Head, skull–neck and extrinsic eye musculature of the dicraeosaurid sauropod *Bajadasaurus pronuspinax*

JUAN PABLO GARDERES[1,2]
NÉSTOR TOLEDO[1,3]
JOHN ANDREW WHITLOCK[4,5]
MARIANO MILITELLO[1,3]
PABLO ARIEL GALLINA[1,2]

1. Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). Ciudad Autónoma de Buenos Aires, Argentina.
2. Centro de Ciencias Naturales, Ambientales y Antropológicas (CCNAA), Universidad Maimónides (UMAI). Ciudad Autónoma de Buenos Aires, Argentina.
3. División Paleontología Vertebrados (DPV), Unidades de Investigación Anexo Museo, Facultad de Ciencias Naturales y Museo (FCNyM), Universidad Nacional de La Plata (UNLP). La Plata, Buenos Aires, Argentina.
4. Science and Mathematics Department, Mount Aloysius College. Cresson, Pennsylvania, USA.
5. Section of Vertebrate Paleontology, Carnegie Museum of Natural History. Pittsburgh, Pennsylvania, USA.

HEAD, SKULL–NECK AND EXTRINSIC EYE MUSCULATURE OF THE DICRAEOSAURID SAUROPOD *BAJADASAURUS PRONUSPINAX*

JUAN PABLO GARDERES[1,2], NÉSTOR TOLEDO[1,3], JOHN ANDREW WHITLOCK[4,5], MARIANO MILITELLO[1,3], AND PABLO ARIEL GALLINA[1,2]

[1]Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). Ciudad Autónoma de Buenos Aires, Argentina.

[2]Centro de Ciencias Naturales, Ambientales y Antropológicas (CCNAA), Universidad Maimónides (UMAI). Ciudad Autónoma de Buenos Aires, Argentina. *garderes.juanpablo@maimonides.edu*; *gallina.pablo@maimonides.edu*

[3]División Paleontología Vertebrados (DPV), Unidades de Investigación Anexo Museo, Facultad de Ciencias Naturales y Museo (FCNyM), Universidad Nacional de La Plata (UNLP). La Plata, Buenos Aires, Argentina. *ntoledo@fcnym.unlp.edu.ar*; *marianomilitello91@gmail.com*

[4]Science and Mathematics Department, Mount Aloysius College. Cresson, Pennsylvania, USA. *jwhitlock@mtaloy.edu*

[5]Section of Vertebrate Paleontology, Carnegie Museum of Natural History. Pittsburgh, Pennsylvania, USA.

JPG: https://orcid.org/0000-0002-9876-1232; **NT:** https://orcid.org/0000-0002-6833-3165; **JAW:** https://orcid.org/0000-0002-1118-2925; **MM:** https://orcid.org/0009-0007-6967-6585; **PAG:** https://orcid.org/0000-0001-9604-3694

Abstract. Cranial muscles perform important roles triggering diverse paleobiological faculties, such as feeding, communication, alert postures, etc. Within Sauropoda, a clade with high specializations in skull architectures, and several partially complete skulls recovered, detailed reconstructions of the cranial muscles are mainly limited to two of the most famous taxa of the clade: *Diplodocus* and *Camarasaurus*. The cranial musculature for Dicraeosauridae, a minor group within the clade, has been gingerly described, based on the few suitable specimens. Herein, the craniomandibular, extrinsic eye, and cervicocranial musculatures of *Bajadasaurus pronuspinax* are inferred, resulting in the first detailed reconstruction for Dicraeosauridae on these muscular groups, and these are compared with previous inferences in Dicraeosauridae and with other Sauropoda and non-avian dinosaurs. The musculature of *Bajadasaurus* shows a shift of angle in the temporal musculature when passing through the inferior temporal window (probably indicating the presence of a cartilage for support), an important role of the orbitotemporal muscles in a hypothetical cranial kinesis (which, if true, would allow pseudo-palinal movements in a rostral direction during the feeding process), an avian-like configuration of the eye muscles, and high lateroflexor moment arms for the skull-neck complex. Dicraeosauridae show clear osteological correlates for a high number of the craniomandibular and cervicocranial muscles, albeit some of these correlates might not be exclusively dedicated for musculature, and could be indicating the presence of alternative soft tissues.

Key words. *Bajadasaurus*. Dicraeosauridae. Sauropoda. Cranial musculature. Paleoecology.

Resumen. MUSCULATURA DE LA CABEZA, CABEZA-CUELLO Y OCULAR EXTRÍNSECA DEL SAURÓPODO DICRAEOSÁURIDO *BAJADASAURUS PRONUSPINAX*. Los músculos craneanos cumplen roles importantes impulsando diversas facultades paleobiológicas, tales como alimentación, comunicación, posturas de alerta, etc. Dentro de Sauropoda, un clado con una alta especialización en la arquitectura craneana, y numerosos cráneos recuperados parcialmente completos, las reconstrucciones detalladas de la musculatura craneana están principalmente limitadas a dos de los taxa más famosos del clado: *Diplodocus* y *Camarasaurus*. La musculatura craneana de Dicraeosauridae, un grupo menor dentro del clado, ha sido cautelosamente descripta, basado en los pocos especímenes aptos. En este artículo, las musculaturas craniomandibular, ocular extrínseca y cervicocranial de *Bajadasaurus pronuspinax* son inferidas, resultando en la primera reconstrucción detallada para Dicraeosauridae para estos grupos musculares, siendo comparada con inferencias previas en Dicraeosauridae, otros Sauropoda y dinosaurios no avianos. La musculatura de *Bajadasaurus* presenta un cambio de ángulo en la musculatura temporal tras atravesar la ventana temporal inferior (probablemente indicando la presencia de un cartílago de soporte), un rol importante de la musculatura orbitotemporal en una hipotética quinesis craneana (la cual, de ser real, permitiría movimientos pseudo-palinales en dirección rostral durante el proceso alimentario), una configuración aviana de la musculatura ocular, y altos brazos de momento lateroflexores para el complejo cráneo-cuello. Los Dicraeosauridae muestran claros correlatos osteológicos para un gran número de músculos tanto craniomandibulares como cervicocraneales, aunque algunos de estos correlatos podrían no estar exclusivamente relacionados a musculatura, pudiendo indicar la presencia de tejidos blandos alternativos.

Palabras clave. *Bajadasaurus*. Dicraeosauridae. Sauropoda. Musculatura craneana. Paleoecología.

INTRODUCTION

The herald cranial musculature study of sauropod dinosaurs was conducted on the diplodocid *Diplodocus* (Haas, 1963), where a comparative analysis based on extant reptiles (Crocodylia and Lepidosauria) was performed. In the following decades, the knowledge on this topic increased

with the recovery of different sauropod cranial remains (*e.g.*, Salgado & Calvo, 1992; Zheng, 1996; Sereno et al., 2007; Holliday, 2009; Young et al., 2012; Nabavizadeh, 2020), primarily focusing on the adductor muscle groups (both temporal and palatal), which are of great importance in the biomechanical properties related to the jaw-closing and bite forces faculties (*e.g.*, Barrett & Upchurch, 1994; Calvo, 1994; Young et al., 2012; Button et al., 2016). However, other cranial muscle groups have been poorly studied in Sauropoda, with the exception of the nuchal muscles of *Diplodocus* and *Camarasaurus* (Button et al., 2014), despite the abundance of exquisitely preserved specimens in the clade (*e.g.*, *Abydosaurus* DINO 16488; *Diplodocus* CM 11161; *Nemegtosaurus* Z.PAL MgD-I/9; *Nigersaurus* MNN GAD512; *Sarmientosaurus* MDT-PV 2; *Tapuiasaurus* MZUSP 807—previously referred to as MZSP-PV), some of which also include ossicles of a scleral ring (*sensu* Franz-Odendaal, 2018; *Diplodocus* CM 11161; *Smitanosaurus* USNM 5384). Specifically, within Dicraeosauridae, the only taxa for which the cranial musculature was partially reconstructed are *Amargasaurus* (Salgado & Calvo, 1992) and *Dicraeosaurus* (Nabavizadeh, 2020), despite the increase in the total number of specimens recovered (or reassigned) since the beginning of the 21st century (Harris & Dodson, 2004; Tschopp & Mateus, 2013; Xu et al., 2018; Gallina et al., 2019; Whitlock & Wilson Mantilla, 2020).

