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From Toad to Frog, a CT-based Reconsideration of *Bufo servatus*, an Eocene
Anuran mummy from Quercy (France)

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RH: LEMIERRE ET AL.—EOCENE ANURAN FROM FRANCE

ABSTRACT—In the XIXth century, natural mummies of amphibians were discovered in the Quercy Phosphorites. The specific collection site was never formally reported, which hampers precise dating of these specimens. Still, the name *Bufo servatus* was erected based on the external morphology of one of the mummified specimen.

A tomography of similarly preserved specimen revealed a preserved skeleton, soft-tissues and gut contents. We analyze here the holotype of *Bufo servatus* using CT-scanning in order to investigate its potentially preserved internal features. Like the previous specimen, a subcomplete articulated skeleton was identified in the *B. servatus* holotype. Surprisingly, this skeleton is almost identical to that of *Thaumastosaurus gezei*, an Eocene anuran from Western Europe to which other specimens from this mummy series were previously assigned. The few differences between the specimen skeletons highlight ontogenetic and intraspecific variations, making *T. gezei* a junior synonym of *B. servatus* and creating the new combination *Thaumastosaurus servatus*. Given its association with previously described Quercy specimens, this redescribed anuran is probably from the same time interval as *T. gezei*.

Previous phylogenetic analyses assigned *T. servatus* to Ranoides, with natatanuran affinities. Using data from this newly described specimen, we tested here further its taxonomic affinities. Our analyses confirm this position, and formally identify *T. servatus* as a Natatanuran member of Pyxicephalidae (currently endemic of Equatorial Africa) and more precisely, a stem-Pyxicephalinae. This result confirms the origin of *Thaumastosaurus*, a member of the African herpetofauna occupying Western Europe before the Grande Coupure at the Eocene/Oligocene transition.

INTRODUCTION

The Quercy Phosphorites consist of an extensive series of limestones fissures within the Quercy plateau (southwestern France) that are infilled with clayey phosphates (Fig. 1A-B; Pélissié and Sigé, 2006). Mining of these phosphates for use as fertilizer began in 1871, with the number of active quarries expanding until 1886 when the operations began to decline. Almost all quarries were closed by 1893 (Thevenin, 1903; Gèze, 1949). The Quercy Phosphorites quickly became known for their highly diverse assemblages of vertebrate fossils (e.g., Filhol, 1877) whose ages range from the Early Eocene to Early Miocene (Sigé et al., 1991; Legendre et al., 1992) but with a concentration between the Middle-Late Eocene to the Late Oligocene. This age distribution makes these fossils especially valuable for understanding the role of climate change in the “Grande Coupure” – the faunal turnover and moderate extinction event that marks the approximately 33.9 Ma Eocene-Oligocene transition (Stehlin, 1909).

The Quercy Phosphorites are best known for their highly diverse mammalian fauna (Pélissié and Sigé, 2006) and great density of amphibians (Rage, 2006), both of which are based largely on disarticulated skeletons. However, four anurans, an urodele and six snake fragments present exceptionnaly well-preserved tissues in 3D (Laloy et al. 2013; Tissier et al. 2016, 2017). At the time of their initial description in the late 1800s, only the external soft-tissues were known and they were referred to as “natural mummies” (see e.g. Filhol, 1877 for a brief description of the anuran skin). They were originally given or sold to Professor Henri Filhol by A. Lafont (or Lafon), a pharmacist in Villeneuve (Aveyron, France; see Fig. 1C) during the early 1870s (see first mention in Filhol, 1873). They remained part of the private collection of H. Filhol, which housed numerous fossils from the Quercy, including the holotypes of the taxa he erected until his sudden death in 1903. Edmond J. de Rothschild then bought the entire collection to prevent its dispersal and donated it to the MNHN the same year

(1903). Given their striking aspect, they were placed in the paleontological gallery of the Museum, where they remain visible to the public even now.

Reliant wholly on external morphological features, early studies assigned the anuran mummies to two different species, *Rana plicata* and *Bufo servatus* (Filhol, 1876, 1877). In the 2010s, two amphibian mummies were further analyzed using classical micro-computed tomography (on the anuran MNHN.F.QU17279; Laloy et al., 2013) and synchrotron light micro-computed tomography (on the urodele MNHN.F.QU17755; Tissier et al., 2016, 2017). Both studies evidenced internal subcomplete and articulated skeletons, soft tissues (e.g. organs) and diet contents, facilitating more complete redescriptions and assessments of their phylogenetic affinities (Laloy et al., 2013; Tissier et al., 2016). MNHN.F.QU17279, initially described by Filhol (1876) under the name *Rana plicata*, turned out to be the most complete specimen of the Eocene *Thaumastosaurus gezei* Rage and Roček, 2007, previously known only from a subcomplete skull and fragmentary remains (Rage and Roček, 2007). Later, a second mummy (MNHN unnumbered) was also assigned to *T. gezei*, based on external shape and a few visible dermal bones (Rage, 2016).

Here we focus on the third anuran specimen discovered in the 1870s and unstudied since the end of the XIXth century: MNHN.F.QU17381. This specimen was originally described as the holotype of “*Bufo servatus*” Filhol 1877. The assignment of this taxon to Bufonidae was questioned by multiple authors (e.g. Sanchiz, 1998; Rage, 2016) as its identification was based only on its external aspect. As for other exceptionally preserved specimens from Quercy, tomography revealed a subcomplete skeleton and soft tissues, enabling us to reassess the identification of MNHN.F.QU17381 and the validity of *B. servatus*. Several phylogenetic analyses are performed on this taxon as a means to discuss its general affinities among anurans. Finally, we discuss the paleobiogeographical and

evolutionary implications of these phylogenetic conclusions and their impact on the anuran fossil record.

GEOLOGICAL CONTEXT

Locality—The specimen MNHN.F.QU17381, like the other Quercy “mummies” (Filhol, 1877), is part of the MNHN ‘old collection’ lacking information on its original location and stratigraphic assignment. However, the brief descriptions given by Filhol (Filhol, 1873, 1876, 1877) seem to indicate that all mummies come from a single quarry. We conclude that this quarry most likely belongs to one of the two localities discussed below.

The first locality is the town of Villeneuve (Fig. 1), where the first seller (A. Lafont) lived. The hypothesis that this locality produced the mummies is supported by the statement of Filhol (1873) that the series came from the department of Aveyron. This information was also repeated in at least two local newspapers. Both the “Journal de l’Aveyron” and the “Journal de Villefranche” published an identical small article in January 1874 based on a talk given by Filhol in Paris (1873) that placed this discovery in Aveyron. Moreover, Filhol mentioned in his talk that he had just received the fossils. It is possible that he indicated Aveyron as the origin of the mummies simply because the seller came from this place.

Near Villeneuve, approximately ten quarries are known (Fig. 1C, gray squares). Among them, one (Vielase) can be ruled out due to the nature of the phosphatic matrix, a tectonized karstic breccia (Simon-Coicon and Astruc, 1991; Legendre et al., 1992) that is clearly incompatible with the observed thin-scale phosphate replacement of the animal structures. Only one tunnel in Vielase could have housed phosphatic fillings, but it is now

inaccessible, and no information exists anymore on this tunnel (T. Péliissié, pers. com). The remaining quarries are either azoic, or devoid of any phosphatic matrix still in place for comparison.

The second locality is the village of Escamps in the Lot department (Fig. 1C). This locality was first mentioned in a local newspaper, the “Journal du Lot” on January 13th, 1874, in an article that discussed a future talk by Filhol at the ‘Société des Sciences Physiques et Naturelles de Toulouse’. Filhol indeed presented on February 6th, 1874 some exquisitely preserved fossil of anurans coming from a quarry in the Lot. The Bulletin of the above-mentioned Society gives an account of this talk, mentioning three anuran fossils (Jeanbernard, 1874). These three fossils can only correspond to the mummy series. The apparent change in the locality of origin for these fossils that occurred between Filhol’s talk in Paris (Filhol, 1873) and southern France (Toulouse) could reflect new information he received from the seller—after his 1873 talk at the Academy of Sciences (Paris). In addition to the press releases and society bulletin, there is a local memory of a discovery of a “stone” anuran in the village of Escamps, dating back to the late XIXth century (T. Péliissié and E. Cassan pers. com. October, 2020). A young miner, Emile Dutheil discovered a stony anuran corresponding to the mummy description inside a cavity in a quarry near the town, either in the site ‘les Rosières’ or ‘les Tempories’ (Fig. 1C). This fossil was soon exchanged against a bottle of wine and might have ended in the hands of A. Lafont. The other mummies might have been discovered shortly thereafter. Six sites are regrouped under the name ‘les Rosières’ (Fig. 1C) and are dated from Late Eocene MP17a (37.8 to 37.4 Ma) to MP19 (34.5 to 33.5 Ma; Aguilar et al., 1997; Vandenberghe et al., 2012). They have been partially studied in the previous decades (Remy et al., 1987), without any discovery of a new mummy. The other site, ‘les Tempories’ is dated from the MP19 (Late Eocene, 34.5–33.5 Ma). In situ layers of phosphorites are still visible today (T. Péliissié pers. com.) but most of the site was drained

during its exploitation and later used as a landfill. If the series came from a layer within the quarry, this layer may have been completely cleared out more than a century ago.

Another possibility is that the series came from elsewhere in the Lot. Fossils discovered in these quarries were often appreciated by local notables and thus experienced local dispersement through exchanges or sales with surrounding towns and villages. Some of these fossils were then sold to known museum curators or even exchanged for favors (T. Pélissié pers. com.).

Until a precise account of the MNHN.F.QU17381 discovery is found that includes locality information, each of these provenance hypotheses will remain somewhat viable with its geographic (and stratigraphic) origins somewhat ambiguous. The strongest support is for the locality of Escamps, especially given the local memory of such a discovery, which does not occur in the vicinity of Villeneuve. We putatively identify the locality as the village of Escamps, Lot (France) and assign a Late Eocene age to the mummy series.

Stratigraphic Range—The genus *Thaumastosaurus* (to which two of the mummies have been attributed so far) is known from various localities in Western Europe (Vasilyan, 2018). The earliest remains of *Thaumastosaurus* are from the MP16 (Late Middle Eocene ~39.5 Ma) from two Swiss localities, and the genus is present throughout the Late Eocene, with most of the localities located in the Quercy Phosphorites. The geologically most recent record of *Thaumastosaurus* is from the MP20 (~33.5 Ma, Priabonian, latest Eocene) from Escamps, in France. The complete list of the localities where *Thaumastosaurus* has been identified was compiled by Vasilyan (2018: table S1).

A recent study presented disarticulated bones from the Upper Turonian (Early Late Cretaceous) and attributed a fragmentary maxilla to *Thaumastosaurus* (Ősi et al., 2019: fig. 6A–E) and a vertebra to an *Anura* indet. The tentative attribution of the vertebra to

Thaumastosaurus is based on the presence of a ventral keel also possibly present in *T. gezei* (Laloy et al., 2013: fig. 5C; Ősi et al., 2019: fig. 6F–G). However, this ventral keel is actually the ridge of the neural spine, visible by transparency. In addition, in the vertebral column of MNHN.F.QU17381, there is no ventral keel on the vertebrae (see below). Furthermore, given the fragmentary state of this vertebra, the specimen cannot be attributed to a more exclusive clade than Batrachia (Duellman and Trueb, 1994; Tissier et al., 2016). Also, the ornamentation composed of irregular pits and ridges on the maxilla described by Ősi et al. (2019) occurs in numerous Cretaceous anuran clades (Roček and Nesso, 1993; Roček, 2008; Company and Szentesi, 2012; Báez and Gómez, 2018) as well as more recent anurans and other vertebrate taxa (e.g. squamates, crocodilians, various early stegocephalians; Buffrénil et al., 2015) and is therefore not diagnostic of *Thaumastosaurus*. Finally, the oval foramen located near the processus pterygoideus (if the fragmentary element is indeed a maxilla) as mentioned by Ősi et al. (2019) is present in other anurans (Biton et al., 2016). This makes the attribution of these Upper Cretaceous fragments to the Eocene *Thaumastosaurus* unlikely and currently unsupportable. Instead, these specimens may belong to a wide range of Mesozoic anuran clades. We therefore conclude that *Thaumastosaurus* has a stratigraphical range from the Late Middle Eocene (~39.5 Ma) to the Terminal Late Eocene (~33.5 Ma).

MATERIALS AND METHODS

Institutional Abbreviations—IC2MP: Institut de Chimie des Milieux et Matériaux de Poitiers, Poitiers, France; **MHNT.PAL:** Muséum d’histoire Naturelle de Toulouse, Toulouse, France; **MNHN:** Muséum National d’Histoire Naturelle, Paris, France; **MNHN.F.QU:** Collection number for specimens from the ‘old’ Quercy Phosphorites

collection, located within the paleontological collection of the MNHN; **NHMB**: Naturhistorisches Museum Basel, Basel, Switzerland; **UM. PRR**: Université de Montpellier, France, specimens from the Perrière site.

