeuxia* sp. (sample NHMW 1986/0024/0028).

166x226mm (300 x 300 DPI)

Figure 5. Holotype skull of *Mystriosuchus steinbergeri* sp. nov. (NHMW 1986/0024/0001) in right lateral (A), posterior (B), medial cross-sectional (C), dorsal (D) and ventral (E) views.

165x165mm (600 x 600 DPI)

Figure 6. Holotype skull of *Mystriosuchus steinbergeri* sp. nov. (NHMW 1986/0024/0001), line drawings in right lateral (A), posterior (B), medial cross-sectional (C), dorsal (D) and ventral (E) views. Abbreviations: ant.fen, antorbital fenestra; bsptg, basipterygoid process; ch, choana; ect, ectopterygoid; exn, external naris; f, frontal; jg, jugal; lc, lacrimal; lpmx, left premaxilla; ltf, laterotemporal fenestra; max, maxilla; n, nasal; pa, parietal; op.sq, opisthotic process of the squamosal; pal, palatine; pf, postfrontal; po, postorbital; pop, paraoccipital process; ppsq, parietal process of the squamosal; prf, prefrontal; ptg, pterygoid; ptoc.fen, pteroccipital fenestra; qd, quadrate; qdf, quadrate foramen; qdj, quadratojugal; rpmx, right premaxilla; smx, septomaxilla; sns, sinus; so.fen, suborbital fenestra; sq, squamosal; stf, supratemporal fenestra; sut.fen, subtemporal fenestra.

182x175mm (300 x 300 DPI)

Figure 7. Referred partial skull and probably associated partial mandible (NHMW 1986/0024/0005, NHMW 1986/0024/00016) of *Mystriosuchus steinbergeri* sp. nov. The specimen is preserved in two blocks, which are shown in articulation in A, whereas in B and C the smaller of the blocks (containing the post-premaxilla part of the skull) is shown separately. A, skull in ventral view, with probably associated partial mandible. B, right lateral view of preserved post-premaxilla part of the skull. This surface articulates with the other block that forms this specimen (see A). C, ventral view of preserved post-premaxilla part of the skull. Abbreviations: ant.fen, antorbital fenestra; cho, choana; ect, ectopterygoid; exn, external naris; imp.pmx, impression of the premaxillae; lect, left ectopterygoid; lmax, left maxilla; lpmx, left premaxilla; ltf, laterotemporal fenestra; mnd, mandible; orb, orbit; pal, palatine; pmx, premaxillae; ptg, pterygoid; rmax, right maxilla; so.fen, suborbital fenestra; v, vomers.

165x125mm (300 x 300 DPI)

Figure 8. Referred partial skull and probably associated mandibular remains (NHMW 1986/0024/0006a, b) of *Mystriosuchus steinbergeri* sp. nov. A, partial skull (NHMW 1986/0024/0006b) in ventral view. B, mandibular material (NHMW 1986/0024/0006a). Abbreviations: alv, alveoli; ch, choana; ect, ectopterygoid; jg-qdj, jugal-quadrate; jg-qdj, jugal-quadrate; l.alv, last alveolus; pal, palatine; pmx, premaxillae; ptg, pterygoid; qd, quadrate; so.fen, suborbital fenestra; sut.fen, subtemporal fenestra.

165x121mm (600 x 600 DPI)

Figure 9. Paired anterior premaxillae (NHMW 1986/0024/0004) of *Mystriosuchus steinbergeri* sp. nov. in ventral (A), left lateral (B), right lateral (C) and dorsal (D) views.

165x143mm (600 x 600 DPI)

Figure 10. Articulated mandibles (NHMW 1986/0024/0002), missing posterior end of right mandible, of *Mystriosuchus steinbergeri* sp. nov. A, dorsal view. B, left dorsolateral view. C, dorsal view of the symphyseal region. D, lateral view of the right external mandibular fenestra. Abbreviations: emf, external mandibular fenestra; gl, glenoid; il, ilium; ret, retroarticular process.

165x225mm (600 x 600 DPI)

Figure 11. Humeri of *Mystriosuchus steinbergeri* sp. nov. NHMW 1986/0024/0007, nearly complete left humerus, in anterior (A), lateral (B), posterior (C), and medial (D) views. NHMW 1986/0024/0008, proximal end of a left humerus, in anterior (E) and posterior (F) views. NHMW 1986/0024/0009, distal end of a left humerus, in posterior (G) and anterior (H) views. Abbreviations: dpc, deltopectoral crest; ectg, ectepicondylar groove; msc, muscle scar; sup, supinator process.

165x171mm (600 x 600 DPI)

Figure 12. Left ulnae of *Mystriosuchus steinbergeri* sp. nov. NHMW 1986/0024/0010 in lateral (A) and medial (B) views. NHMW 1986/0024/0011 in lateral (C) and medial (D) views.

165x118mm (600 x 600 DPI)

Figure 13. Left ilium (NHMW 1986/0024/0003) of *Mystriosuchus steinbergeri* sp. nov. in lateral view.
Abbreviation: saf, supraacetabular flange.

165x69mm (300 x 300 DPI)

Figure 14. Femora of *Mystriosuchus steinbergeri* sp. nov. NHMW 1986/0024/0012, complete right femur, in anterolateral (A), medial (B), proximal (C), distal (D), posteromedial (E) and lateral (F) views. NHMW 1986/0024/0013, proximal right femur, in posteromedial (G), anterolateral (H) and proximal (I) views. Asterisks in G and H mark the plane of the histological cross section shown in Figure 17. Abbreviations: cf, attachment site for the caudofemoralis musculature; pmt, posteromedial tuber.

165x96mm (600 x 600 DPI)

Figure 15. Left tibia (NHMW 1986/0024/0014) and osteoderm (NHMW 1986/0024/0015) of *Mystriosuchus steinbergeri* sp. nov. Left tibia in medial (A), proximal (B), distal (C) and lateral (D) views. Osteoderm in dorsal (E) and ventral (F) views.

165x116mm (300 x 300 DPI)

Figure 16. Thin-section images of femur shaft (NHMW 1986/0024/0013) in normal transmitted light. A, thick and well-preserved part of the cortex composed of parallel-fibred bone tissue in the anterior (up) and medial (left) quadrants. Note that lines of arrested growth (LAGs) are marked with white arrow heads and numbers. B, Close-up of thick transitional zone in lateral quadrant showing numerous erosion cavities and secondary osteons. C, close-up of the longitudinal and reticular vascularisation of the parallel-fibred bone tissue. Abbreviations: eb, endosteal bone; ec, erosion cavity; mc, medullary cavity; pfb, parallel-fibred bone; po, primary osteon; so, secondary osteon; svc, simple vascular canal.

104x218mm (300 x 300 DPI)

Figure 17. Strict consensus of eight most parsimonious trees from Jones & Butler (2018). Positions of *Mystriosuchus steinbergeri* sp. nov. and the genus *Mystriosuchus* are indicated.

Figure 18. Life reconstruction of *Mystriosuchus steinbergeri* sp. nov. in the Dachstein Limestone depositional environment. Copyright Mark Witton.

2822x1763mm (72 x 72 DPI)