Bajadasaurus pronuspinax (Gallina et al., 2019) is a dicraeosaurid sauropod whose holotype (MMCh-PV 75) includes a partially complete skull and cervical vertebral elements (Gallina et al., 2019; Garderes et al., 2023). Hitherto, this dicraeosaurid taxon is the only one known to preserve a complete lower hemimandible. Therefore, previous attempts to address the cranial musculature among the clade have been strictly limited to those extrapolating the mandibular morphology from closely related taxa, such as diplodocids (*e.g.*, Nabavizadeh, 2020), albeit the post-dentary morphology of Dicraeosauridae and other diplodocoids (which includes diplodocids) differ significantly (*e.g.*, Garderes et al., 2023). Among Dicraeosauridae, *Bajadasaurus* differs from other taxa in several cranial traits, such as the medially extended post-temporal fenestra, extremely elongate and thin basipterygoid processes, and an expanded rostroventral lamina in the quadrate (Gallina et al., 2019; Garderes et al.,

2023), while other traits of the skull are not comparable, such as the angular being longer than the surangular (synapomorphy in Gallina et al., 2019). The overall preservation of this specimen represents a remarkable opportunity for expanding the knowledge on several paleobiological features of this taxon, such as the muscular architecture and variability among Dicraeosauridae, its feeding paleobiology (based on the muscular reconstruction and the morphological analysis of the kinetic joints), and putative ecological strategies (defensive or survival directed). Moreover, due to the fact that *Bajadasaurus* is the only dicraeosaurid with preserved post-dentary elements, it is the best candidate for representing the muscular architecture of the clade.

MATERIALS AND METHODS

The 3D digital models of *Bajadasaurus* were segmented in Garderes et al. (2023) based on the holotype of this taxon (MMCh-PV 75). From these original models, a retrodeformed digital model (Fig. 1) was produced following Lautenschlager et al. (2014) in order to perform a biomechanical test and a reconstruction of the musculature, using the software Blender (V. 2.90.0). This involved: a) the filling of the spaces where elements were broken but spatially close (and contacts between the parts were recognizable); b) the symmetrization of plastic-deformed traits (such as the basipterygoid processes); c) the reorientation and articulation of disarticulated elements; and d) the complete reconstruction of missing elements (*e.g.*, palatine) based on the morphology of closely related taxa with the missing element preserved (*e.g.*, for the palatine, *Diplodocus* CM 11255 was used as a model; Whitlock et al., 2010). The cranial musculature (Fig. 2) was reconstructed following Lautenschlager (2013), which represents a four-stepped workflow involving: a) the mapping of osteological correlates (when recognizable); b) the application of a topological criterion (when osteological correlates are not recognizable); c) the application of a neurovascular criterion (when the topological criterion fails); and d) the application of a homological criterion (when the neurovascular criterion fails), assisted by the Extant Phylogenetic Bracketing (EPB; Witmer, 1995). The muscles were reconstructed using the software Avizo (7.0).
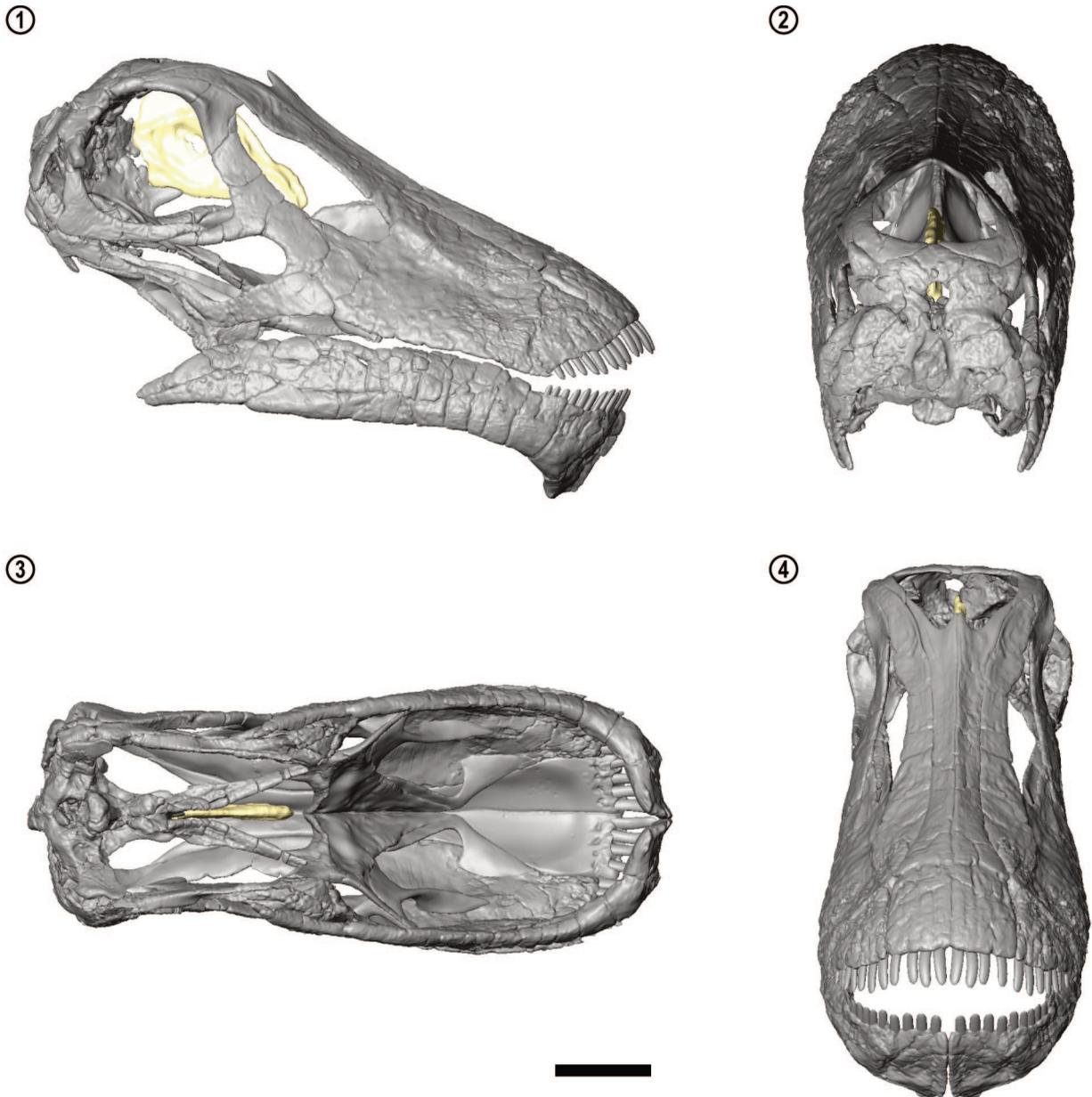
Figure 1. Retrodeformed skull of *Bajadasaurus pronuspinax*. 1, right lateral view; 2, dorsal view; 3, ventral view; 4, frontal view. Colour pattern: grey, skull; light yellow, interorbitary septum. Scale= 5 cm.

Nomenclature of the adductor musculature (orbitotemporal, palatal and temporal) follows Holliday (2009). As for the extrinsic eye musculature, a nomenclature following Smith-Paredes & Bullar (2019) was used. Lastly, the nomenclature for the axial and depressor muscles follows Militello et al. (2026) and Garderes et al. (2022), based on Tsuihiji (2010), and are included within the term cervicocranial—rather than the formerly used term craniocervical (*e.g.*, Snively & Russell, 2007a)—based on a proximo-distal-attachment-naming criterion, as in each of the muscles gathered under this term (*e.g.*, *transversospinalis capitis* originating from the neural spines and inserting on the skull), and other muscular groups. The proximal attachment, where the origin attaches, is placed on the most static part of the lever system, whereas the distal is placed on the most dynamic part of the system.