The mummy MNHN.F.QU17381, currently displayed in the paleontology gallery of the National Natural History Museum in Paris (France), was micro-CT scanned at the PLATINA Plateforme Instrumentale d'Analyses (PLATINA platform) at the IC2MP (Poitiers, France). A microfocus beam of 160 kV of the CT-scanner was used with the following parameters: voltage, 130 kV; current, 180 μ A; voxel size, 0.024 μ m; slice resolution, 1346 $\times$ 2525 pixels. A total of 1750 virtual slices showing internal structures were reconstructed using XAct (RX solution). These slices were imported in the 3D reconstruction software Mimics 21.0 (Materialise, Leuven, Belgium). Before the importation, the slices were cropped to maximally remove the empty spaces. To decrease data size, slices were converted from 16 to 8 bits. The dataset thus includes 1256 slices with an image resolution of 1527 $\times$ 2391 pixels and a voxel size of 2.4 μ m for the volume file (see Appendix S1 in Supplement Data 1). The 3D model was produced by segmentation of each bone using the 'thresholding' function (using the contrast on greyscale images). We used the same voxel resolution of 2.4 μ m, with a smoothing factor of 3 for one iteration, to homogenize the model resulting from manual segmentation. Data produced by segmentation were exported in the software 3matic 9.0 as a separate file (see Appendix S2 in Supplement Data 1).

Tomography revealed the internal preservation of soft tissues replicated in calcium phosphate (e.g. part of the brain and of the spinal cord, potential muscles and nerves). Unfortunately, most of the soft internal structures are either too degraded, or too similar to other structures in density and/or capacity to absorb X-rays (resulting in poor contrast) to be confidently segmented and described here. The external structures will be described in detail in a future study (N. Robin, unpublished data) and are only briefly presented here; our

description focuses on the skeleton. The skull preserved inside the mummy lost its anteriormost region (snout) but is otherwise complete. Some hyobranchial bones are preserved, along with many postcranial bones, excepting the limbs and pelvic girdle (Fig. S1). An isolated ilium (UM.PRR 2002) collected in 1984 (Rage, 1984a) was recently attributed to *Thaumastosaurus* (Vasilyan, 2018) and was used here for phylogenetic analysis. This is justified given the remarkable similarity of the postcranial skeleton of the two species of *Thaumastosaurus* described in the Quercy, *T. gezei* Rage & Roček, 2007 and *T. botti* De Stefano, 1903 (Vasilyan, 2018).

The anatomical terminology used herein is based on Roček (1980) and Biton et al. (2016) for cranial features, Roček et al. (2016) for the middle ear apparatus, Sanchiz (1998) for postcranial ones, Gardener et al. (2010) for iliac characters.

Phylogenetic Analyses—Our data matrix includes 85 taxa and 143 morphological characters (62 cranial and 68 postcranial characters, 12 from the hyobranchial apparatus, and one from soft-tissues) and is derived from that of Báez and Gómez (2018; see Appendix S3 in Supplement Data 1 for the list of characters). We added 14 new extant natatanuran taxa (see Appendix S4 in Supplement Data 1) to better represent the major natatanuran clades inferred from recent molecular phylogenies (Frost et al., 2006; Pyron and Wiens, 2011; Jetz and Pyron, 2018). The new taxa were scored from both literature (Procter, 1919; Clarke, 1981; Scott, 2005; Evans et al., 2014) and 3D-models available on MorphoSource by the Blackburn Laboratory (Florida, USA) as part of the OVert program (Cross, 2017; for more information see the website: <https://www.floridamuseum.ufl.edu/overt/>).

All analyses were performed using TNT v.1.5 (Goloboff and Catalano, 2016). Half of the analyses was performed using equal weighting, whereas the other half was performed using implying weighting. Some analyses were conducted with all characters unordered and others with cline characters ordered (characters 3, 9, 10, 14, 26, 34, 51, 52, 68, 93, 112, 121,

124, 125 and 126), with or without topological constraints. All analyses consisted of heuristic searches with 1000 random addition sequences of taxa, followed by tree bisection reconnection (TBR) branch swapping, holding 10 trees per repetitions. The final trees were rooted on *Ascapthus truei* (Ascaphidae) and, when more than one tree was obtained, a strict consensus was obtained.

Implied weighting was used to minimize the influence of homoplastic characters in the dataset, and achieved a better resolution of the different uncertainties recovered in the analysis under equal weighting (Goloboff, 1993, 1997), mostly for morphological characters (Goloboff et al., 2018a) and several values of k were used ($k = 1-20$) to assess sensitivity of the results due to variations of the strength of the function (Goloboff et al., 2008). Some controversies remain on the effectiveness of this method, especially when compared to Bayesian models (O'Reilly et al., 2016; Congreve and Lamsdell, 2016; Puttick et al., 2017), but some recent evidence indicates implied weighting performs well (Goloboff et al., 2018a, b). Consequently, we chose to use both equal and implied weighting parsimony methods and then compare their results. Cline characters were ordered in all but one analysis (see Appendix S5 in Supplement Data 1), as recent studies (Rineau et al., 2015, 2018) have shown that analyses using ordered morphocline characters outperformed analyses using unordered characters even if the ordering scheme includes some errors (Rineau et al., 2018). Constrained analyses were performed with ordered characters including both equal and implied weights ($k = 7$), using the topology of Jetz and Pyron (2018) as a constraint for extant taxa (Fig. S2). The same was done using the topology (Fig. S3) presented in Feng et al. (2017), with extinct taxa as floating taxa, in both cases. Node supports were expressed using Bremer support and standard bootstrap, with traditional searches of 1000 replicates, collapsing groups below 5% frequency. Bremer support uses tree fit score (Bremer, 1994; Goloboff and Farris, 2001). However, in

implied weighting analyses, Bremer support is expressed in fractions due to the different weights that reflect the character fit (Goloboff, 1997; Jones and Butler, 2018).

SYSTEMATIC PALEONTOLOGY

ANURA Duméril, 1805

NEOBATRACHIA Reig, 1958

RANOIDES Frost et al., 2006

NATATANURA Frost et al., 2006

PYXICEPHALOIDEA Bonaparte, 1850

PYXICEPHALIDAE Bonaparte, 1850

PYXICEPHALINAE Bonaparte, 1850

Genus *THAUMASTOSAURUS* De Stefano, 1903

Type Species—*Thaumastosaurus bottii* De Stefano, 1903

Revised Diagnosis—Hyperossified natatanuran exhibiting cranial ornamentation, composed of pits and ridges, on the frontoparietals, maxillae, nasals, squamosals and sphenethmoid; the paired nasals and frontoparietals co-ossified with each other respectively and with the sphenethmoid and prooticoccipital (frontoparietals only), rhomboid dorsal fenestra on the skull allowing a dorsal exposure of the sphenethmoid; palatines (neopalatines of Trueb, 1973) present, in medial contact with each other (by their medial margin); anterior tip of the cultriform process of the parasphenoid does not extend between palatines; processus

posterolateralis and ramus paroticus of squamosal merged, articulating with the crista parotica of the otic capsules; arteria occipitalis of either side piercing the frontoparietal; medial ramus of the pterygoid well-developed, overlapping the parasphenoid alae; zygomatic ramus (lamella alaris + processus maxillaris) of the squamosal well-developed, articulating with the maxilla.

Differs from *Pyxicephalus* Tschudi, 1838 and *Aubria* Boulanger, 1917 in lacking fang-like lamellar projections on the dentaries, in having the alary process of the premaxillae oriented dorsally (posterodorsally oriented in *Pyxicephalus* and *Aubria*), the craniomandibular joint at the same level as the occiput (posterior to the occiput in *Pyxicephalus* and *Aubria*) and the clavicles oriented anteromedially to the sagittal axis (perpendicular to the sagittal axis in *Pyxicephalus* and *Aubria*).

Differs further from *Pyxicephalus* in having the alae of the parasphenoid perpendicular to its cultriform process (posterior to the cultriform process in *Pyxicephalus*), a large dorsal exposure for the sphenethmoid (in *Pyxicephalus*, the sphenethmoid is not visible in dorsal view), cotyles of the atlas fully confluent (Type III of Lynch, 1971 (instead of juxtaposed Type II in *Pyxicephalus*), bicuspid teeth on the maxillae (monocuspid teeth on the maxillae in *Pyxicephalus*) and in lacking a lateral wall of the neurocranium ossified around the optic foramen (lateral wall ossified around the optic foramen in *Pyxicephalus*).

Differs from *Aubria* in having a distinct postchoanalis processus of the vomers (no distinct process in *Aubria*).

THAUMASTOSAURUS SERVATUS Filhol, 1877 comb. nov.

Bufo servatus Filhol, 1877:493, fig. 412 (413 in error) of Filhol (1877), MNHN.F.QU17381 (original description).

Bufo serratus Filhol, 1876: 28, Filhol, 1877: fig. 412 (413 in error) (nomen nudum)

Rana plicata Filhol, 1876: 27, Filhol, 1877:figs. 401, 402, 404, 405.

Thaumastosaurus gezei Rage and Roček, 2007, figs 1, 7A.

Rana cadurcorum Martín et al., 2012: 163. Filhol, 1877: figs. 401, 402, 404, 405 (new combination).

Holotype—The holotype is MNHN.F.QU17381, a nearly complete specimen lacking the snout, appendages and pelvic region. Unrecorded locality (likely Escamps) of the Quercy Phosphorites, southwestern France. Age uncertain, but probably late Middle to Late Eocene.

Referred Specimens—MNHN.F.QU17748, right squamosal missing anterior tip of lamella alaris (Rage and Roček, 2007: fig. 2); MNHN.F.QU17376, holotype of *Thaumastosaurus gezei*, articulated skull missing anterior end, right side of palate, much of the right cheek region, parts of parasphenoid and both otic capsules (Rage and Roček, 2007: figs. 1, 7A); MNHN.F.QU17279, holotype of *Rana plicata*, nearly complete specimen lacking the appendages and pelvic region (Laloy et al., 2013:fig.1A–C); MNHN.F.QU17280, forelimb (Laloy et al., 2013: fig. 1D, E); MNHN unnumbered, specimen preserving the head and part of the trunk.

Revised Diagnosis—Differs from *T. wardi* by having a longer anterior extension of the squamosal alongside the dorsal margin of the maxilla, forming the whole ventral margin of the orbit; a medial margin of the lamina horizontalis of the maxilla convex rather than flat in medial view and in having the ridge separating the fossa maxillaris from the posterior part of the maxillae oriented posteriorly (instead of anteriorly).

Differs from *T. bottii* by having an elongate and slender medial process of the premaxillae, no ventral longitudinal ridge on this same process, and a groove for the vena jugularis interna shallower and wider.

DESCRIPTION

External Preservation—As part of the Quercy old collection mummies, MNHN.F.QU17381 displays an exceptional three-dimensional preservation including most of its external soft-tissues replicated in calcium phosphate. These include the two eyeballs (Fig. 2A) and the skin laying over 3D-preserved muscular series (Fig. 2B–F), the striations of which are locally visible ventrally (e.g., right submaxillary muscles) (Fig. 2F). The specimen is about 6 cm from the snout to the sacrum, with its right side almost fully preserved. Hindlimbs and forelimbs are only proximally preserved. Posterior to each of the eyeball, a 1.3 cm long and 0.6 cm wide large ovoid swelling is present (Fig. 2D, represented by a red/gray arrow and outline). This was at first identified as the outer visible deformation of a parotoid gland, typical for bufonids (Duellman and Trueb, 1994). However, other studies cast doubt on the presence of these glands in MNHN.F.QU17381 (Piveteau, 1927; Rage, 2006). The 3D model (Fig. 3) shows that this swelling is caused by the posterior process of the squamosals, which stretches the skin in this area (Fig. 3). This structure might have been caused by desiccation (N. Robin, unpublished data).

The outer tissues of MNHN.F.QU17381 are heterogeneously preserved. The skin is best preserved on the ventral and lateral sides of the specimen with fine sub-millimetric foldings. The latter concentrate on the mandible/maxillary complex, as well as posterior to the eye (Fig. 2B–D). These folds, absent on extant anurans when alive, must result from post-mortem deformation of the outer tissues. Dorsally, the replicated surface tissues reveal a glassy aspect reflecting a different phosphatized texture (Fig. 2C, E). In this region, the skin and inner tissues do not retain their in vivo volume but appear to be collapsed over the spine

and underlying bony structure. The desiccation (or differential chemical transformation) of this dorsal part of the integument during early decay may have occasioned laterally the wrinkling of the skin resulting in observed microfolds. The left eyeball shows at the bottom a clear demarcation of the eye from the surrounding skin membrane (Fig. 2D). Elsewhere, no distinction between the eye and the eyelid is apparent.

Two other specimens of *T. servatus* display this level of exceptional 3D preservation in calcium phosphate. MNHN.F.QU17279 shows well-preserved eyelids covering the eyes fossilized in their original direction (Fig. 4A, C). On this specimen, the skin is more stretched and homogenously preserved over the specimen surface, revealing thinner skin (compared to MNHN.F.QU17381) microfolds and a local bulbous texture that looks original to the structure (Fig. 4A–C). Larger skin ridges extend posteriorly from the eyes onto the dorsal surface of the trunk (Fig. 4B). About 1 mm in width, these skin ridges correspond to the original dorsolateral folds present in many anuran taxa (Duellman and Trueb, 1994), especially in ranoids (e.g. in Pyxicephalidae, see Poynton, 1964; Channing and Baptista, 2013; Channing et al., 2016; see Dubois and Ohler, 2005 for other ranoids). On the left side of the specimen MNHN.F.QU17279, in a region between the posterior process and the postero-lateral side of the squamosal, the skin bears a slight demarcation with a faint outline (Fig. 4C). Given the preservation of the skin on this region (Fig. 4A–C), we do not interpret this delimitation as a reflection of the underlying bones but rather as the borders of the tympanic membrane (Duellman and Trueb, 1994).