A 2D analysis of the mean inclination of the lines of action of the muscles was performed. The lines of action
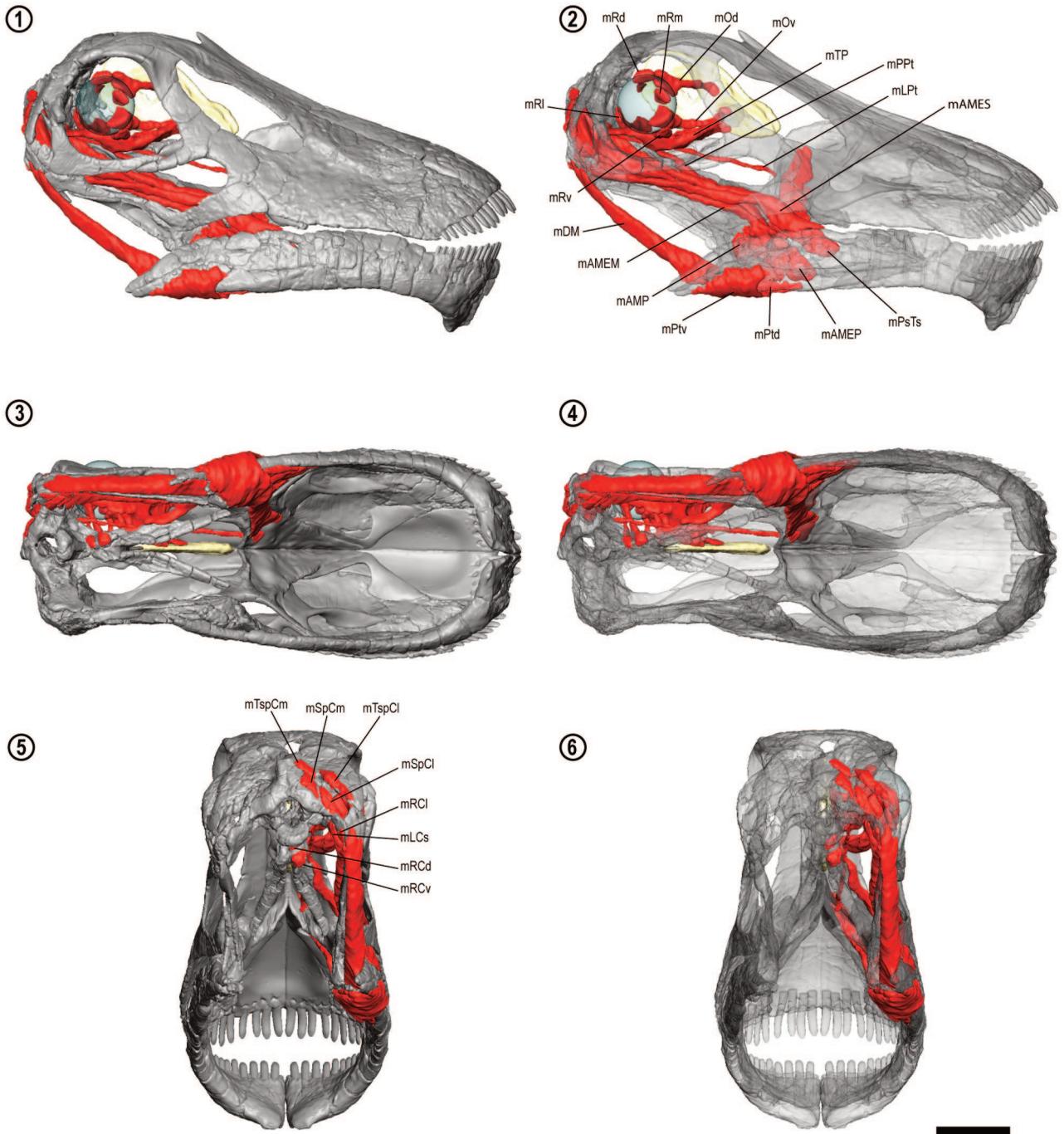
Figure 2. Cranial musculature of *Bajadasaurus pronuspinax*. 1–2, lateral view; 3–4, ventral view; 5–6, caudal view. Abbreviations: mAMEM, muscle *adductor mandibulae externus medialis*; mAMEP, muscle *adductor mandibulae externus profundus*; mAMES, muscle *adductor mandibulae externus superficialis*; mAMP, muscle *adductor mandibulae posterior*; mDM, muscle *depressor mandibulae*; mLCs, muscle *longissimus capitis superficialis*; mLPt, muscle *levator pterygoideus*; mOd, muscle *obliquus dorsalis*; mOv, muscle *obliquus ventralis*; mPPt, muscle *protractor pterygoideus*; mPsTs, muscle *pseudotemporalis superficialis*; mPtd, muscle *pterygoideus dorsalis*; mPtv, muscle *pterygoideus ventralis*; mRCd, muscle *rectus capitis dorsalis*; mRCl, muscle *rectus capitis lateralis*; mRCv, muscle *rectus capitis ventralis*; mRd, muscle *rectus dorsalis*; mRl, muscle *rectus lateralis*; mRm, muscle *rectus medialis*; mRv, muscle *rectus ventralis*; mSpCl, muscle *splenius capitis lateralis*; mSpCm, muscle *splenius capitis medialis*; mTP, muscle *tensor periorbitae*; mTspCl, muscle *transversospinalis capitis lateralis*; mTspCm, muscle *transversospinalis capitis medialis*. Colour pattern: grey, skull; light blue (in transparency), inferred eye; light yellow, interorbitary septum; red, muscle. Scale= 5 cm.

were inferred by connecting the middle points at the lines where a muscle attachment shows its higher extension (one at the origin and one at the insertion). These lines of action are estimated in lateral view (the extended projection regarding the sagittal plane) and with the lower jaw in resting position (*i.e.*, in occlusion) using the software Fiji (ImageJ v. 1.54p). Then, the angle between the estimated line of action and the projected line of the orthal plane (in lateral view) was estimated, resulting in the mean apparent inclination of the muscle fibers. This analysis was only applied to the palatal and temporal muscles, as these are of key importance for the biomechanical analysis performed here, and are the only inferred muscles—aside from the depressor musculature—that pass through the orthal plane. The inclination of the estimated line of action is defined based on the proximo-distal direction given by the position of the origin and the insertion of each individual muscle.

Institutional acronyms. CFA-OR, Fundación de Historia Natural Félix de Azara, Colección Ornitológica, Buenos Aires, Argentina; **CM,** Carnegie Museum of Natural History, Pennsylvania, USA; **DINO,** Dinosaur National Monument, Colorado, USA; **MACN-Pv N,** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Colección Nacional de Paleontología de Vertebrados (Neuquén), Ciudad Autónoma de Buenos Aires, Argentina; **M.BR.,** Museum für Naturkunde der Humboldt-Universität, Berlin, Germany; **MDT-PV,** Museo Desiderio Torres, Colección de Paleontología de Vertebrados, Chubut, Argentina; **MMCh-PV,** Museo Municipal de Villa El Chocón "Ernesto Bachmann", Colección de Paleontología de Vertebrados, Neuquén, Argentina; **MNN GAD,** Musée National du Niger, Gadoufaoua, Niamey, Republic of Niger; **MUVC AL,** University of Missouri, Vertebrate Colection, Alligator specimens, Missouri, USA; **MZUSP,** Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; **USNM,** United States National Museum, Washington, USA; **Z.PAL MgD,** Palaeobiological Institute of the Polish Academy of Sciences, Collection of Mongolian Dinosaurs, Warsaw, Poland.

Anatomical abbreviations. CN, cranial nerve; **ITW,** inferior temporal window; **mAME,** muscle *adductor mandibulae externus*; **mAMEM,** muscle *adductor mandibulae externus medialis*; **mAMEP,** muscle *adductor mandibulae externus profundus*; **mAMES,** muscle *adductor mandibulae externus superficialis;* **mAMP,** muscle *adductor mandibulae posterior*; **mCID,** muscle *constrictor internus dorsalis;* **mDM,** muscle *depressor mandibulae;* **mLCs,** muscle *longissimus capitis superficialis;* **mLPt,** muscle *levator pterygoideus;* **mOd,** muscle *obliquus dorsalis;* **mOv,** muscle *obliquus ventralis;* **mPPt,** muscle *protractor pterygoideus;* **mPsTp,** muscle *pseudotemporalis profundus;* **mPsTs,** muscle *pseudotemporalis superficialis;* **mPt,** muscle *pterygoideus;* **mPtd,** muscle *pterygoideus dorsalis;* **mPtv,** muscle *pterygoideus ventralis;* **mRCd,** muscle *rectus capitis dorsalis;* **mRCl,** muscle *rectus capitis lateralis;* **mRCv,** muscle *rectus capitis ventralis;* **mRd,** muscle *rectus dorsalis;* **mRl,** muscle *rectus lateralis;* **mRm,** muscle *rectus medialis;* **mRv,** muscle *rectus ventralis;* **mSpC,** muscle *splenius capitis;* **mSpCl,** muscle *splenius capitis lateralis;* **mSpCm,** muscle *splenius capitis medialis;* **mTP,** muscle *tensor periorbita*e; **mTspC,** muscle *transversospinalis capitis;* **mTspCl,** muscle *transversospinalis capitis lateralis;* **mTspCm,** muscle *transversospinalis capitis medialis.*

RESULTS
Muscular reconstruction

From the preserved cranial remains of *Bajadasaurus*, the orbitotemporal, palatal, temporal, depressor (partially), extrinsic eye and cervicocranial (partially) muscle groups were reconstructed.

Orbitotemporal muscles

Muscles connecting the neurocranium and the palate, derivate from the mCID (Holliday, 2009) (Figs. 3.1–5).
Muscle *tensor periorbitae* (CN V3). Alternative nomenclature= muscle *levator bulbi* (Lessner & Holliday, 2020). This muscle is present both in extant Crocodylia and Aves (Holliday & Witmer, 2007; Holliday, 2009; Smith-Paredes & Bullar, 2019; Lessner & Holliday, 2020), forming a muscular separation between the orbit and the jaw muscles (Van den Berge & Zweers, 1993). In these clades, it originates from the lateral surface of the laterosphenoid in a prominent crest, and inserts onto the rostral portion of the interorbitary septum or the preotic pillar, although in some *Alligator mississippiensis* specimens (MUVC AL031; Lessner & Holliday, 2020) the mTP originates rostral to the origin of the mRl, caudal to the foramen of the CN II. This muscle is inferred
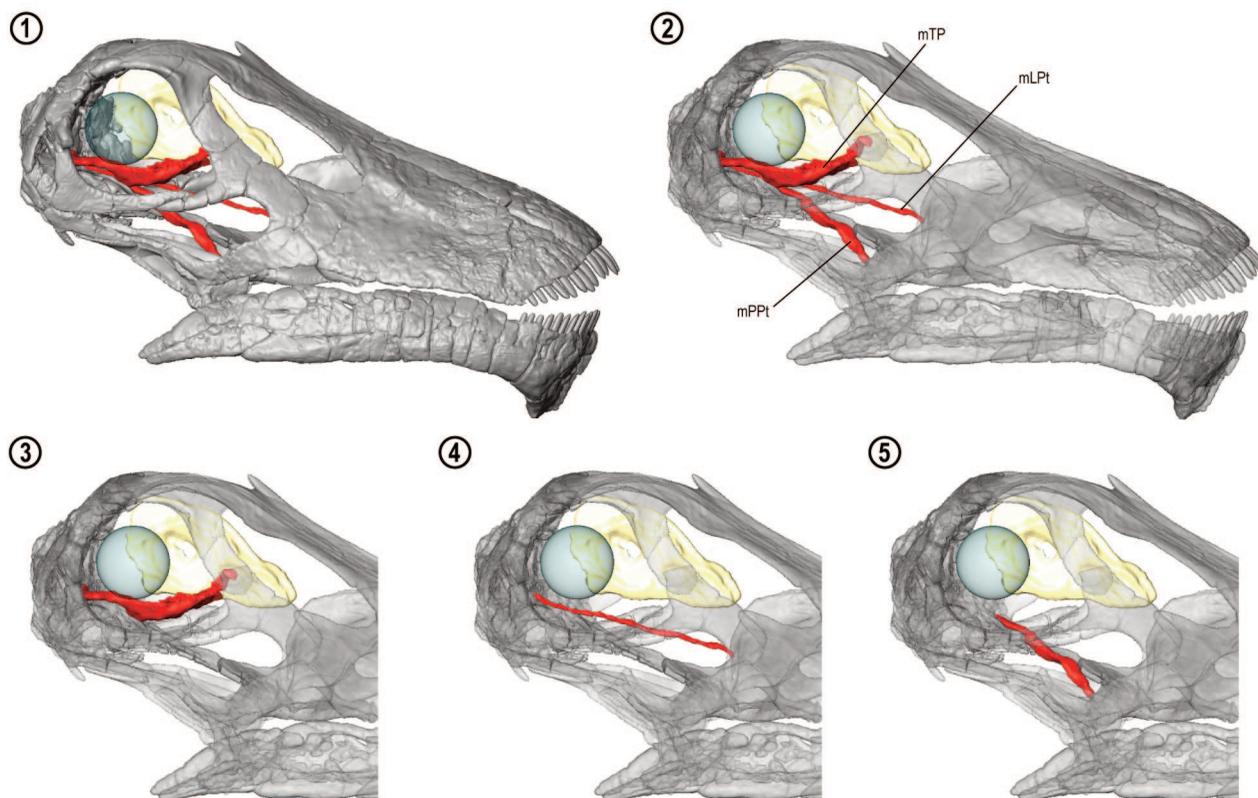
Figure 3. Orbitotemporal musculature. 1–2, general display in lateral view; 3, muscle *tensor periorbitae* (mTP); 4, muscle *levator pterygoideus* (mLPt); 5, muscle *protractor pterygoideus* (mPPt). Colour pattern: grey, skull; light blue (in transparency), inferred eye; light yellow, interorbitary septum; red, muscle. Scale= 5 cm.

to be present in non-avian dinosaurs, originating from the lateral expansion of the laterosphenoid (*crista prootica*; Holliday, 2009).

The mTP in *Bajadasaurus* was reconstructed with an origin on the lateral process of the laterosphenoid (Fig. 3.3), whose presence is considered as the osteological correlate in other non-avian dinosaurs (Holliday, 2009). The insertion of this muscle is inferred to attach to the interorbitary septum as in Aves and Lepidosauria, probably related to the fascia infratemporalis (Witzmann et al., 2019) (Fig. 3.3), as in other non-avian dinosaurs, the presence of mTP in *Bajadasaurus* represents a level I/II' inference.

Muscle *levator pterygoideus*. The mLPt tentatively develops in non-avian dinosaurs where the epipterygoid bone is present (Holliday, 2009), including some neosauropod taxa. However, it is not present in extant Crocodylia and Aves. This muscle would originate on the laterosphenoid, dorsal

to a foramen and the ophthalmic groove, inserting on the medial surface of the pterygoid and the epipterygoid, nearby the ascending process of the pterygoid, allowing the elevation of the dorsocaudal portion of the pterygoid.

The origin of mLPt in *Bajadasaurus* was reconstructed on the ascending process of the pterygoid on a clear osteological correlate as a small and subcircular fossa, placed on the rostral surface of the medial area of the crista prootica, dorsocaudal to the foramen for CN V (Fig. 3.4). The insertion of mLPt is inferred to attach to the caudal portions of the dorsal ascending process of the pterygoid (Fig. 3.4). The presence of mLPt in *Bajadasaurus* represents a level III/III' inference.

Muscle *protractor pterygoideus*. The mPPt originates at the base of the interorbitary septum, ventral to the ophthalmic groove, and inserts both on the pterygoid and the quadrate, allowing the protraction of the palatoquadrate bridge in

Aves; in Crocodylia, this muscle is absent (Holliday, 2009; Smith-Paredes & Bullar, 2019).

The origin of mPPt in *Bajadasaurus* was inferred to attach on the rostral surface of the ventral portion of the crista prootica, on the leaf-like expansion (Fig. 3.5), characteristic of Dicraeosauridae. This muscle inserts on the medial surface of the quadrate process of the pterygoid and the pterygoid process of the quadrate, leaving no clear osteological correlate (Fig. 3.5). The presence of this muscle in this taxon represents a level II/II' inference.

Palatal musculature

This muscular group includes those muscles originating from the internal arcade of the upper jaw (Figs. 4.1–6).

Muscle *pseudotemporalis profundus*. The mPsTp is lost in non-avian dinosaurs where the epipterygoid element is lost (Holliday, 2009). The attachment surface of the origin varies among the related extant taxa: it attaches onto the epipterygoid in Lepidosauria, on the laterosphenoid in Crocodylia, and on the quadrate in Aves (Holliday & Witmer, 2007; Jones et al., 2009). Its insertion attaches to a more conservative topological locus, on the coronoid eminence or its analogue (Holliday & Witmer, 2007). If it is present, the presence of the muscle in non-avian dinosaurs would represent a level I or I' inference. In non-avian dinosaurs where it was inferred (Holliday, 2009; Lautenschlager, 2013), its insertion attaches to the coronoid eminence. In Sauropodomorpha, the mPsTp was not inferred for *Diplodocus*, *Camarasaurus* nor *Plateosaurus* (Button et al., 2014, 2016; Lautenschlager et al., 2016; Nabavizadeh, 2020), although it was suggested that its origin migrated from the base of the epipterygoid to the supratemporal fossa (Nabavizadeh, 2020).

In the present study, the mPsTs was not reconstructed in *Bajadasaurus*, given the space limitations within the adductor supratemporal fossa. Both in the quadrate and the laterosphenoid, no osteological correlate tentatively assignable to the origin of this muscle was found, although we do not rule out the possibility of a correlate in the non-preserved, rostrodorsal surface of the quadrates. Moreover, the limited space in the passage through the ITW suggests that, even if this muscle was present, its cross-sectional area would be negligible compared to other adductor muscles. If its origin attached to the lateral surface of the quadrate, as in some extant Aves, the mPsTp would also have a minor volume given its topological constraints by the medial limits of the ITW (medially), the mAME group (laterally) and the mPt group (ventrally). The absence of an osteological correlate within the mandibular adductor fossa does not suggest the presence of mPsTp as an isolated muscle. An alternative possibility is that, as in Crocodylia (Holliday, 2009; Smith-Paredes & Bullar, 2019), the distal portion of the mPsTp merges its fibers with other temporal muscles, before it crosses the ITW.

Muscle *pterygoideus dorsalis*. In non-avian dinosaurs, the mPtd has been inferred to originate on the dorsal surface of the pterygoid and the palatine, as in Crocodylia and Aves (Holliday & Witmer, 2007; Smith-Paredes & Bullar, 2019), and inserting onto the medial surface of the retroarticular process, leaving clear osteological correlates on both surfaces (Holliday, 2009). In *Diplodocus*, *Camarasaurus*, *Plateosaurus* and *Shunosaurus* (Zheng, 1996; Young et al., 2012; Button et al., 2014, 2016; Lautenschlager et al., 2016) the mPtd was inferred to originate on the dorsal and rostral surfaces of the pterygoid, in some cases extending over the ectopterygoid, inserting on the ventromedial surface of the retroarticular process.