The second best-preserved specimen, MNHN.F.QU17376, consists solely of a head whose preservational quality varies gradually from snout (best preserved) to neck (Fig. 4D–E), with visible snout bony ornamentation (part of the nasals; Fig. 4D). Posterolaterally, the skin looks pristine, with bulbous textural components. The aforementioned external aspects indicate that MNHN.F.QU17381 (Fig. 2) may plausibly have undergone a longer period of

decay/exposure time span prior to burial than MNHN.F.QU17279 (Fig. 4A–C) and one comparable with, or shorter than MNHN.F.QU17376 (Fig. 4D–E).

Skull

The skull is incomplete, missing the anteriormost part of the snout and the premaxillae (Figs. 2, 3, 5). The preserved cranial bones are all articulated.

Dermal Bones—The frontoparietals, squamosals, maxillae, nasals and the dorsal part of the sphenethmoid bear an ornamentation composed of deep oval to subcircular pits and ridges with a constant thickness (Fig. 5A). The ornamentation on the sphenethmoid is much less marked than on the other bones.

Frontoparietals—The frontoparietals are fused into a single bone, in the shape of a truncated rhomboid, longer than wide, without any clear trace of a median suture. However, anteriorly, at the posterior end of a deep notch on the midline of the nasal margin, a shallow depression on the dorsal and ventral face seems to mark the limit between the bones (Fig. 6A). Anterolaterally, they articulate with the nasals by the external end of the nasal margin, and anteromedially, with the posteromedial margin of the dorsal exposure of the sphenethmoid. The lateral margin bears on its mid-length an external expansion (a peak), the tectum supraorbitale (Fig. 6A–B). There is no contact between frontoparietals and squamosals (Fig. 5A), but the lateral expansion of the tectum may indicate these two bones were joined by a ligament that would have delimited the posterior margin of the orbit, as observed in some extant anurans (Roček, 1980).

Posteriorly, the frontoparietals are fused to the prooticoccipital complex (Fig. 5D). The processus lateralis of the frontoparietals are difficult to distinguish from the crista parotica of the prootic but seem to form an almost straight margin (Figs. 5A, 6A).

Posterolaterally, the processus paraoccipitalis of the frontoparietals is fused to the dorsal face of the prominentia ducti semicircularis posterioris of the prootic, forming a prominent ridge (Fig. 5D). Medially, the processus paraoccipitalis delimits the foramen for the arteria occipitalis canal (Fig. 5D). As in several extinct and recent anurans (Sanchiz, 1998), the posterior process of the frontoparietals consists of a horizontal lamina. This lamina extends the midlength of the bone posterior margin and forms a small spike-like surface that covers the dorsal exposure of the prooticooccipital (Fig. 6A).

In ventral view, the anterolateral pars contacta is a vertical lamina extending from the ventral surface of the frontoparietals (Fig. 5B) and is fused to the dorsolateral part of the sphenethmoid (Fig. 5B, 6A). The pars contacta increases in size posteriorly, forming a thin vertical lamina that is fused to the prootic ventrally and to the processus lateralis of the frontoparietals dorsally where it covers the prootic anterolaterally (Fig. 5B).

Ventrally, the incrassatio frontoparietalis presents two structures, the facies cerebraalis anterior, and the facies cerebraalis posterior (Fig. 6B). The facies cerebraalis anterior is an unpaired lanceolate structure, extending from the posterior margin of the sphenethmoid/frontoparietals suture. The posterior limit of this structure is not clear. The facies cerebraalis posterior is an unpaired circular impression, located postero-laterally on the left side of the bone. In another mummy (MNHN.F.QU17381), a similar condition was found for the facies cerebraalis anterior, but the facies cerebraalis posterior was a paired circular impression on each side (Laloy et al., 2013: fig. 4D). This condition is reminiscent of ranoids (Jarošová and Roček, 1982). In our specimen, the unpaired condition of the facies cerebraalis posterior might be due to a non-preservation of the impression, or a lesser ossification of the right frontoparietal.

Squamosals—In lateral view, the lamella alaris is arch-shaped; it expands bilaterally at the base and tapers and descends ventrally towards the processus maxillaris (Fig. 6C). It

forms a thin strip of bone separating the maxilla from the orbit (Fig. 5B). This configuration is similar to that of MNHN.F.QU1729, which also bears an elongate thin extension of the lamella alaris (Laloy et al., 2013) but is proportionally shorter than that of the holotype of *Thaumastosaurus gezei* (MNHN.F.QU17376; Rage and Roček, 2007). The anterior end of the lamella alaris forms a shallow groove with the lateral end of the nasal, identified as the groove for the nasolacrimal duct (Fig. 5B).

The processus maxillaris is antero-posteriorly elongated (Fig. 6C). The processus zygomatico-maxillaris of the maxilla is inserted into an incisura lateral to this processus maxillaris, fully overlapping it. This is not visible in lateral view, as it is overlapped by the lamella alaris (Fig. 5B). The orbital margin is concave dorsally, forming the ventral wall of the orbit (Fig. 5A–B). Laterally, the lamella alaris extends posteroventrally into a spike-like extension, reaching the anterior part of the processus posterolateralis of the squamosals.

Medially, the ramus paroticus is a broad dorsoventrally flat lamina, fused to the crista parotica of the otic capsule dorsomedially (Fig. 5A). It narrows medially and ends in an almost straight margin (Fig. 5A). The posterior process of the squamosal is short and rounded distally (Figs. 5A–B, 6B). The processus posterolateralis is elongate and slender. In dorsal view, the surface between the ramus paroticus and the processus posterolateralis is concave (Fig. 5A), and most likely forms the lateral wall of the tympanic cavity (Roček and Lamaud, 1995). The processus posterolateralis bears a medial flange fused to the ramus posterior of the pterygoid, making it difficult to digitally segment them (Fig. 5B–C). The distal end of the processus posterolateralis is fused to the dorsolateral surface of the quadratojugal (Fig. 5B).

Maxillae—The left maxilla is incomplete, lacking its anterior length starting at the level of the processus frontalis. The right maxilla, however, is almost complete, missing only its anterior tip. The posterior process of the maxillae is long, slender and has a groove posteromedially to articulate with the quadratojugal (Figs. 5B, 6D). The processus

pterygoideus, visible in medial view, is short and marked by a small posterior prominence from the lamina horizontalis. This processus delimits ventro-medially a large pit, which faces posteriorly. The lamina horizontalis is straight with a convex medial margin, moderately thickened anteriorly, where it extends onto the dorsal margin of the lamina anterior and develops into an anterodorsal anterior spine (Fig. 6D). Posterior to the processus pterygoideus, the lamina horizontalis narrows considerably, ending in a thin, poorly marked strip extending onto the lower margin of the posterior process of the maxillae (Fig. 6D).

In lateral view, a flattened smooth processus zygomatico-maxillaris and a well-developed processus frontalis are visible dorsally (Fig. 6E). The dorsal margin of the pars facialis is almost straight. A weakly-pronounced notch is visible on the midline of the medial (= inner) surface of the pars facialis (Fig. 6E). This notch was also observed in non-articulated maxillae in *Thaumastosaurus* (Roček and Lamaud, 1995; Vasilyan, 2018). The recessus vaginiformis is overlapped by a medial crista extending up to the tip of the processus frontalis. Anteriorly, the fossa maxillaris is shallow (Fig. 6D).

The ventral margin of the lamina horizontalis delimits the base of the crista dentalis up to a triangular anterior facet of the maxillae in medial view (articulation of the premaxilla; Roček and Lamaud, 1995: fig. 6D). The teeth are present, but they are difficult to discern on either maxilla and it is not possible to determine if the tooth crowns are uni- or bicuspid, and whether or not they were pedicellate. However, Holman and Harrison (2002) described a partial maxilla attributed to *Thaumastosaurus*, where the teeth are pedicellate and bicuspid. The pedicellate condition was also retrieved in another partial maxilla (Holman and Harrison, 2003). The tooth row ends anterior to the posterior margin of the lamina horizontalis.

The anteriormost portion of the right maxilla and therefore details about the end of the lamina anterior, the rostellum and the anterior extension of the crista dentalis, are not preserved.

Nasals—The nasals are in close contact anteromedially and diverge from each other posteromedially, leaving the sphenethmoid exposed (Fig. 5A). This puts them in a transitional state between the condition found in the first mummy (MNHN.F.QU17279; Laloy et al., 2013), in which they are separated by an empty space, and the condition of MNHN.F.QU17376, where they are wholly fused, without midline sutures (Rage and Roček, 2007). The nasals are fused to the dorsal surface of the sphenethmoid. Both the maxillary and orbital margins are concave, with the processus paraorbitalis oriented posterolaterally at its distal end (Fig. 5A, 6F). The processus paraorbitalis has no ornamentation distally, where it is delimited ventrally by the anterior extension of the lamella alaris of the squamosal to form a groove for the nasolacrimal duct (Fig. 5B, 6F). The parachoanal process is a small protuberance, located at midlength of the maxillar margin (Fig. 6F). The dermal sculpture of the nasals appeared to be more deeply pitted near the orbital margin.

Quadratojugals—The quadratojugals are elongate with an anterior slender and elongate processus jugularis. The quadratojugals articulate with the maxillae along a triangular facet, on the lateral side of the processus jugularis for nearly one half of the length of the quadratojugals (Fig. 5B, 7A). In ventral view, the processus jugularis curves anteromedially and extends up to 80% of the lateral border of the pterygoid fossa. Posteriorly, the bone forms a thick bulge, extending medially, and with a medial groove on its posterior surface (Fig. 5B). This bulge is interpreted as the quadrate (ossified portion of the palatoquadrate; Špinar, 1972; Duellman and Trueb, 1994; Roček, 2003). The palatoquadrate is mostly cartilaginous in anurans, but its posterior region can ossify as the quadrate. In anurans whose quadratojugals are present, the quadrates are fused to them, forming a quadratojugal+quadrate complex. The quadrate is overlapped posterodorsally by the posterolateral process of the squamosals and medially by the ramus posterior of the pterygoid. In MNHN.F.QU17279, it is also possible to see these ossified quadrates fused to the

quadratojugals, with a thin suture visible between the two bones in ventral view (Laloy et al., 2013; fig. 3B).

Suspensory Bones

Angulosplenials—Both angulosplenials are incompletely preserved. The left angulosplenial represents less than $\frac{1}{4}$ of the whole bone (compared to the one described in Laloy et al., 2013), and the right one represents around $\frac{2}{3}$ of a complete angulosplenial. The processus coronoideus is dorsoventrally oriented as an oval flattened plate, whereas the crista paracoronoidea is poorly developed (Fig. 7B). The crista mandibulae externa is marked laterally. The groove for Meckel's cartilage is visible on the lateral side of the angulosplenial where it widens posterodorsally (extremitas spatulata, Fig. 7B). In dorsal view, the articular is preserved in the posterior region of the bone. Remaining mandibular bones are not preserved in this specimen.

Articular—This bony element forms, with the quadrate, the jaw joint in anurans (Roček et al., 2016). The articular is an irregularly shaped, anteroposteriorly elongate element (Fig. 7C). The poor ossification of this element made it difficult to delineate from the surrounding matrix in the CT data. The articular is in ventral contact with each angulosplenial but is not fused to this element. It is covered dorsally by the quadratojugal+quadrate. The quadrate and articular are not in contact, but this might be due to poor ossification/preservation of the two elements.

Palate Bones

Palatines—The palatines (neopalatines of Trueb, 1973) are elongate, dorsoventrally flattened, sub-cylindrical elements that are oriented perpendicular to the sagittal axis of the skull. In ventral view, the paired palatines articulate medially in the midline of the sphenethmoid (slightly separated by a very narrow fissure), as in MNHN.F.QU17376 (Rage and Roček, 2007). The processus palatines maxillae extends posterolaterally on the palatoquadrate groove of the maxilla (Figs. 5C, 7D). The medial process ventrally contacts the lateral process of the sphenethmoid and nearly contacts the anterior tip of the parasphenoid posteriorly.

Vomers—Both vomers are preserved in situ and articulate with the ventral face of the sphenethmoid and with each other by their lamina medialis, forming a flat lamina that extends posteromedially (Fig. 5C). The medial margin is convex and almost in contact with the palatine. The left vomer is damaged anterolaterally and at least half of it is missing; a few teeth are visible in ventral view (Fig. 5C). Vomerine teeth were not visible on the right vomer during the segmentation, but their presence was observed by Laloy et al. (2013) in their segmentation of MNHN.F.QU17279. The anterior process extends anterolaterally towards, but fails to contact, the anterior spine of the lamina horizontalis of the maxilla. The processus choanalis anterior is very elongate and extends laterally without reaching the maxilla. The processus choanalis posterior is a small flattened lamina, with a crest extending dorsally (Fig. 7E). The choanal margin (margo choanalis in Roček, 1994) is well-marked with an acute angle that indicates a moderately large choanal opening (Biton et al., 2016).

Parasphenoid—The parasphenoid is fused to the prooticooccipital complex posterolaterally and to the sphenethmoid anteriorly. The cultriform process is long and slender, without any longitudinal ridges on its ventral surface. Posteriorly, the alae (processus lateralis) are short, lie perpendicular to the cultriform process, and bear a transversal and arched keel ventrally (Fig. 7F). The posterior margin is curved (convex anteriorly) towards a

short, medially borne spear-like posterior process. The parasphenoid is fused to the pterygoids by the anterolateral margin of the alae. This suture was difficult to discern during segmentation, but the alae are extensively overlapped by the ramus interior of the pterygoid anteriorly (Fig. 5C).

Pterygoids—The pterygoids are of the standard triradiate shape for anurans (Fig. 5A). The ramus posterior is an elongated vertical lamina (partly fused to the processus posterolateralis of the squamosal) in contact distally with the quadrate (Fig. 5C). The ramus interior bears a posterodorsal flange that forms a part of the posterior wall of the orbit (Fig. 5D). A deep sulcus extends dorsally from the ramus posterior to the ramus anterior on the maxillar margin called the sulcus pterygoideus (Fig. 7G). The ramus anterior is well-developed, robust, and slightly flattened dorsoventrally.

Endocranium

Sphenethmoid—The sphenethmoid is an unpaired bone, pentagonal in dorsal view. Most of its dorsal surface is overlapped by, and fused to, the nasals and frontoparietals. The exception is a small, rhomboid, median part that is visible dorsally (Fig. 5A). This exposure is covered with low and poorly defined ornamentation composed of pits and ridges, nearly identical to the one covering the dermal bones (Figs. 5A, 8A). In extant anurans, the ornamentation of the sphenethmoid (and other bones as well) thickens during growth and thus serves as an ontogenetic marker (Buffrénil et al., 2015, 2016). An even weaker ornamentation characterizes MNHN.F.QU17279 (Laloy et al., 2013), indicating that it is less mature than our specimen.

Among extant anurans, a dorsal exposure of the sphenethmoid occurs in various taxa (Duellman and Trueb, 1994; Paluh et al., 2020). However, this dorsal exposure is rarely

ornamented like the neighboring dermal bones (e.g. *Aubria masako*, where the dorsal exposure is reduced to a minute rhomboidal fenestra, devoid of ornamentation). In addition, the dorsal exposure is reduced or absent in most extant or extinct hyperossified taxa (Duellman and Trueb, 1994; Sheil, 1999; Nicoli, 2019; Paluh et al., 2020), where the nasals and frontoparietals overlap the sphenethmoid. In contrast, the exposure in MNHN.F.QU17381 is rather large.

An exposed and ornamented sphenethmoid occurs in extant hylids (casque-headed tree frogs) from South America, Pelobatidae and Bombinatoridae (Trueb, 1970; Roček, 1980; Smirnov, 1997). Analysis of the ontogeny and skeletogenesis of this region in Hylidae and Bombinatoridae has shown the presence of a dermal bone called the dermal sphenethmoid (Trueb, 1966, 1970; “internasofrontal”, Smirnov, 1997). This rhomboidal neomorphic element develops by intermenbranous ossification in the lower dermis (Trueb, 1966) and then cossifies with the sphenethmoid to form a single bone mass (Trueb, 1966, 1970; Smirnov, 1997). The presence of this bone is contested in Pelobatidae (Roček, 2003), as the sphenethmoid can be covered by adjacent dermal bones. Periosteal ossification of the sphenethmoid could also result in a secondary ornamentation such as for the neighboring nasals and frontoparietals. The presence of a dermal sphenethmoid is highly speculative in MNHN.F.QU17381, as it can only be differentiated in premetamorphic specimens (Trueb, 1970).

Anteriorly, the bone is divided into two chambers (cavitas nasalis) separated medially by the bony septum nasi (Fig. 8C). The sphenethmoid is elongate posteriorly, reaching close to the mid-level of the cultriform process of the parasphenoid (Fig. 5C). Despite the overall hyperossification of the skull, the sphenethmoid does not reach the prooticooccipital, leaving a part of the lateral walls of the braincase unossified.

Posteriorly, the dorsal fenestra frontoparietalis forms a notch for the insertion of the facies cerebralis anterior (Fig. 8A) of the frontoparietals, bearing a dorsal impression of the forebrain. Ventrally, the sphenethmoid is fused to the anterior tip of the parasphenoid and to the palatines. The lateral processes are distally short, with the posterior wall extending slightly laterally (Fig. 8A). The dorsal surface of these processes extends slightly postero-laterally to form a poorly developed lamina supraorbitalis (Fig. 8A). The lateral wall of each anterior chamber is pierced by an orbitonasal foramen, which conveyed the ophthalmic nerve (canalis ramus medialis nervi ophthalmici) into a large cavitas nasalis (= anterior chamber) (Fig. 8B).

Several portions of the anterior sections of the sphenethmoid are partially ossified, which is characteristic of hyperossification. The septum nasi is ossified, without any anterior thickening, reaching the anterior part of the nasals (Fig. 8C), and the tectum nasi is oriented anterodorsally, forming a triangular flattened area in dorsal view (Fig. 8A). The solum nasi (ventral surface of the cavitas nasalis) bears a broad dorsal prominence, the sella amplificans (Fig. 8C). The surface of the solum nasi and septum nasi appears smooth in the segmentation. This most likely indicates that a cartilaginous part was present (Roček and Lamaud, 1995; Duellman and Trueb, 1994). The rest of the anterior part of the sphenethmoid was most likely cartilaginous or poorly ossified, and therefore neither the postnasal wall nor anterior wall of the nasal capsule were preserved. In ventral view, the sphenethmoid is subcruciform, with the lateral expansion of the anterior chamber perpendicular to both the posterior chamber and the bony anterior extension of the septum nasi.

Prooticooccipital Complex—The prootic, occipital and exoccipital are fused into a single complex that constitutes the posterior part of the braincase and skull (Fig. 5D). The otic capsules are poorly ossified ventrally, as indicated by their irregular ventral surface (Fig. 8G).

The foramen magnum is large and oval (slightly compressed dorsoventrally). The two occipital condyles are crescentic, with a small dorsal ridge connecting them to the

prominentia ducti semicircularis posterioris (Fig. 8D). The latter is naturally flattened mediolaterally and extends as an elongate protuberance oriented ventrolaterally. The prominentia ducti semicircularis are flanked medially by a depression (oriented dorsoventrally) that is delimited dorsally by a small median keel (Fig. 8D). This keel is similar to one found in MNHN.F.QU17376 (Rage and Roček, 2007: fig. 5B) and NHMB V.R31 (Vasilyan, 2018: fig. 3) but this keel was not visible in MNHN.F.QU17279 (Laloy et al., 2013).

Two large jugular foramina are partially hidden in posterior view by the occipital condyles (Fig. 8D). They open in the lateral wall of the cavum cranii and in the otic capsule. The fenestra ovalis is located on the lateral wall of the prootic (Fig. 8D).

Dorsally, the crista parotica extends laterally into a dorsoventrally flattened processus (ramus lateralis sensu Špinar, 1978) (Fig. 8D–E). A horizontal groove (perilymphatic groove in Fig. 8) extends laterally from the jugular foramen on the posterior surface of the otic capsules and might have housed a perilymphatic canal. This groove is visible in both specimens MNHN.F.QU17279 and MNHN.F.QU17376 (Rage and Roček, 2007; Laloy et al., 2013). The parietal fenestra is large and completely covered dorsally by the frontoparietals.

Anteriorly, the prootic foramen is large and undivided (unlike in MNHN.F.QU17376; see Rage and Roček, 2007:fig.7). The groove for the vena jugularis is visible, extending from this foramen to the lateral margin of the anterior surface of the prooticooccipital. This groove is shallow and poorly delimited (Fig. 8F), making it similar to the groove in MNHN.F.QU1376 (Rage and Roček, 2007: fig. 7A), and slightly different from that of MNHN.F.QU17279 (Laloy et al., 2013). On the left side of the prooticooccipital, the groove for the vena jugularis ends laterally in a small notch on the lateral side of the prootic. In MNHN.F.QU17376 and two other incomplete braincases of *Thaumastosaurus* (see Rage and Roček, 2007: fig. 7), two unidentified foramina penetrate the anterior surface of the

prooticooccipital, piercing the groove for the vena jugularis. In two of the braincases (Rage and Roček, 2007: fig. 7A, C), the most lateral of these foramina forms a notch on the lateral border of the prootic, in a similar location to the notch in MNHN.F.QU17381. These foramina are not known in MNHN.F.QU17279 (Laloy et al., 2013). Medial to the anterior surface of the prominentia ducti semicircularis posterioris, a small depression is present, as in MNHN.F.QU17279 (Fig. 8E). This small depression might be another part of the otic canals.

The lateral wall of the cavum cranii is pierced by three foramina. As mentioned earlier, the posteriormost foramen is connected to the jugular foramen. A large, irregularly-shaped opening that leads to the otic capsules is present ventrally at approximately the midlength of the lateral wall. We interpret this single opening to have conveyed both branches of the acoustic nerve (Duellman and Trueb, 1994; Rage and Roček, 2007) whose specific bony paths are not visible due to poor preservation in this region of the otic capsule. A small rounded foramen, dorsal to this irregular opening, is interpreted as the perilymphatic foramen.

Columellae—Only the ossified portion of the columellae, the plectrum (~stapes), was identified and segmented. Both preserved plectra have the same orientation and position on each side of the braincase, implying they are in anatomical position. The posterior region of the plectrum is bifurcated, with a notch on its medial margin (Fig. 8H). This posterior region is interpreted as the ossified pars interna plectri ('footplate' of Duellman and Trueb, 1994), with the notch on the medial surface serving as an insertion point for the cartilaginous operculum (Bolt and Lombard, 1985; Roček et al., 2016). The pars media plectri is a curved, slender rod that extends laterally between the posterior and posterolateral processes of the squamosal, where the tympanic annulus is located in anurans (Duellman and Trueb, 1994; Sheil, 1999; Roček et al., 2016). The tympanic annulus has not been identified in MNHN.F.QU17381 and MNHN.F.QU17279, although a tympanic membrane was identified in the latter specimen (Fig. 4C), implying that a cartilaginous tympanic annulus was present

(Pereyra et al., 2016). As MNHN.F.QU17381 is attributed to the same taxon (see in Taxonomy), we conclude that a tympanic annulus was present in MNHN.F.QU17381.

Hyobranchial Skeleton

Hyoid Bones—The cartilaginous hyoid plate is not visible in the scan data. However, two slender bony elements, the thyrohyal bones, corresponding to the posteromedial processes of hyoid plate, are present. The two elements are oriented anteromedially with their proximal parts almost in contact. They widen at both ends (proximal and distal; Fig. 8I). They are placed ventrally under the first three vertebrae and the exoccipital, and dorsal to the coracoids and clavicle.

Vertebral Column

The vertebral column is similar to the one found and described inside the mummy by Laloy et al. (2013). It is composed of eight presacral vertebrae, one sacral vertebra and an urostyle (Fig. 9). The seven first presacral vertebrae are procoelous (anterior cotyle and posterior condyle; Fig. 10A, B) and the last presacral (eight vertebra) is biconcave (Fig. 10C), indicating an amphicoelous condition. The sacral vertebra is biconvex, with an anterior cotyle and two posterior cotyles (Fig. 10D, E). These conditions of the presacral and sacral vertebrae are characteristics of a diplasiocoelous vertebral column.

Atlas—The atlas articulates with the exoccipitals by two large and laterodorsal-ventromedially elongated cotyles (Fig. 10A), which fuse medially to a protruding lip at the midline, forming a large articular facet with the skull (type III of Lynch, 1971). The vertebral canal is large, with thin lateral walls and thicker ventral and dorsal walls; the latter forms a

large base for the short and posteriorly inclined neural spine (Fig. 9B). The postzygapophyses are poorly developed, with a flattened articular surface inclined medioventrally. The centrum is flattened dorsoventrally and possesses a small elliptical condyle in posterior view (Fig. 10B).

Post-atlantal Vertebrae—The centra of the post-atlantal vertebrae are longer than wider and flattened dorso-ventrally (Fig. 9B–C). The centrum of vertebrae II–VII is concave anteriorly and convex posteriorly, indicating a procoelous condition. No vertebra bears ribs.

In lateral view, the neural arch is thin, anteriorly notched, with an enlarged base (Fig. 9B). Arches are non-imbricated. The vertebral canal remains broad until the fifth post-atlantal vertebra. The neural spines are dorsally elongated and inclined posteriorly, but do not extend beyond the posterior margin of the postzygapophysis. The posteriormost post-atlantal vertebrae (vertebra VI to VIII) possess a shorter neural spine, which are oriented less posteriorly. The zygapophyses have flat articular processes.

The first post-atlantal vertebra (Vertebra II) possesses a pair of large transverse processes, a bit shorter than the sacral transverse processes. In dorsal and ventral views, this first pair of transverse processes are slightly posteriorly arched (Fig. 9A, C). The processes are thicker at their mid-length, with a crest appearing on the anterior face. The second post-atlantal vertebra (Vertebra III) possesses the largest transverse processes. They are oriented posterolateroventrally and are moderately widened distally. The transverse processes of vertebra IV have the same distal extension as the sacral apophyses and are oriented lateroposteriorly. The presacral vertebrae V–VII are similar in possessing transverse processes that are thinner and narrower distally than proximally. On vertebra V, they are slightly oriented posterodorsally (Fig. 9B). On vertebrae VI and VII, they are roughly perpendicular to the long axis of the column. Presacral vertebra VIII bears thin transverse processes similar to the one of the previous presacral vertebrae. However, this vertebra is amphicoelous.