The mPtd was inferred in *Bajadasaurus* to originate on the dorsal surface of the pterygoid, rostral to the quadrate process of this element (Fig. 4.3). It is possible that this attachment extended rostrally, along the total lateral surface of the rostral process of the pterygoid, not preserved in the holotype. The attachment leaves a clear osteological correlate on the lateral surface of the element (Fig. 4.3). The insertion of mPtd attaches to the ventromedial surface of the retroarticular process and the medial portions of the angular, after the passage of the muscle through the ITW, leaving a clear osteological correlate as a depressed surface in the ventral area of the angular and prearticular (Fig. 4.3). The presence of mPtd in *Bajadasaurus* represents a level I/I inference. In lateral view, the mPtd orients almost parallel to the skull roof, and perpendicular to the plane containing the rostrum. Its fibers run laterally to the same of mPtv and medially to those of mAMP.

Muscle *pterygoideus ventralis*. The origin of mPtv attaches to the caudoventral surface of the pterygoid in Crocodylia
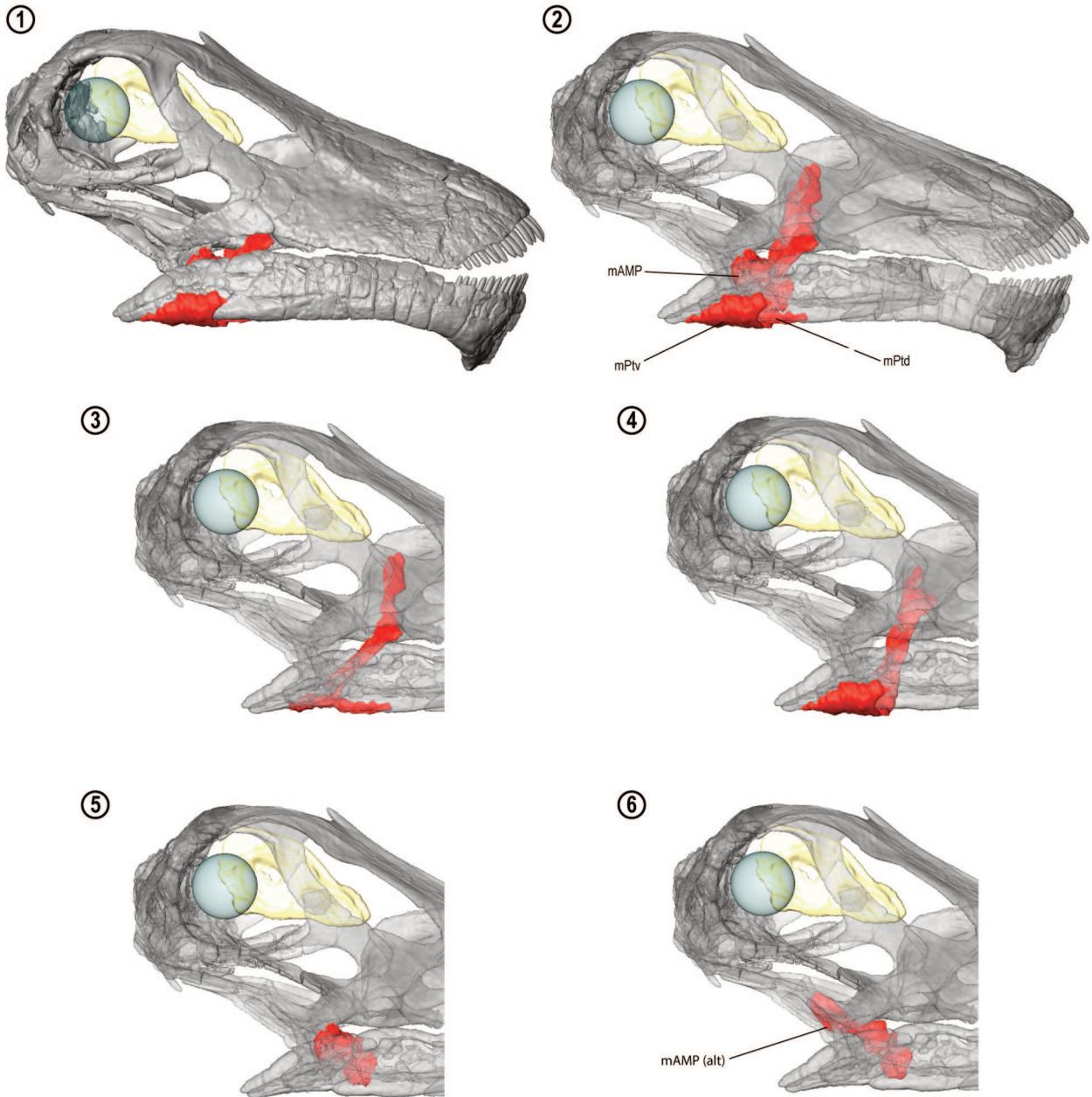
Figure 4. Palatal musculature. 1–2, general display in lateral view; 3, muscle *pterygoideus dorsalis* (mPtd); 4, muscle *pterygoideus ventralis* (mPtv); 5, muscle *adductor mandibulae posterior* (mAMP); 6, alternative reconstruction for mAMP. Colour pattern: grey, skull; light blue (in transparency), inferred eye; light yellow, interorbitary septum; red, muscle. Scale= 5 cm.

and Aves (Holliday, 2009; Smith-Paredes & Bullar, 2019), Lepidosauria (Daza et al., 2011) and *Sphenodon* (Jones et al., 2009). The locus of insertion of the muscle varies depending on the extant group. It attaches to the lateroventral surface of the retroarticular process, up to the surangular, in Lepidosauria, Crocodylia and Aves (Holliday & Witmer, 2007; Daza et al., 2011); however, with exceptions in Neognathae

(Smith-Paredes & Bullar, 2019), or the medioventral surface of the same process in *Sphenodon* and Neognathae (Jones et al., 2009; Smith-Paredes & Bullar, 2019). In non-avian dinosaurs (*e.g.*, Holliday, 2009; Young et al., 2012; Lautenschlager, 2013; Button et al., 2014, 2016; Lautenschlager et al., 2016) the mPtv has been inferred to have the same configuration as in Aves and Crocodylia, with

variable extensions of its insertion along the lateral surface of the caudal portion of the lower jaw.

In *Bajadasaurus*, the mPtv originates from the ventral surface of the pterygoid, evidenced by a strong, rugose and elevated surface as a clear osteological correlate, rostral to the quadrate process of the element (Fig. 4.4). The fibers of the mPtv extend along the medialmost area of the oral cavity, wrapping the lower jaw, and as a consequence, its insertion attaches to its lateral surface, surrounding laterally the retroarticular process, including both the angular and the surangular. This attachment leaves a depression and a change of inclination of the surface as an osteological correlate on the lateral surface of the lower jaw (Fig. 4.4). The presence of the mPtv in *Bajadasaurus* represents a level I/I inference. Its inclination in lateral view replicates the same of mPtd, as its major axis is perpendicular to the plane including the rostrum, and is almost parallel to the plane containing the skull roof.

Muscle *adductor mandibulae posterior*. The mAMP is topologically consistent in Aves, Crocodylia, Lepidosauria and *Sphenodon* (Holliday, 2009; Jones et al., 2009; Daza et al., 2011; Smith-Paredes & Bullar, 2019). Its origin in all related extant taxa attaches to the rostrolateral surface of the quadrate, while it inserts on the mandibular adductor fossa. In Aves, this muscle sometimes varies on its insertion, as there are differences between Neognathae—dorsolateral surface of the lower jaw—(Holliday, 2009; Smith-Paredes & Bullar, 2019) and Palaeognathae—dorsomedial surface of the lower jaw (Smith-Paredes & Bullar, 2019). In non-avian dinosaurs, the mAMP has been consistently inferred to originate on the rostrolateral surface of the quadrate, and to insert onto the mandibular fossa (*e.g.*, Rybczynski et al., 2008; Holliday, 2009; Lautenschlager, 2013; Button et al., 2014, 2016; Taylor et al., 2017; Nabavizadeh, 2020).

In *Bajadasaurus* the mAMP is inferred to originate from the ventrolateral surface of the quadrate, rostral to the articular process of the element (Fig. 4.5). The dorsal extension of this origin is limited by the reduced space of the caudal area of the ITW, restricted by the tight articulation between the quadrate and the quadratojugal, as well as by the passage of the mAME through the ITW rostrally. No clear osteological correlate for the origin was observed; however, this origin attaches onto the laminar expansion connecting the articular and pterygoid processes of the quadrate, a putative autapomorphic trait of *Bajadasaurus* (Garderes et al., 2023). The insertion of the mAMP attaches to the caudal area of the mandibular adductor fossa, rostral to the temporomandibular joint (Fig. 4.5). The presence of mAMP in *Bajadasaurus* represents a level I/I inference. In lateral view, the major axis of this muscle aligns perpendicular to the plane including the skull roof, and, among the adductor musculature, the mAMP is the shortest.