Sacral Vertebra—The sacral vertebra possesses two small, well-separated, posterior circular condyles that articulate with the urostyle, and one dorsoventrally flattened elliptical anterior condyle that articulates with the posterior cotyle of the last presacral vertebra (Fig. 10D–F). On the anterodorsal border of the neural arch, a well-developed lamina extends from the base of the prezygapophyses to the base of the neural spine (Figs. 9A, 10D). This kind of lamina is also present on the posterior border of the neural arch (Fig. 10D–E). The sacral transverse processes are subcylindrical in cross section, slightly flattened dorsoventrally, and do not widen posterodistally. A small notch is visible dorsally at the distal margin of each transverse process (Fig. 9A). The neural spine is reduced and anterodorsally oriented.

Urostyle—The urostyle is posteriorly incomplete. The anterior portion of the bone is articulated with the sacral vertebra with two well-separated circular anterior cotyles (fossa cotylae), which protrude laterally from the main shaft of the urostyle (Fig. 10G). The vertebral canal is moderately high, accounting for half the height of the neural arch. The neural arch bears a well-developed thick dorsal process. This also marks the cranial end of a tall and thin dorsal crest that extends throughout the whole preserved portion of the bone and slightly decreases in size posteriorly (Fig. 10H). A spinal foramen is present on each side of the base of the dorsal crest, posteroventrally to the thick dorsal process (Fig. 10H). No transverse processes are present.

Pectoral Girdle

All pectoral bony elements are present in anatomical position (Fig. 11).

Cleithra-Suprascapulae Complexes—The cleithrum and the ossified portion of the suprascapula are fused together, forming a single compound element dorsomedial to the scapula. The cleithrum represents the anterior thickened portion of the compound, and the

suprascapular (a mostly cartilaginous element) is ossified on its ventral and posterior margins (Fig. 12A, B). The ramus anterior of this compound bone is long with a thickened anterior margin by the presence of a long lamina recurvata (sensu Špínar, 1972). The margins scapularis and posterior surface of the compound are rounded. There is no ramus posterior.

Scapulae—The scapulae are transversally elongated, with a moderately widened distal end of the processus suprascapularis (Fig. 12C, D). The anterior margin is concave (Fig. 12C). There is no crest on both anterior or posterior margins of the scapulae. The processus acromialis and the processus glenoidalis are separated by a moderately wide sinus interglenoidalis (Fig. 12E). The processus acromialis is wider than the processus glenoidalis and has a rounded lateral margin; in dorsal view, it hides the processus glenoidalis and the sinus interglenoidalis. In medial view, a well-developed medial crest is present on the processus glenoidalis and extends from the ventral border to the base of the processus anterior (Fig. 12C). No lamina is present on the processus anterior. The glenoid fossa is moderately extended dorsoventrally (Fig. 12C).

Coracoids—The coracoids are transversally oriented, with a thickened, cylindrical processus glenoidalis. This latter of both coracoids and scapulae are almost in contact with each other, leaving a gap for the paraglenoid cartilage. The processus epicoracoidalis is flat and anteroposteriorly enlarged (much larger than the processus glenoidalis) and bears a convex medial margin (Fig. 12F). The processus epicoracoidalis extends anteriorly, forming a hook that extends close to the medial end of the clavicles. Both coracoids are in contact with each other medially, but do not overlap (Fig. 11). This is characteristic of a firmsternal condition (sensu Cope, 1864; Boulanger, 1886). The left coracoid is badly damaged, with the processus glenoidalis broken off from the main shaft (Fig. 12G–H). On the anterior and posterior margins of the main shaft, vertical laminae can be observed, forming a bony callus

linking the two broken parts. This callus is also visible in ventral view, expanding the width of the shaft of the coracoid (Fig. 12G–H). This damage can be linked to the missing part of the left clavicle. The near-absence of disarticulated bones (except the ilia) and the presence of a mineralized skin on this part of the specimen seems to exclude the diagenesis hypothesis. The absence of any hole indicating a missing part in the area of the coracoid and clavicle (the nearest holes are located anteriorly on the ventral face of the specimen) excludes the extraction hypothesis. This leaves only the hypothesis of a damage received before the burial of the animal. In extant anurans, the healing process for bone fractures is slow compared to mammals (Cameron et al., 2012; Egawa et al., 2014). Given that the broken coracoid seems partially fused back and bears a bony callus, this may represent a scar from a wound received during the life of the animal.

Clavicles—The right clavicle is completely preserved, whereas the left clavicle only preserves its lateral part (Fig. 11). This could be linked to the injury visible on the left coracoid. The clavicles are almost as long as the coracoids and slightly arched anteriorly. In dorsal view, the lateral part is bifurcated and articulates with the processus acromialis and processus glenoidalis of the scapulae, forming a part of the articular fossa for the humeri. The sulcus cartilagine praecoracoidealis extends posteriorly on the length of the bone (Fig. 12I). The clavicles are in contact, slightly overlapping dorsoventrally the processus glenoidalis of the coracoids. The extremitas medialis of the clavicle is not in contact with the medial part of the coracoids (Fig. 11).

Sternum—The sternum is fully ossified as an elongate slender element. The sternum is expanded both anteriorly and posteriorly with the former being larger than the latter. (Fig. 12J). It is strongly similar to the one found in *Pyxicephalus adspersus* (Sheil, 1999: fig. 5B).

Omosternum—The omosternum is ossified, denoting a firmisternal condition of the girdle (Cope, 1864; Boulanger, 1886; Duellman and Trueb, 1994). It is an inverted “Y”-shaped bone with a bifurcated posterior end (Fig. 12K).

Forelimb

Humeri—Only the proximal parts of both humeri are preserved, although badly damaged. Only the proximal articular facet of the right humerus is preserved with the glenoid fossa of the pectoral girdle. The left humerus, however, is more completely preserved, with both its proximal head and part of the diaphysis (Fig. 13A). The left humerus displays a moderately developed crista ventralis, and lacks a proximal crista paraventralis (Fig. 13A).

Pelvic Girdle

Ilia—The two ilia are partially preserved. The left one is only a fragment of the distal part (around 1.4 mm in length), but the right one is more completely preserved, which represents about half or more of the complete iliac shaft (= ilial shaft of Gómez and Turazzini, 2016). It bears a high and well-developed dorsal crest (Fig. 13B). Unfortunately, the rest of the ilium (distal half) is not preserved, as in the first mummy (MNHN.F.QU17279; Laloy et al., 2013).

TAXONOMY

MNHN.F.QU17381 is the holotype and only known specimen of *Bufo servatus*, erected and illustrated by H. Filhol (1876; 1877: pl. 51; fig. 412) based on a first description

done in 1873 (Filhol, 1873). Filhol named the specimen *Bufo servatus* (Filhol, 1876) without giving characters to diagnose the taxon or differentiate it from the other *Bufo* species. He placed it in Bufonidae based on the presence of parotoid glands (see Filhol, 1876, 1877). Martín et al. (2012) considered the name *B. servatus* as valid and did not discuss the criteria of validity. Sanchiz (1998) considered the name a nomen vanum (Mones, 1989), a taxonomic term considered in the ICZN as referring to a name based on a type inadequate for definitive diagnosis, but he did not question its validity. Our work shows that the specimen is informative, hence *B. servatus* cannot be a nomen vanum. The specimen has been figured, and according to the article 12.2.7 of the International Code of Zoological Nomenclature (ICZN), this supports the validity of a name if published before 1931. The name *B. servatus* can therefore be considered as valid. Moreover, this name has been cited several times since its original description (Piveteau, 1927; Tihen, 1962; Sanchiz, 1998; Rage, 2006) and its validity was not often discussed.

Attribution to *Bufo* was based on the presence of what Filhol identified as two parotoid glands located right behind the eyes (Filhol, 1876, 1877). However, several studies (Piveteau, 1927; Tihen, 1962; Rage, 2006, 2016) considered this observation as erroneous. We here confirm this proposition and suggest that the structures interpreted by Filhol as parotoid glands are artefactual skin ridges caused by post-mortem desiccation during the natural mummification process. In addition, on specimen MNHN.F.QU17381, we observed teeth on the maxillary, which are lost in Bufonidae (Duelleman and Trueb, 1994). Moreover, the vertebral column is diplasiocoelous, which is characteristic of Ranoidea. Finally, the presence of a firmisternal pectoral girdle as well as an ossified omosternum also reinforce the attribution to a ranoid taxon. We therefore conclude that MNHN.F.QU17381 cannot be attributed to Bufonidae or *Bufo*. Furthermore, the skeleton of specimen MNHN.F.QU17381 is almost morphologically identical to the one of MNHN.F.QU17279 and to the skull of

MNHN.F.QU17376, both of which have been attributed to the genus *Thaumastosaurus* as *T. gezei* (Roček and Lamaud, 1995; Laloy et al., 2013). We therefore attribute the specimen MNHN.F.QU17381 to *Thaumastosaurus* De Stefano, 1903 by the following combination of characters: (1) dermal bones covered with ornamentation that differs from the one found in *Latonia*, *Pelobates*, *Eopelobates* and *Ceratophrys*; (2) nasals (partially) and frontoparietals co-ossified with each other and with sphenethmoid and frontoparietals co-ossified with prooticooccipital; (3) rhomboid part of sphenethmoid exposed on skull roof; (4) no bony contact between the frontoparietal and squamosal; (5) anterior tip of the parasphenoid does not extend between palatines; (6) processus posterolateralis and ramus paroticus of squamosal merged, articulating with the crista parotica of the otic capsules (Rage and Roček, 2007; Vasilyan, 2018).

At the species level, MNHN.F.QU17381 differs from *Thaumastosaurus bottii* and *T. wardi* by having the lamella alaris of the squamosal extending anteriorly along the entire ventral margin of the orbit (lamella alaris ends anteriorly at the midlength of the orbit in *T. bottii* and *T. wardi*). However, the lamella alaris of the squamosal of the neotype of *T. bottii* (Roček and Lamaud, 1995: fig. 5) is almost entirely broken off, and the length of its anterior extension cannot be assessed. Other squamosals attributed to *T. bottii* are either broken or present as an eroded anterior part of the bone (Vasilyan, 2018: fig. 4G–H), making comparison difficult. This difference on the squamosals might only result from a different preservation, as no skull of *T. bottii* is as complete as the holotype of “*T. gezei*”. This difference is not attributed to ontogeny.

The specimen MNHN.F.QU17381 furthermore differs from *T. bottii* by having a shallow, poorly delimited groove for the vena jugularis interna on the prooticooccipital complex (Fig. 8F), whereas *T. bottii* possesses a narrower and more sharply delimited groove (Roček et Lamaud, 1995; Vasilyan, 2018). Other proposed morphological differences for the

two Quercy species are located on the premaxilla (Vasilyan, 2018), which is unfortunately lost in MNHN.F.QU17381, thus preventing any further comparison with *T. bottii*.

Among the mummies attributed to *Thaumastosaurus*, MNHN.F.QU17381 presents strong resemblances with MNHN.F.QU17279, the former holotype of “*Rana plicata*” (attributed to *Thaumastosaurus gezei* by Laloy et al., 2013), with the anterior extension of the squamosal separating the maxillary from the orbit by a thin strip, and a postcranial identical in both mummies. It also presents a strong resemblance to MNHN.F.QU17376, with the palatines medially in contact with each other and a groove for vena jugularis interna, which also resembles the one of MNHN.F.QU17279 (Laloy et al., 2013). However, a few differences can be seen between the skull of MNHN.F.QU17381 and those of MNHN.F.QU17279 and MNHN.F.QU17376. First, the nasals are partially fused in MNHN.F.QU17381 whereas they are separated in MNHN.F.QU17279 and fully fused in MNHN.F.QU17376. The ornamentation of the sphenethmoid in MNHN.F.QU17381 is more developed than in MNHN.F.QU17279 (Laloy et al., 2013: fig. 3A) but less than in MNHN.F.QU17376, where the limits between the sphenethmoid and the neighboring dermal bones are obscured by the ornamentation (Rage and Roček, 2007: fig. 1A). As in MNHN.F.QU17279, the prootic foramen is not divided into two portions. However, as mentioned in the description, a notch can be observed on the lateral margin of the anterior surface of this bone of MNHN.F.QU17381, which is continuous with the groove for the vena jugularis and the unknown foramina found in MNHN.F.QU17376 and other *Thaumastosaurus* sp. skulls (Rage and Roček, 2007: fig.7A–C). The extension of the lamella alaris in MNHN.F.QU17381 is also thinner than in MNHN.F.QU17376, resembling the one found in MNHN.F.QU17279. Those differences can be linked to ontogeny (see Ontogenetic Assessment below).

MNHN.F.QU17381 shares with both MNHN.F.QU17376 and MNHN.F.QU17279 (attributed to *T. gezei*) the anterior extension of the squamosal forming the whole lateral wall of the orbit and the shape of the groove for the vena jugularis interna which is shallow and wide; these are listed in the revised diagnosis. The specimen MNHN.F.QU17381 can therefore be assigned to “*Thaumastosaurus gezei*”.

A consequence of this attribution is that *T. gezei* and *B. servatus* are subjective synonyms. Considering the available names and excluding those invalidated by homonymy, *Bufo servatus* Filhol, 1877 is the oldest valid name. We therefore here consider the new combination *Thaumastosaurus servatus* (Filhol, 1877).

ONTOGENETIC ASSESSMENT

Based on Rage and Roček (2007) and Laloy et al. (2013), the following cranial characters can be used to assess the skeletal maturity of *T. servatus* specimens: relation between the nasals, palatines, and ornamentation of the sphenethmoid. In skeletally mature (sensu Griffins et al., 2021) *T. servatus*, the contralateral nasals are fused medially, as are the palatines where only a suture is still visible between the bones, and the ornamentation of the sphenethmoid is well developed, with a similar pattern present in the surrounding bones. These conditions are also present in MNHN.F.QU17376 (Rage and Roček, 2007). This specimen can therefore be considered skeletally mature. In MNHN.F.QU17279, the lack of contact between the nasals (and similarly for the palatines), and the subdued ornamentation of the sphenethmoid demonstrate skeletal immaturity (sensu Laloy et al., 2013). In MNHN.F.QU17381, the slight medial contact between the nasals, the separation of palatines by a thin fissure, and the faint ornamentation of the sphenethmoid suggest a slightly greater

skeletal maturity than MNHN.F.QU17279. MNHN.F.QU17381 is therefore more skeletally mature than MNHN.F.QU17279, but less than MNHN.F.QU17376.

PHYLOGENY

Thaumastosaurus servatus was first suggested to have affinities with Leptodactylidae, especially the South American Ceratophryidae, based on cranial characters (Roček and Lamaud, 1995; Rage and Roček, 2007). Later, Laloy et al. (2013), based on a subcomplete skeleton found within the mummy, MNHN.F.QU17279, carried out a phylogenetic analysis, using a matrix modified from Báez et al. (2009). This latter dataset (see Báez et al., 2009) was itself based on the matrix proposed by Fabrezi (2006), modified for ceratophryid phylogeny. The dataset from Báez et al. (2009) includes 42 taxa, 3 of which are extinct taxa, scored for 75 characters. Laloy et al. (2013) enlarged the sample by adding 40 taxa from Evans et al. (2008), whose matrix was also modified from the dataset of Fabrezi (2006; see Evans et al., 2008 for modifications) and included genera as OTUs. Evans et al. (2008) deleted one character (the dorsal exposure of sphenethmoid) and redefined another (character 1 in Evans et al., 2008; Laloy et al., 2013). Laloy et al. (2013) found *Thaumastosaurus* within the Natatanura, as the sister-taxon of a clade that contains *Pyxicephalus* and *Cornufer* (a ceratobatrachid).

Báez and Gómez (2018) modified the dataset from Báez et al. (2009) by adding 29 neobatrachian taxa and redefining some characters to test the impact of hyperossification characters within the dataset. The taxon sample was greatly enlarged (from 42 to 71 taxa), and 68 characters were added (for a total of 143 characters), and several characters from the old dataset were redefined. Among the taxa, *T. servatus* (“*T. gezei*” in the dataset of Báez and

Gómez, 2018) was included, using the new information from MNHN.F.QU17279 described by Laloy et al. (2013). They also found *T. servatus* within hyperossified Natatanuran, but as more closely related to *Pyxicephalus adspersus* Tschudi, 1838 (African bullfrog) than to *Cornufer guentheri* Boulanger, 1884 (Solomon island leaf frog). This topology could be explained by the limited inclusion of only five extant natatanurans taxa in their dataset. We therefore expanded the dataset of Báez and Gómez (2018) with 15 extant natatanurans taxa (See Materials and Methods). We added seven more taxa from Pyxicephalidae (*Arthroleptella lightfooti*, *Aubria subgillata*, *Cacosternum boettgeri*, *Cacosternum namaquense*, *Natalobatrachus bonebergi*, *Strongolypus grayii* and *Tomopterna tuberculosa*), represented previously only by *Pyxicephalus adspersus* (the sister-taxon to *T. servatus*, according to Báez and Gómez, 2018).

Most extant anurans are placed within Neobatrachia (Feng et al., 2017), which includes two clades, Hyloides and Ranoides. The latter clade can be divided into three subclades: Microhylidae (*Hylambates*, *Dermatonotus*, and *Asterophrys* in our dataset), Afrobatrachia (*Arthroleptis* and *Hylambates* in our dataset) and Natatanura (represented by 19 taxa in our matrix, of which 14 were not included in any of the matrices mentioned above). The phylogenetic relationship among these three clades remains contentious. Natatanura represents the vast majority of extant Ranoides (Frost et al., 2006; Pyron and Wiens, 2011), but its fossil record is scarce and mostly composed of isolated fragmentary bones (Rage, 1984b; Sanchiz, 1998; Gardner and Rage, 2016). Given the good preservation and completeness of *T. servatus* fossils and their geological age, understanding its precise position within Natatanura is essential to better understanding the evolution of the clade and assessing the timing of its diversification. For this, several phylogenetic analyses were performed.

Unconstrained Analysis

Equal Weight Analysis, Unordered—We obtained 140 MPTs (most parsimonious trees) of 1355 steps (CI = 0.122; RI = 0.326) with the analysis performed under equal weight, with all multistate characters treated as unordered (Fig. S4A). The strict consensus shows numerous polytomies, with Neobatrachia not recovered. *Thaumastosaurus servatus* is recovered as a sister-taxon to a trichotomy composed of hyperossified ranoides, *Pyxicephalus adspersus*, *Aubria subsigillata* and *Cornufer guentheri* (Fig.S4A). The clade is supported by 26 synapomorphies. Many of them have been considered to be associated with Ranoides and Natatanura, which are not recovered in this analysis.

Equal Weight Analysis, Ordered—With cline characters ordered, we obtained 90 MPTs, of 1373 steps (CI = 0.137; RI = 0.422; Figs. 14A, S4B). The strict consensus is more resolved than with unordered states, but it still presents numerous polytomies. A majority of the ranoids taxa (excluding the three microhylids) are clustered together (Figs.14A, S4B), forming a “Ranoides” clade. This restricted “Ranoides” is supported by nine synapomorphies but has poor bootstrap support (less than 5%) and moderate Bremer support. Among those synapomorphies, the ossification of omosternum (101: 0→1) is uniquely shared by members of this clade; it is present in almost all taxa forming the “Ranoides” clade, except in *Cacosternum*. Another one, non-overlapping coracoids (104: 0→1), is convergent with only the Microhylids (see Appendix S in Supplement Data 1 for the detailed list).

The presence of an ossified omosternum is particularly important in several phylogenies of Ranoides and Natatanura, as various authors have proposed it as a synapomorphy for either clade (Lynch, 1973; Laurent, 1986; Scott, 2005; Frost et al., 2006). Most natatanuran taxa display this character, although it is lost in some taxa typically ranked as genera. It is present in the Afrobatrachia but not in the Microhylidae. Another interesting synapomorphy recovered for both “Ranoides” clade and Microhylidae is the presence of non-overlapping epicoracoids (present in all extant Ranoides, as mentioned in Trueb, 1973;

Lynch, 1973; Frost et al., 2006). This character represents a firmisternal condition for the pectoral girdle, classically associated with Ranoides (Lynch, 1973; Trueb, 1973; Duellman and Trueb, 1994). However, this condition is also found as a synapomorphy for Dendrobatidae (Trueb, 1973; Frost et al., 2006).

Thaumastosaurus servatus is found within “Ranoides”, recovered as a sister-taxon to a trichotomy composed of the extant hyperossified Ranoides (Fig. 14A). Nine synapomorphies were recovered, almost all of them based on cranial elements, and six of which are hyperossification-linked characters, like the presence of a supraorbital flange on the frontoparietals (6: 0→1), a contact between squamosals and nasals (11: 0→1; lost in *Cornufer guntheri*) and the presence of a heavily ornamented external surface of the pars facialis of the maxillae (50: 0→2; see Appendix S6 in Supplement Data 1 for the detailed list). This clustering of hyperossified ranoids seems mainly moderately supported by the convergent evolution of hyperossification characters present on the skull, and is quite similar to the previous analysis, where *T. servatus* was recovered, close to extant hyperossified ranoids (Laloy et al., 2013; Báez and Gómez, 2018).

The two afrobatrachians (*Arthrolepis adolfifriederici* and *Hylambates verrucosus*) are recovered in a clade with *Arariphrynus placidoi* (Fig. 14A), which is poorly supported by the loss of the ossified style of the sternum (102: 1→0), the reduction of the width of the glenoid fossa (112: 1→2; relative to the width of the shaft), the loss of the posterolateral process of the hyoid plate (67: 1→0) and the reduction of the posterodorsal expansion of the ischium (131: 1→0). Of those four synapomorphies, only the reduction of the glenoid fossa is scored for *A. placidoi*. The latter is recovered as the sister-taxon of *Phlyctimantis*, supported by three synapomorphies, which are the reduction of the length of the urostyle (92: 1→0), relative to the presacral vertebral length, a pars facialis of the maxillae which decrease abruptly in height in the orbital region (49: 0→1) and a change in the shape of the occipital condyles, which

become stalked (40: 0→1). In addition, the *A. placidoi* postcranial is not well-known, and the synapomorphies for the “Ranoides” clade recovered (mentioned earlier) are not known in this taxon.

Implied Weighted Analyses, Ordered—When using implied weighting with a low concavity constant ($k = 3$), we obtained one fully resolved tree of 91.30 steps (CI = 0.164; RI = 0.533; Fig. S5). Neobatrachia was recovered as monophyletic, with *Heleophryne* as a sister-taxon to all others neobatrachian. The neobatrachian clade is poorly supported by six synapomorphies, including the presence of palatines (27: 0→1; see Appendix S6 in Supplement Data 1 for the detailed list). Although not unique to the clade, this synapomorphy is commonly used, along other characters coded here but not recovered as synapomorphies for the clade (the loss of free ribs in adults and a bicondylar articulation between the sacral vertebra and the urostyle; Báez et al., 2009) to characterize neobatrachian taxa. Another synapomorphy proposed for this clade, the presence of a taeniae tecti medialis in the frontoparietal (Haas, 2003) was not recovered, likely for the fact that this character was not scored for a majority of the taxa in the dataset.

We recovered a monophyletic “Ranoides” (excluding Microhylidae), still supported by seven synapomorphies, including six found previously. *T. servatus* is placed as a sister-taxon to the crown-clade of Pyxicephalinae (Fig. S5 in Supplement Data 1). This clade is moderately supported by 12 synapomorphies on cranial and postcranial characters (see Appendix S6 in Supplement Data 1 for the detailed list). One of them, the presence of a contact between squamosals and nasals (11: 0→1), is interesting as it is considered a marker for hyperossification (Báez and Gómez, 2018; Paluh et al., 2020) and is recovered only in Pyxicephalinae and Ceratophryidae.

When using a higher constant value ($k = 7$), we obtained two MPTs of 66.96 steps (CI = 0.168; RI = 0.548). In the strict consensus (Fig. 14B; Fig. S6), *T. servatus* is placed within

Pyxicephalinae, as a sister-taxon to *Aubria subsigillata* (brown ball frog). This clade is poorly supported by a single synapomorphy, the absence of odontoids on palatines (reversion to the plesiomorphic state). Pyxicephalinae is supported by three synapomorphies, the development of a contact between nasals and squamosals (11: 0→1), the ossification of the planum anteorbitale of the sphenethmoid (33: 0→1) and the development of a process lateral to the anterior process of the hyale (anterior process of Duellman and Trueb, 1994; such as e.g. on *Morerella cyanophthalma*, Rödel et al., 2009: fig. 5a; 64: 0→1; unknown in *T. servatus*). Only one of these was found in the previous analysis (contact between nasals and squamosals). As mentioned above, this character is retrieved as a synapomorphy for the Ceratophryidae (Báez and Gómez, 2018). *Cornufer guentheri* was placed as a sister-taxon to Pyxicephalinae (including *T. servatus*), supported by ten synapomorphies. Many of these were recovered in the equal weighting analysis, and are linked to hyperossification characters like the contact of nasals along most of their medial margin (3: 0→2), the development of tectum supraorbitale on the frontoparietals (6: 0→1) or the development of the ramus paroticus of the squamosals, overlapping prootics (14: 1→2; see Appendix S6 in Supplement Data 1 for the detailed list).

When using an even higher constant value ($k=12$), we retrieved one fully resolved MPT of 50.89 steps (CI = 0.171, RI = 0.558; Fig. S7). *T. servatus* is recovered in the same position as before, within Pyxicephalinae, with *C. guentheri* as the closest taxon to all Pyxicephalinae. *A. placidoi* is placed once again within Afrobatrachia (as when using equal weight), supported by the same synapomorphies.

Constrained Analyses

Relationships within Ranoides and Natatanura have always been controversial (Clarke, 1981; Lynch, 1973; Scott, 2005; Frost et al., 2006; Pyron and Wiens, 2011), with various clades lacking morphological synapomorphies. This can be observed in our analysis as well, as we did not recover the Ranoides as a clade, but only a subset of these excluding microhylids (see Figs. S4–S7).

However, molecular datasets have yielded a better resolution of their relationships, especially with large dataset (Frost et al., 2006; Pyron and Wiens, 2011; Feng et al., 2017; Jetz and Pyron, 2018). Some uncertainties remain, with some clades still lacking clear support (see Pyron and Wiens, 2011). Conflict still exists around the position of Afrobatrachia, either as a sister-taxon to Microhylidae (Pyron and Wiens, 2011; Jetz and Pyron, 2018) or to Natatanura (Feng et al., 2017). We choose constrained analyses under two topologies, to see if changes in the relationship inside Ranoides could impact the placement of *T. servatus*.