An alternative reconstruction (Fig. 4.6), with its origin attaching to the medial surface of the quadrate, would allow an increase in the dorsal extension of the muscle. However, this interpretation is less parsimonious, as this muscle attaches onto the medial face of the quadrate in few extant taxa, including *Salvator merianae* (Gröning et al., 2013).

Temporal musculature

Group of muscles including those that originate from the supratemporal fossa (Figs. 5.1–6).

Muscle *adductor mandibulae externus superficialis*. The mAMES in extant related taxa originates on different elements, being either the squamosal or the quadrate in Aves, the quadrate in Crocodylia, on in the upper temporal bar, mostly formed by the postorbital and the squamosal in Lepidosauria (Holliday & Witmer, 2007; Smith-Paredes & Bullar, 2019; but see Daza et al., 2011). In *Sphenodon*, this origin surface potentially expands ventrally attaching to a fascia related to the infratemporal fenestra (Jones et al., 2009), an attachment that is considered as an alternative, differentiated muscle in Lepidosauria: the muscle *levator anguli oris*—not developed in Aves and Crocodylia (Holliday, 2009). The insertion of the mAMES on the lower jaw consistently attaches to the dorsolateral surface and the dorsal margin of the surangular (Holliday, 2009). In non-avian dinosaurs, and particularly in Sauropodomorpha, the mAMES has been inferred as originating by attaching to the medial surface of the upper temporal bar, and inserting onto the dorsolateral surface of the surangular, caudal to the coronoid, if present as an isolated element, or the coronoid eminence (Rybczynski et al., 2008; Holliday, 2009; Young et al., 2012; Lautenschlager, 2013; Button et al., 2014, 2016; Taylor et al., 2017; Nabavizadeh, 2020).

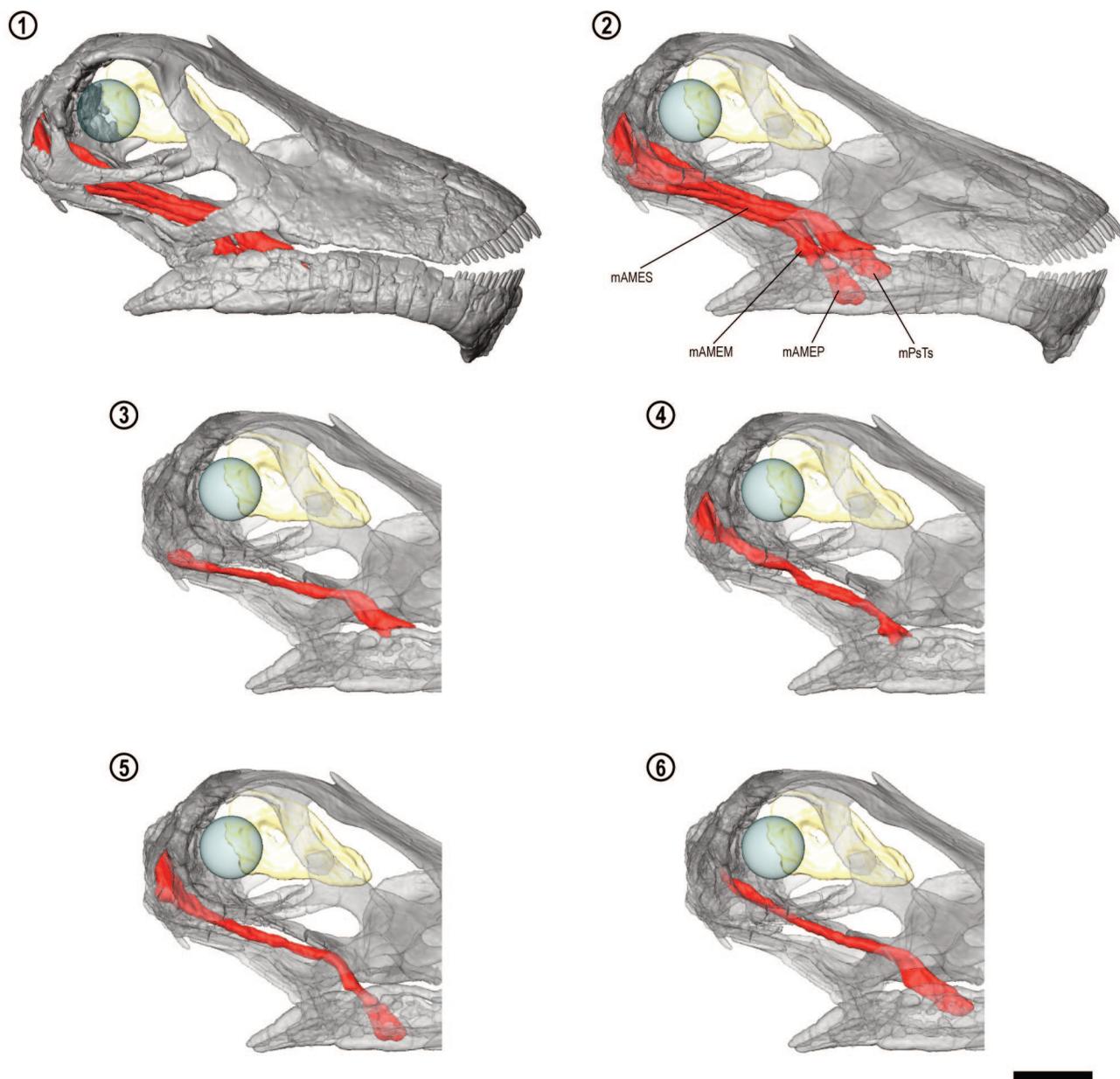The mAMES in *Bajadasaurus* is inferred to have its origin

Figure 5. Temporal musculature. 1–2, general display in lateral view; 3, muscle *adductor mandibulae externus superficialis* (mAMES); 4, muscle *adductor mandibulae externus medialis* (mAMEM), 5, muscle *adductor mandibulae externus profundus* (mAMEP); 6, muscle *pseudotemporalis superficialis* (mPsTs). Colour pattern: grey, skull; light blue (in transparency), inferred eye; light yellow, interorbitary septum; red, muscle. Scale= 5 cm.

attaching to the medial and ventral areas of a crest on the medial face of the upper temporal bar, and inserting onto a smooth surface on the dorsal margin of the surangular, rostral to the insertion of the mAMEM and caudal to the anterior surangular foramen (Fig. 5.3). The presence of a mAMES in this taxon represents a level I/I inference. In lateral view, the major axis of the mAMES is rostroventrally inclined regarding the orthal plane. After passing the ITW, its angle slightly increases towards the same plane, becoming more vertical.

Muscle *adductor mandibulae externus medialis*. The presence of the mAMEM and its attachments in extant taxa is ambiguous. In Crocodylia, this muscle originates on the quadrate, while its insertion attaches to the coronoid

eminence, fusing its fibers with those of mAMES and mAMEP, while in Aves, and mainly in Neognathae, the mAMEM does not differentiate (Holliday & Witmer, 2007). In *Sphenodon* and Lepidosauria (Holliday, 2009; Jones et al., 2009; Daza et al., 2011), the mAMEM originates attaching to the lateral surface of the bodenaponeurosis. In *Sphenodon* and Ratites, this muscle divides into several muscle bundles (Holliday & Witmer, 2007; Daza et al., 2011). In non-avian dinosaurs, the origin of the mAMEM has been inferred to attach to the caudomedial surface of the dorsotemporal fossa and the elements defining the fenestra, as in Lepidosauria (Holliday, 2009), inserting onto the medial surface of the surangular, probably sharing its attachment surface with other muscles such as mPsTs and mAMEP (Holliday, 2009). Regarding Sauropodomorpha, the mAMEM was reconstructed for *Plateosaurus*, *Diplodocus* and *Camarasaurus* (Young et al., 2012; Button et al., 2014, 2016; Lautenschlager et al., 2016). In these taxa the origin was inferred to attach onto the caudal area of the supratemporal fossa, and with an insertion onto the dorsomedial surface of the surangular.

The origin of the mAMEM of *Bajadasaurus* is inferred to attach onto the medial and dorsal surface of the supratemporal fossa, probably projecting rostrally reaching the rostral limits of this fossa (Figs. 5.4, 6.1–2). This attachment is represented by an osteological correlate as a crest running through the ventral surface of the parietal (Fig. 6.2), indicating the division of the origin of the mAMEM and mAMEP. The mAMEM inserts onto the dorsal and dorsomedial surfaces of the surangular, caudal to the same of mAMES, leaving no clear osteological correlate (Fig. 5.4). The presence of this muscle in *Bajadasaurus* represents a level II/II' inference, according to the EPB (Witmer, 1995), given the ambiguity related to its homology in extant Aves. In lateral view, the mAMEM and mAMES show similar inclinations regarding the orthal plane and the same kind of variation in inclination after passing through the ITW, although the verticalization of the major axis in the mAMEM is higher than that of mAMES.

Muscle *adductor mandibulae externus profundus*. The mAMEP is present in both extant phylogenetically related groups to non-avian dinosaurs, usually originating onto the caudomedial surface of the supratemporal fossa and

the prootic (Holliday, 2009). This muscle is also present in more distantly related groups, such as Lepidosauria and *Sphenodon* (Jones et al., 2009; Daza et al., 2011), with its origin attaching onto the caudomedial surface of the supratemporal fossa. The insertion of the mAMEP attaches to the coronoid or the coronoid eminence (Holliday, 2009). In Lepidosauria the muscle inserts both onto the adductor mandibular fossa and the bodenaponeurosis, which contacts the coronoid eminence (Gröning et al., 2013). In non-avian dinosaurs, the mAMEP was inferred to have an origin on the caudomedial surface of the supratemporal fossa, attaching to the sagittal crest (if present), and inserting on the medial surface of the coronoid process of the surangular or the coronoid (Rybczynski et al., 2008; Holliday, 2009; Lautenschlager, 2013; Button et al., 2014, 2016; Lautenschlager et al., 2016; Taylor et al., 2017).

The mAMEP in *Bajadasaurus* is inferred to have an origin attaching to the ventral surface of the parietal and the rostromedial surface of the otooccipital, in the caudal area of the supratemporal fossa (Fig. 5.5). This attachment is rostrolaterally limited by the crest on the ventral surface of this fossa, limiting with the mAMEM. Its insertion attaches to the rostral half of the adductor mandibular fossa in the lower jaw, limited rostrally by the splenial and caudally by the insertion of the mAMP (Fig. 5.5). The presence of mAMEP in *Bajadasaurus* represents a level I/I inference. In lateral view, as in other muscles originating from the supratemporal fossa, the major axis of the mAMEP presents a rostroventral inclination regarding the occlusal plane, tilting ventrally after passing through the ITW. In this fashion, the mAMEP shows the higher change of inclination within the temporal musculature.

Muscle *pseudotemporalis superficialis*. The mPsTs is highly variable in extant taxa, both in closely and distantly related ones. It originates on the medial wall of the dorsotemporal fossa in Ratites, Lepidosauria and *Sphenodon*, or exclusively from the laterosphenoid in Neognathae and Crocodylia (Holliday & Witmer, 2007; Holliday, 2009; Jones et al., 2009; Smith-Paredes & Bullar, 2019). In both scenarios, the origin of the mPsTs is the rostralmost within the temporal musculature. In these extant groups, the mPsTs does not produce clear osteological correlates in its insertion, which attach onto the medial surface of the surangular, the
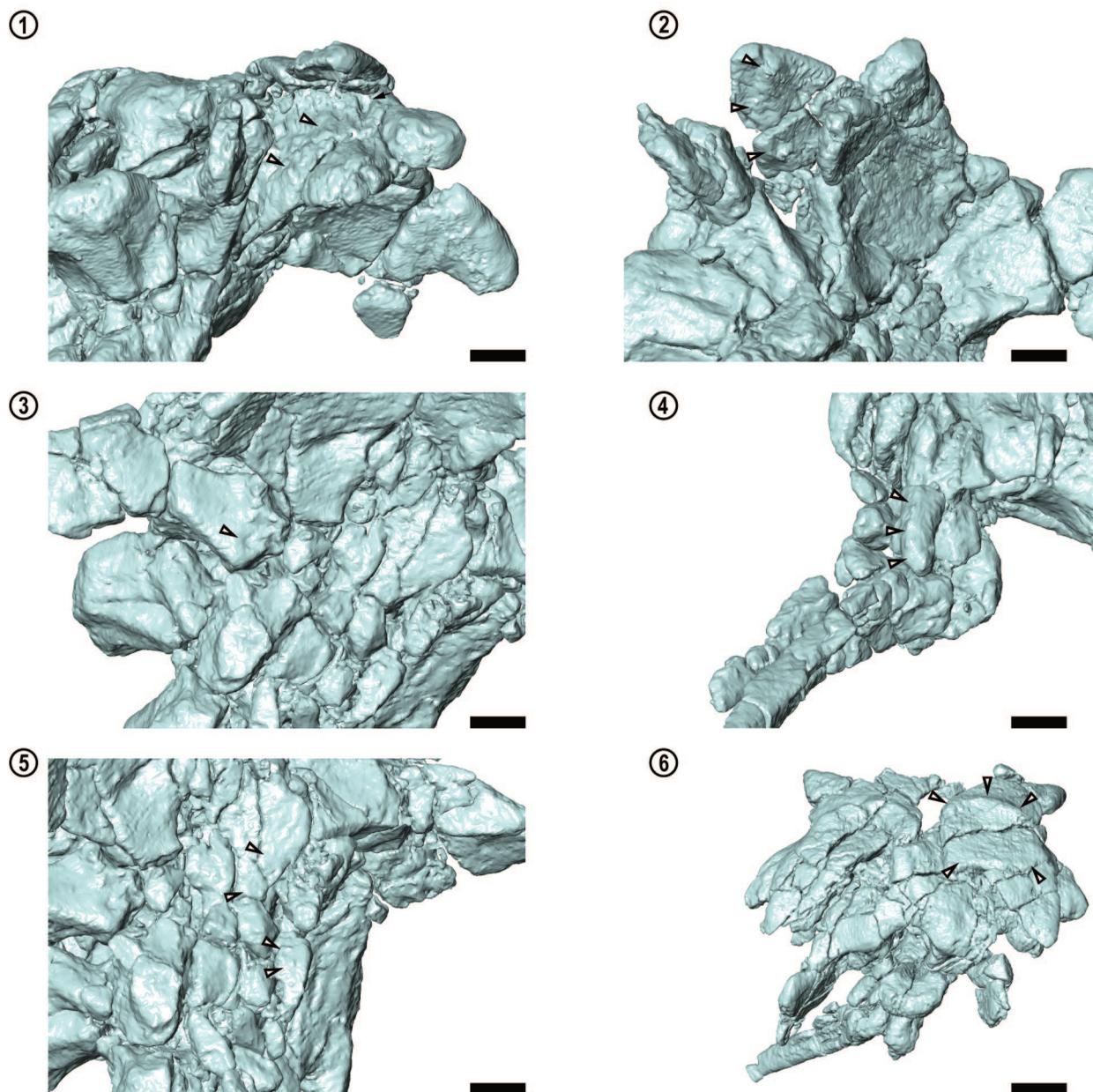
Figure 6. Clear osteological correlates on the neurocranium of *Bajadasaurus*. 1, ridge dividing mPsTs-mAMEM; 2, ridge dividing mAMEM-mAMEP; 3, origin for mLPt; 4, origin for mPPt; 5, origin for mRd and mRv; 6, dorsal depression of the parietal considered as a whole as the insertion for mTspCm in previous analyses. The white-filled dark arrows indicate the stronger portions of the correlates. Scale= 1 cm for 1–5 and 2 cm for 6.

coronoid, or directly onto de adductor mandibular fossa (Holliday & Witmer, 2007; Holliday, 2009; Jones et al., 2009; Gröning et al., 2013). In Lepidosauria, the insertion of this muscle attaches to the bodenaponeurosis (Gröning et al., 2013), while in extant Crocodylia, depending on the homologies of the muscle portions, either if the muscle *intramandibularis* is part or not of the mPsTs (Holliday &

Witmer, 2007; Bona & Desojo, 2011), the insertion of the mPsTs varies between the medial wall of the adductor mandibular fossa (former scenario) or the *transiliens* cartilage (later scenario). In previous reconstructions in non-avian dinosaurs, the mPsTs was inferred to attach its origin to the supratemporal fossa, with a rostromedial projection along the dorsal surface of the lateral wing of the

laterosphenoid (antotic process) or the frontal (when this participates of the rostral limits of the fossa; Young et al., 2012; Button et al., 2014, 2016; Taylor et al., 2017). The rostral extension of this muscle is discussed, as it was suggested that the rostrodorsal surface of the supratemporal fossa was free of muscle attachments in Theropoda, Ceratopsia and *Diplodocus* (Holliday et al., 2019), and related to other vascularity-related tissues. The insertion of the mPsTs attaches to the rostral area of the adductor mandibular fossa in Sauropodomorpha (Lautenschlager et al., 2016; Holliday et al., 2019) and *Psittacosaurus* (Taylor et al., 2017), while in other non-avian dinosaurs it inserts onto the medial surface of the coronoid eminence (Rybczynski et al., 2008; Holliday, 2009).

The mPsTs in *Bajadasaurus* originates on the ventral margin of the antotic process of the laterosphenoid (Fig. 5.6). This is not evidenced by an osteological correlate other than the presence of the crista antotica. It inserts on the rostrodorsal area of the adductor mandibular fossa, rostrodorsal to the insertion of the mAMEP, and, even though it does not leave an osteological correlate, it is surrounded by the elevations given by the splenial (rostrally), and by a dorsal thickening of the medial surface of the surangular (Fig. 5.6). A rostral projection on the origin surface of this muscle is dismissed, as in lateral view, such projection implies a shift on the major axis of the muscle of about 90°. This hypothesis is discarded based on the absence of an osteological correlate along the dorsal surface of the frontal, and the absence of a trochlear surface of the edge of the crista antotica. As in other temporal muscles, the major axis of this muscle is rostroventrally inclined towards the orthal plane. This muscle differs, however, in that its major axis does not change its inclination regarding the aforementioned plane when passing through the ITW. The presence of mPsTs in *Bajadasaurus* represents a level I/I' inference.