Equal Weight Analysis, Ordered—When using a topology inferred on the phylogeny of Jetz and Pyron (2018) as a constraint, we recovered 22 MPTs with a score of 1586 steps. The strict consensus (CI = 0.149, RI = 0.479) places *T. servatus* in a trichotomy with the two pyxicephalines (Fig. S8). The clade is strongly supported by thirteen synapomorphies, including the presence of a contact between nasals and squamosals (11: 0–>1), the expansion of the zygomatic ramus of the squamosals, allowing for its articulation with the maxillae (10: 1–>2), the presence of a distal expansion of the crista parotica (39: 0–>1) and the enclosure of the pathway for the occipital artery into a canal (7: 0–>2; see Appendix S6 in Supplement Data 1 for the detailed list). Neither Ranoides nor Hyloides are recovered as a clade. This is linked to the instability of one taxon, *A. placidoi*, which is recovered either as an hyloid (in 72% of the trees) or as a ranoid. When excluding this taxon, we recovered 6 MPTs with a score of 1580 (CI = 0.158, RI = 0.481). In the strict consensus,

we recovered both Ranoides and Hyloides, and *T. servatus* is placed in the same trichotomy, supported by the same synapomorphies (Fig. S9)

When using a topology inferred on the phylogeny proposed by Feng et al. (2017) as a constrain, we recovered 4 MPTs, with a score of 1574. In the strict consensus tree (CI = 0.137, RI = 0.425; Fig. S10), *T. servatus* was recovered in the same position as with a topology inferred on the phylogeny of Jetz and Pyron (2018), in a trichotomy with the two pyxicephalinae taxa, supported by seventeen synapomorphies, thirteen of them recovered in the previous analysis, with an additional four, the partial ossification of the septum nasi of the nasal capsule (34:0→1), the ossification of the crista parotica (38: 0→1), the translocation of the craniomandibular joint to a position well posterior to occiput (61: 0→2) and the presence of anterolateral processes on the hyoid plate (64: 0→1; not scored for *T. servatus*).

Implied Weight Analyses (k = 7), Ordered—When using implied weights, and using a topology inferred on the phylogeny of Jetz and Pyron (2018) as a constraint, we obtained one tree of 72.01 steps (CI = 0.150, RI = 0.459), with *T. servatus* still found within Pyxicephalidae, as a sister-taxon to the extant Pyxicephalinae (Figs. 15, S11), a placement similar to the one found with a low constant value (k = 3) using implied weighting (Fig. S4). This clade is well-supported by the same 13 synapomorphies recovered in the previous analysis constrained on the same topology.

When constraining the analysis using the topology inferred from the analysis of Feng et al. (2017), we also obtained one tree of 71.79 steps (CI = 0.151, RI = 0.486) fully resolved (Fig. S12). The position of *T. servatus* is identical as before, as the closest taxon to the Pyxicephalinae, well supported by the same thirteen synapomorphies.

Discussion—The various analyses confirm the placement of *Thaumastosaurus* within Ranoides, more precisely within Natatanura. This position is mainly justified by several

postcranial characters, such as the ossified omosternum and non-overlapping coracoids. This placement highlights the importance of postcranial characters to reduce the impact of homoplasy found in the skull characters of anurans (Duellman et Trueb, 1994; Báez and Gómez, 2018) and to correctly assess the position of extinct taxa.

In most analyses, *T. servatus* is recovered as a sister-taxon to Pyxicephalinae, or within this clade. In addition, the hyperossified *Cornufer guentheri* is also recovered close to Pyxicephalinae and *T. servatus* with both equal and implied weight, except when using a low k value (punishing heavily homoplasy; Figs. 14A, B, S4–7). However, one difference can be observed between equal and implied weight analyses. With equal weights, *T. servatus* is placed as the sister-taxon to a trichotomy of the three extant taxa, whereas with implied weights, *C. guentheri* is recovered as a sister-taxon to *T. servatus* and Pyxicephalinae. This clustering of hyperossified ranoids is mostly likely driven by convergence, as the clades are based mainly on hyperossified characters (see Appendix 6 in Supplemental Data 1). However, when using implied weight, the placement of *T. servatus* as close to Pyxicephalinae (based only on one synapomorphies on an hyperossified character) has relatively high Bremer and moderate bootstrap supports. This could be an effect of the implied weight, which tends to favor resolved trees, which may lead to false topologies. This can be observed when using low k value ($k = 3$), where *C. guentheri* is not recovered close to the other hyperossified ranoids, but also not close to its position proposed by molecular phylogenies (Fig. S4; Jetz and Pyron, 2018). To minimize this problem, several authors proposed to use higher k value (Goloboff et al., 2018a, b). In the constrained analysis, *Thaumastosaurus* is also placed within the Pyxicephalidae, a clade composed of Pyxicephalinae and Cacosterninae. However, no osteological synapomorphy is known for this clade, because the presence of a medial lingual process on the tongue (presumed synapomorphy; Frost et al., 2006) is not known in *Thaumastosaurus*.

Conversely, as already proposed by Clarke (1981), Pyxicephalinae is supported by four morphological synapomorphies (Frost et al., 2006). One of them, the presence of an occipital canal, was also recovered as a synapomorphy for this clade in our analyses, while another one, a well-developed ramus interior (medial ramus; Clarke, 1981) of the pterygoids overlapping the parasphenoid alae, is present on *Thaumastosaurus*. The other two synapomorphies for the clade are a well-developed zygomatic ramus (= lamella alaris) of the squamosals (longer than its ramus paroticus) articulating with the maxillae, and a cranial exostosis (sensu Trueb, 1973). This latter in its typical state (a reticulate pattern of bone deposition, forming an ornamentation) is present only in Pyxicephalinae (in the Natatanura). Indeed, *C. guentheri* presents a modified pattern of exostosis, named casquing (Trueb, 1973). The articulated skulls attributed to *T. servatus* present a reticulated bone ornamentation that can be considered as skull exostosis (Figs. 5, 6; Roček and Lamaud, 1995: fig 1–5; Rage and Roček, 2007: fig.1–6; Laloy et al., 2013: fig. 3), and possess elongated squamosals with a well-developed zygomatic ramus forming the whole ventral margin of the orbit (the maxilla does not contribute to the ventral margin of the orbit; Fig. 5B). This character shared with both *Pyxicephalus adspersus* and *Aubria subsigillata* (both Pyxicephalinae) but not by *C. guentheri*.

Thaumastosaurus servatus shows all the synapomorphies of the Pyxicephalinae and is found in almost all analyses as the closest taxon to the pyxicephaline crown clade. It can therefore be confidently placed within Pyxicephalidae. Furthermore, we can consider *T. servatus* as a stem-Pyxicephalinae.

Several Cretaceous taxa were included in the analyses, including: *Baurubatrachus pricei*, *Eurycephalella alcinae*, *Arariphrynus placidoi*, *Beelzebufo ampinga*, *Uberabatrachus carvalhoi* and *Cratia gracilis*. Their position throughout the analyses are similar to the ones recovered in recent analyses (Báez and Gómez, 2018). *Baurubatrachus pricei* is recovered

within Atrastrobatrachia, close to *Calyptocephalella gayi*. *Eurycephalella alcinae* is recovered as a sister-taxon to the extant Myobatrachidae. *Arariphrynus placidoi* is recovered within the Craugastoridae, but this position is poorly supported, as the taxon was in several analyses placed within various neobatrachian clades, even within the Ranoides, as a sister-taxon to the Afrobatrachia. This variability can be explained by the poorly known postcranial bones, especially around the pectoral girdle, where most critical characters for both Hyloides and Ranoides are found. *Cratia gracilis* is placed in the same position as in previous analyses (Báez et al., 2009; Báez and Gómez, 2018). *U. carvalhoi* is recovered as a sister-taxon to Ceratophryidae, a position that was also recovered in some analyses of Báez and Gómez (2018) but differs from the position they retained as their preferred one (sister-taxon to *B. ampinga* clustered within Myobatrachia). *B. ampinga* is recovered in various positions, but most often as a sister-taxon to all Ceratophryidae, a position proposed by previous analyses (Evans et al., 2008; Evans et al., 2014). However, this was challenged recently (Báez and Gómez, 2018) and this uncertainty may be linked to the scarce post-cranial remains.

PALEOBIOGEOGRAPHIC IMPLICATIONS

Only a few sites from Africa have yielded pre-Pleistocene natatanuran fossils (Gardner and Rage, 2016). However, new material has been published in the last decade, and the fossil record of various natatanuran clades is beginning to be better documented.

The pre-Pleistocene fossil record of Ranoides is scarce, and even fewer fossil specimens older than the Miocene have been assigned to Natatanura (Sanchiz, 1998; Gardner and Rage, 2016). The few Ranoides specimens are moreover mostly fragmentary (de Broin et

al., 1974; Rage, 1984a; Roček and Lamaud, 1995; Báez and Werner, 1996). The origination time estimates in molecular studies for Ranoides are around 90.7 Ma (105.6 to 76.3 Ma, according to Frazão et al., 2015), about mid-Cretaceous, which is compatible with the fossil record given that the first presumed remains attributed to this clade date from the Cenomanian (between 100.5 Ma to 93.9 Ma; Báez and Werner, 1996; Marjanović and Laurin, 2014: fig.4). However, these remains were neither described nor illustrated, making the validity of this attribution difficult to assess. Other remains are from the Santonian (86.3 Ma to 83.6 Ma) of In Beceten, Niger (de Broin et al., 1974; Rage, 1984a) and from the Paleocene (66.0 to 56.0 Ma) from Cernay, France (Estes et al., 1967; Rage, 1984a). More recent remains, clearly attributed to Ranoides, are known in multiple Eocene sites, in northern Africa (Rage et al., 2021) and in the Quercy Phosphorites (Rage, 2016), with *T. servatus* and *T. bottii* (as well as other indeterminate forms; see Rage, 2016) constituting the best-known taxa.

For Natatanura, almost no fossil record is known. *Thaumastosaurus* is the oldest undisputed known taxon, as well as the oldest Ranoides with a valid taxon name (Sanchiz, 1998; Gardner and Rage, 2016; Rage, 2016). The Eocene age of this taxon is substantially more recent than the transition Cretaceous/Paleocene age for Natatanura inferred in the most recent molecular age analysis (Feng et al., 2017).

Although scarce, the fossil record of Ranoides (including Natatanura) is concentrated (in the Mesozoic at least) on the African continent (with a few exceptions in India), which suggests an African origin of the clade (Gardner and Rage, 2016). This hypothesis is strengthened by the presence of extant endemic clades on this continent (Gardner and Rage, 2016), including Pyxicephalidae. The attribution of *Thaumastosaurus*, an endemic clade of Western Europe (Vasilyan, 2018) to Pyxicephalidae extends the geographic range of Pyxicephalidae, which is otherwise limited to Sub-Saharan Africa (van der Meijden et al., 2011) for both extant and extinct taxa (Gardner and Rage, 2016). Moreover, *Thaumastosaurus*

(Middle to Late Eocene, 40.5 to 33.5 Ma) is much older than the other fossils previously attributed to that clade (around 5.1 Ma for the oldest specimen; Gardner and Rage, 2016). However, the attribution of *Thaumastosaurus* to Pyxicephalidae is well supported by our phylogenetic analysis and is compatible with the geological age proposed for the clades by molecular studies. Indeed, Pyxicephalidae diverged from its sister-clade around 60 Ma ago (Early to Middle Paleocene) according to recent molecular age (Feng et al., 2017). Within this clade, Pyxicephalinae diverged from Cacosterninae around 50 Ma ago (Hedges et al., 2015; Feng et al., 2017). The stratigraphic range for *Thaumastosaurus* is compatible with these molecular ages. Furthermore, we confirm the African affinities of *T. servatus*, proposed almost a decade ago (Laloy et al., 2013).

The presence of *Thaumastosaurus* in Europe could be linked to a faunistic exchange through an intermittent connection between Africa to Europe (Rage, 1984b; Gheerbrant and Rage, 2006). Indeed, some adapisoriculid (De Bast et al., 2012) and lousinid mammals (Sudre, 1979) may have immigrated through an intermittent connection between Africa and Eurasia in the Paleocene or Eocene. Starting in the Late Paleocene (Tanrattana et al., 2020), the temperature increased (Sluijs et al., 2006; Bohaty et al., 2009) in Western Europe, and remained warm until the end of the Middle Eocene (Bohaty et al., 2009). During this period, Western Europe was characterized by a subtropical climate, with evergreen forests under warm and humid conditions (Escarguel et al., 2008; Hérán et al., 2010; Tanrattana et al., 2020).

For the herpetofauna, the timing of this wave of immigration in Europe and paleobiogeographic origins of the Early Paleogene herpetological faunas of Europe still is poorly constrained. Numerous taxa appear in Europe at the earliest Eocene (MP7; Folie et al., 2005, 2013; Rage, 2012), but could have arrived during the end of the Paleocene. Bufonidae

already exhibit such a pattern with their earliest record in Europe being from the Paleocene of Cernay (Rage, 2003).

A major cooling is recorded during the Eocene-Oligocene transition (EOT). This is well established in numerous studies using different proxies (Escarguel et al., 2008; Hérin et al., 2010; Lunt et al., 2017; Tanrattana et al., 2020) and is linked to the establishment of permanent ice caps on Antarctica (Vandenberghe et al., 2012; Boscolo Galazzo et al., 2014). In Europe, the climate and environments dramatically changed. The climate became drier, with stronger seasonality and the appearance of a dry season (Escarguel et al., 2008; Tanrattana et al., 2020). The vegetation changed from forests to woodland savannah (Escarguel et al., 2008). This climate change probably triggered a moderate extinction event called the “Grande Coupure” (Stehlin, 1909), which has been particularly well-documented for mammals in Europe (Remy et al., 1987). Most of the subtropical fauna of African origin disappeared in Europe and was replaced by Eurasian taxa adapted to temperate conditions. This event is also documented in the herpetofauna (Delfino et al., 2003; Rage, 2006, 2012; Augé and Smith, 2009; Macaluso et al., 2019). Among amphibians, *Thaumastosaurus* is the best-documented victim of this turnover (Vasilyan, 2018).

CONCLUSION

The tomography and skeletal study of the specimen MNHN.F.QU17381, firstly described as the holotype of the bufonid *Bufo servatus*, yielded numerous data. The anatomical characters led to a new taxonomic attribution to the ranoid taxon *Thaumastosaurus servatus*. MNHN.F.QU17381 is the third mummy from the Old Collections

of the Quercy phosphorites attributed to this taxon, thus making it the best-known anuran in the Eocene of Western Europe.

Previous analyses placed *T. servatus* within the Natatanura, without specifying its position. Our analyses place *T. servatus* with the African hyperossified Pyxicephalinae (and likely as a stem-Pyxicephalinae and sister-taxon to the extant Pyxicephalinae), sharing a peculiar ornamentation as well as a combination of cranial features such as a contact between the squamosals and nasals, which is unique within Natatanura and Ranoides.

The position of *T. servatus* within Natatanura and Pyxicephalinae provides new insights to calibrate molecular dating analyses, as it represents the oldest fossil record for Pyxicephalidae and Pyxicephalinae, previously known only from the Pliocene (around 5 Ma) and Pleistocene respectively, extending therefore the geological range of the Pyxicephalinae of more than 33 Ma and making *T. servatus* one of the few well-known taxa firmly attributed to the Natatanura in the Paleogene. Moreover, Pyxicephalinae were previously considered to be distributed solely in Africa, whereas *T. servatus* is endemic to Western Europe.

Confirmation of these affinities extends the geographical range of pyxicephalines. The main biogeographical hypothesis is that the clade originated in Africa, and then migrated into Europe through dispersal of some natatanurans during the Eocene, making *Thaumastosaurus* a member of the African herpetofauna present in Europe until the Eocene/Oligocene transition, when it was eliminated around the Grande Coupure (Delfino et al., 2003; Rage, 2006, 2012). However, given the scarce fossil record of Ranoides in Africa, especially during the Paleocene and Eocene, other hypotheses cannot be ruled out. Further findings could help to understand the evolution of Ranoides, which represents the majority of extant anurans on the African continent.

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FIGURE CAPTIONS

FIGURE 1. Geographical maps of potential localities for the mummies. **A** map of France, with the Quercy region highlighted in black; **B** map of the Quercy region, with its south-eastern part highlighted in gray square outline (red in online version); **C** close-up on the south-eastern Quercy region, modified from Gèze (1949), with the two-potential locations for sites that yielded the mummies in bold. Black dots indicate phosphorite quarries listed by Gèze (1949), gray (red online) squares indicate putative origin sites for the mummy series near Villeneuve, black arrow indicates the location of the site ‘les Tempories’, transparent circle indicates the area of the Rosières sites. [planned for full page width]

FIGURE 2. External views of the specimen MNHN.F.QU17381, holotype of “*Bufo servatus*” now attributed to *T. servatus* in **A** anterior; **B** right lateral; **C** posterior; **D** left lateral; **E** dorsal and **F** ventral views. ? indicate the area previously identified as a parotoid gland.

Abbreviations: **eb**, eyeball; **nos**, nostril; **hum**, humerus; **vert**, vertebrae; **urst**, urostyle.

[planned for page width]

FIGURE 3. 3D-model of the specimen MNHN.F.QU17381. **A** whole specimen in dorsal view with soft tissue digitally rendered transparent to show the color-coded skeleton; **B** dorsal view of the sole osteological component; **C** whole specimen in right dorso-antero-lateral view with soft tissue digitally rendered transparent to show the color-coded skeleton; **D** same view of the sole osteological component. **Abbreviations:** **ang**, angulosplenial; **fp**, frontoparietals; **hum**, humerus; **il**, ilium; **mx**, maxilla; **na**, nasal; **ptgrd**, pectoral girdle; **qj**, quadratojugal; **sq**, squamosal; **vo**, vomer; **vtc**, vertebral column. [planned for page width]

FIGURE 4. External views of specimens MNHN.F.QU17279 and MNHN.F.unnumbered, both referred to *T. servatus*. **A–C** specimen QU 17279 in **A** dorsal view; **B** close-up of the rectangular region in **A** to show the ridges and folds of the preserved skin on the dorsal surface of the anterior trunk region; **C** same specimen in left lateral view; **D–E** specimen MNHN.F.unnumbered in **D** dorsal; and **E** right lateral views. Black arrow indicates the area of potential tympanic membrane. **Abbreviations:** **eb**, eyeball; **na**, nasals. [planned for page width].

FIGURE 5. The almost complete and articulated skull of the mummy MNHN.F.QU17381.

Shown in **A** dorsal; **B** right lateral; **C** palatal and **D** posterior views. **Abbreviations:** **aroc**, canal for the arteria occipitalis; **cp**, crista parotica; **fm**, foramen magnum; **fp**, frontoparietals; **fpp**, posterior process of the frontoparietals; **grnad**, groove for the nasolacrimal duct; **lma**, lamella alaris; **mch**, choanal margin; **mdp**, medial process; **mfg**, medial flange; **mx**, maxilla; **na**, nasal; **pal**, palatine; **par**, parasphenoid; **pct**, pars contacta; **pdscp**, prominencia ducti semicircularis posterioris; **pg**, processus glenoidalis; **plc**, plectrum; **ppl**, processus posterolateralis; **ppoc**, processus prooticoccipitalis; **ptd**, pterygoid; **qj**, quadratojugal; **qu**,

processus maxillaris; **ppob**, processus paraorbitalis; **ppn**, posterior process of the nasals; **ppoc**, processus prooticoccipitalis; **pptm**, posterior process of the maxilla; **ppl**, processus posterolateralis; **pptd**, processus pterygoideus; **pzg**, processus zygomatico-maxillaris; **rvg**, recessus vaginiformis; **rpa**, ramus paroticus; **sqpp**, posterior process of the squamosal; **su?**, putative suture of the frontoparietals; **tsob**, tectum supraorbitale. [planned for page width]

FIGURE 7. Suspensorium and Palate bones from MNHN.F.QU17381. **A** left quadratojugal in lateral view; **B** right angulosplenial in dorsal view; **C** right angulosplenial and articular in dorsal view; **D** right palatine in ventral view; **E** right vomer in ventral view; **F** parasphenoid in ventral view; **G** left pterygoid in dorsal view. **Abbreviations:** **alae**, alae of the parasphenoid; **art**, articular; **cpcrd**, crista paracornoidea; **cmnex**, crista mandibulae externa; **exs**, extremitas spatulate; **lm**, lamina medialis; **mch**, choanal margin; **mdp**, medial process; **par.pp**, posterior process of the parasphenoid; **par.mp**, posterior margin of the parasphenoid; **pcha**, processus choanalis anterior; **pchp**, processus choanalis posterior; **pcrd**, processus coronoideus; **pcl**, cultriform process; **pj**, processus jugularis; **pmx**, processus palatinus

maxillae; **qu**, quadratum; **mmx**, maxillar margin; **mm**, medial margin; **ra**, ramus anterior; **ri**, ramus interior; **rp**, ramus posterior; **scm**, sulcus pro cartilagine Meckeli; **sptd**, sulcus pterygoideus; **trf**, triangular facet; **vo.pa**, processus anterior of the vomer. [planned for page width]

FIGURE 8. Endocranial bones of MNHN.F.QU17381. **A–C** sphenethmoid in **A** dorsal; **B** right lateral and **C** anterior views; **D–G** prooticoccipital in **D** posterior; **E** dorsal; **F** anterior and **G** ventral views; **H** left stapes in posterior view; **I** right hyoid bone in dorsal view.

Abbreviations: **cp**, crista parotica; **dsph**, dorsal exposure of the sphenethmoid; **ddp**, depression anterior to the prominentia ducti semicircularis posterioris of the prooticoccipital; **ffp**, fenestra frontoparietalis; **feov**, fenestra ovalis; **jf**, jugular foramen; **fm**, foramen magnum; **grvj**, groove for the vena jugularis; **lsorb**, lamina supraorbitalis; **mk**, median keel; **occ**, exoccipital; **orbf**, orbitonasal foramen; **p.n**, notch on the medial surface of the plectrum; **pdscp**, prominentia ducti semicircularis posterioris; **pgr?**, putative perilymphatic groove; **pip**, pars interna plectri; **pmp**, processus medialis plectri; **prf**, prootic foramen; **pro**, prootic; **sam**,

sella amplificans; **sn**, septum nasi; **son**, solum nasi; **sph.lp**, lateral process of the sphenethmoid; **tn**, tectum nasi; **tsy**, tectum synotium; **uf**, unknown foramen?. [planned for page width]

FIGURE 9. Articulated diplasiocoelous vertebral column of MNHN.F.QU17381, without the urostyle in **A** dorsal; **B** left lateral and **C** ventral views. **Abbreviations:** **ns**, neural spine; **n**, notch on the sacral apophyse; **poz**, postzygapophysis; **prz**, prezygapophysis; **sav**, sacral vertebrae; **stp**, sacral transverse process; **tp**, transverse process. [planned for 2/3 page width]

FIGURE 10. Vertebral elements of the column of MNHN.F.QU17381. **A–B** atlas in **A** anterior and **B** posterior views; **C** VIII presacral vertebra in ventral view; **D–F** sacral vertebrae in **D** lateral; **E** anterior and **F** posterior views; **G–H** urostyle in **G** anterior and **H** lateral views. **Abbreviations:** **acd**, anterior condyle; **act**, anterior cotyle; **adp**, anterodorsal process; **atl**, anterior lamina; **dc**, dorsal crest; **dl**, diapophyseal lamina; **ns**, neural spine; **occt**, occipital cotyle; **pcd**, posterior condyle; **poz**, postzygapophysis; **prz**, prezygapophysis; **psl**, posterior lamina; **stp**, sacral transverse process; **vrc**, vertebral canal. [planned for page width]

FIGURE 11. Articulated bony pectoral girdle of MNHN.F.QU17381 in ventral view.

Abbreviations: **cl**, clavicle; **cor**, coracoid; **ost**, omosternum; **scp**, scapula; **sscp+clt**, suprascapular+cleithrum; **st**, sternum. [planned for 2/3 page width]

FIGURE 12. Bony elements of the pectoral girdle of MNHN.F.QU17381. **A–B** left suprascapular + cleithrum complex in **A** lateral and **B** medial views **C–E** right scapula in **C** lateral; **D** medial and **E** ventral views (orientation follows Duellman and Trueb, 1996: 346, fig. 13-35); **F** right coracoid in dorsal view; **G–H** left coracoid in **G** ventral and **H** medial views; **I** right clavicle in dorsal view; **J** sternum in dorsal view; **K** omosternum in dorsal view.

Abbreviations: **cal**, callus; **clt**, cleithrum; **coma**, anterior margin of the coracoid; **comp**, posterior margin of the coracoid; **exm**, extremitas medialis; **gdfo**, glenoid fossa; **ho**, hook; **lrt**, lamina recurvata; **msscp**, margo suprascapularis; **mv**, margo vertebralis; **mc**, medial crest; **pacm**, processus acromialis; **pecd**, processus epicoracoidalis; **pgd**, processus glenoidalis; **psscp**, processus suprascapularis; **ra**, ramus anterior; **scma**, anterior margin of the scapula; **scmp**, posterior margin of the scapula; **sctpcd**, sulcus cartilagine praecoracoidealis; **sigd**, sinus interglenoidalis; **sspcma**, anterior margin of the suprascapular+cleithrium. [planned for page width]

FIGURE 13. Humerus and Ilium of MNHN.F.QU17381. **A** left humerus in lateral view; **B** right ilium in lateral view. **Abbreviations:** **dc**, dorsal crest; **ish**, iliac shaft; **prxh**, proximal head; **vc**, ventral crest. [planned for column width]

FIGURE 14. Reduced consensus trees from two analysis. **A** Simplified strict consensus of 90 MPTs of 1373 steps (CI = 0.137, RI = 0.422) from the analysis under equal weight (EW), multistate characters ordered; **B** Simplified strict consensus of 2 MPTs of 67 steps (CI = 0.168, RI = 0.548) from the analysis under implied weight (IW) with k = 7, multistate characters ordered. The † symbol represents extinct taxa, the red area represents hyperossified ranoid taxa, the blue area represents the “Ranoides”, the yellow area represents the clade

Afrobatrachia + *Arariphrynus placidoi*, the brown area represents the microhylids (all colors visible only online). [planned for 2/3 page width]

FIGURE 15. Simplified MPT from a constrained analysis. Reduced MPT of 72 steps (CI = 0.150, RI = 0.459) using a molecular scaffold tree from Jetz and Pyron (2018), performed under IW with $k = 7$, multistate characters ordered. The † symbol represents extinct taxa. [planned for page width]