Muscle inferential lines of action

Comparing the arrangement of the palatal and temporal muscle groups in lateral view, the former group forms a higher mean angle with the orthal plane (Figs. 7.1–8). The mean angles for mPt are 60.87° (mPtv) and 66.74° (mPtd), both caudoventrally oriented. The mean estimated angle for mAMP, although rostroventrally oriented, is 52.94°.

All of the temporal muscles are rostroventrally oriented, increasing their respective angles, related to the orthal plane, when passing through the ITW. Among these muscles, and proximal to the curvature formed at the ITW, the mAMES shows the lowest angle regarding the orthal plane (almost horizontal, 13.79°; Fig. 7.5), while the remaining muscles diverge from the plane in angles surpassing 20° (Fig. 7). At their distalmost portions, the temporal muscles become vertical, with the angles of their lines of action and the orthal plane increasing by a mean of 24.5°, and, among these, the mAMEP shows the highest angled reorientation (29.57° from the extended inferred line of action of its proximal portion; Fig. 7.7).

Depressor musculature

Muscle *depressor mandibulae* (CN VII). In *Sphenodon* the mDM originates on the caudodorsal edge of the parietal and the squamosal, and from a small portion of connective tissues (Jones et al., 2009). In the same taxon, this muscle sometimes divides in two portions (*medialis* and *lateralis*; Gorniak et al., 1982; Al-Hassawi, 2007). In Crocodylia the mDM originates on the parietal, squamosal, supraoccipital and quadrate (Schumacher, 1973; Bona & Desojo, 2011; Smith-Paredes & Bullar, 2019). In Aves, it originates attaching on the supratemporal fossa (Smith-Paredes & Bullar, 2019). In these three extant groups, the mDM inserts onto the dorsal surface of the retroarticular process. In Sauropodomorpha and other herbivore non-avian dinosaurs, the mDM originates from the distalmost surface of the paroccipital process (Nabavizadeh, 2020), sometimes extending along the caudal surface of the squamosal (Tsuihiji, 2010).

In *Bajadasaurus* the origin of this muscle is inferred to attach to the distalmost portion of the caudal surface of the paroccipital process and the caudal surface of the squamosal (Fig. 8), leaving no clear osteological correlate, in either the lateral or medial limits of the attachment. The insertion of mDM attaches to the retroarticular process, formed by the articular and the surangular, leaving a clear, deep and rostrocaudally elongated osteological correlate (Fig. 8). The mDM is inferred in non-avian dinosaurs (Tsuihiji, 2010; Smith, 2015; Nabavizadeh, 2020), based on its ubiquitous presence in Aves, Crocodylia and other
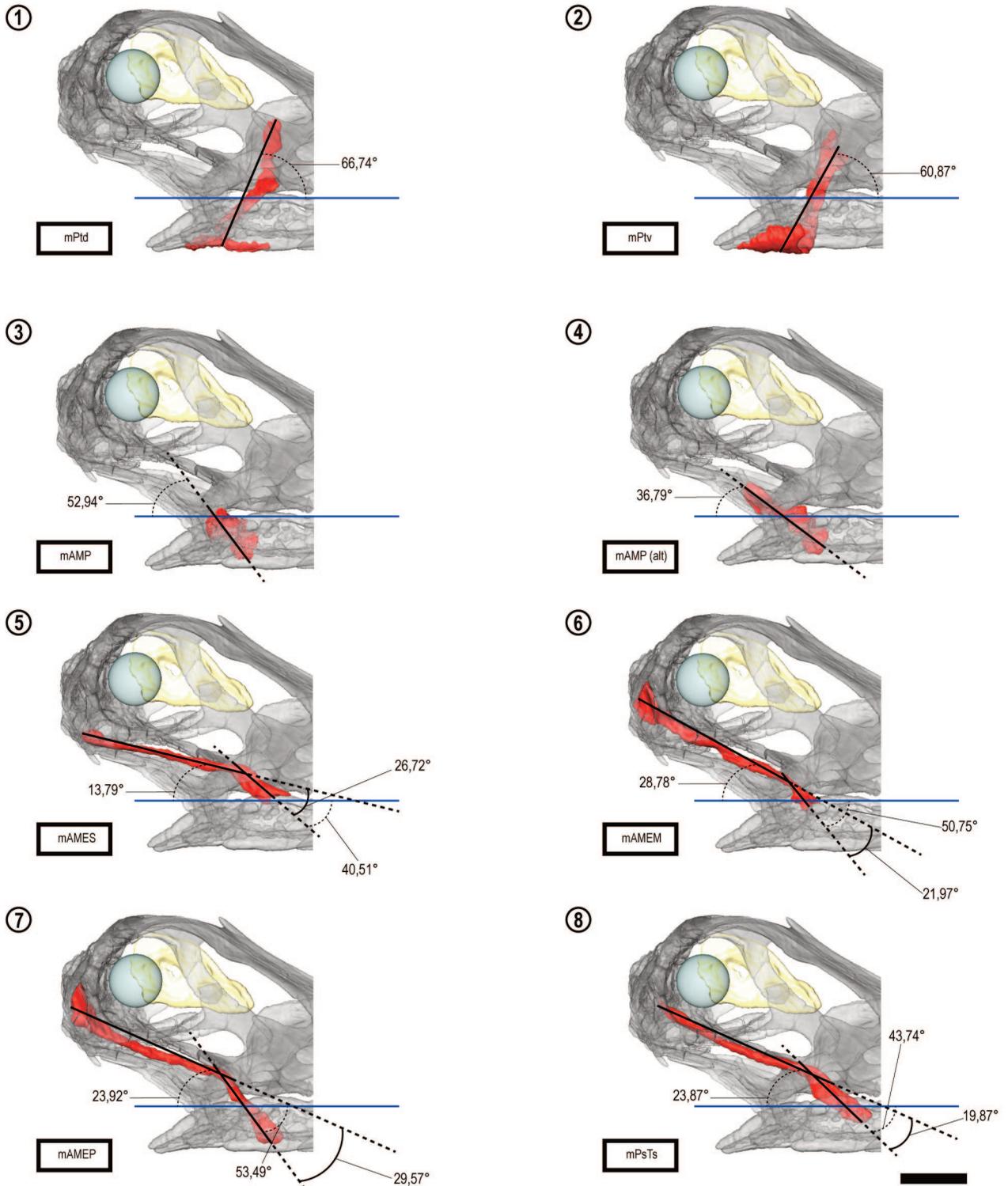
Figure 7. Inferred lines of action of the palatal and temporal muscles in the sagittal plane. 1, mPtd; 2, mPtv; 3, mAMP; 4, mAMP (alternative reconstruction); 5, mAMES; 6, mAMEM; 7, mAMEP; 8, mPsTs. The blue line indicates the projected orthal plane, the dark lines indicate the inferred lines of action of the muscles (being dotted when projected). Abbreviations: mAMEM, muscle *adductor mandibulae externus medialis*; mAMEP, muscle *adductor mandibulae externus profundus*; mAMES, muscle *adductor mandibulae externus superficialis*; mAMP, muscle *adductor mandibulae posterior*; mAMP (alt), alternative reconstruction of the muscle *adductor mandibulae posterior*; mPsTs, muscle *pseudotemporalis superficialis*; mPtd, muscle *pterygoideus dorsalis*; mPtv, muscle *pterygoideus ventralis*. Colour pattern: grey, skull; light blue (in transparency), inferred eye; light yellow, interorbitary septum; red, muscle. Scale= 5 cm.

Sauropsida (*e.g.*, Tsuihiji, 2007; Jones et al., 2009). Under this scenario and based on the osteological correlate on the retroarticular process, the presence of mDM in *Bajadasaurus* represents a level I'/I inference.

Extrinsic eye musculature

In extant Aves, the extrinsic eye musculature originates primarily on the interorbitary septum (Van den Berge & Zweers, 1993; Lautenschlager et al., 2013; Smith-Paredes & Bullar, 2019). In Crocodylia, this musculature attaches primarily to the lateral wall of the neurocranium and the interorbitary cartilage (Wedin, 1953; Smith-Paredes & Bullar, 2019; Lessner & Holliday, 2020). For the purpose of this analysis, the eye globe was reconstructed as a 3D digital model formed by a quasi-perfect sphere (2,454 edges and 1,636 faces; Figs. 9.1–6), with a diameter representing half of the total length of the eye socket, parallel to the plane containing the skull roof. This size estimation of the eyeball is based in the following rationale: a) the ratio between the size of the eye scleral ring of the
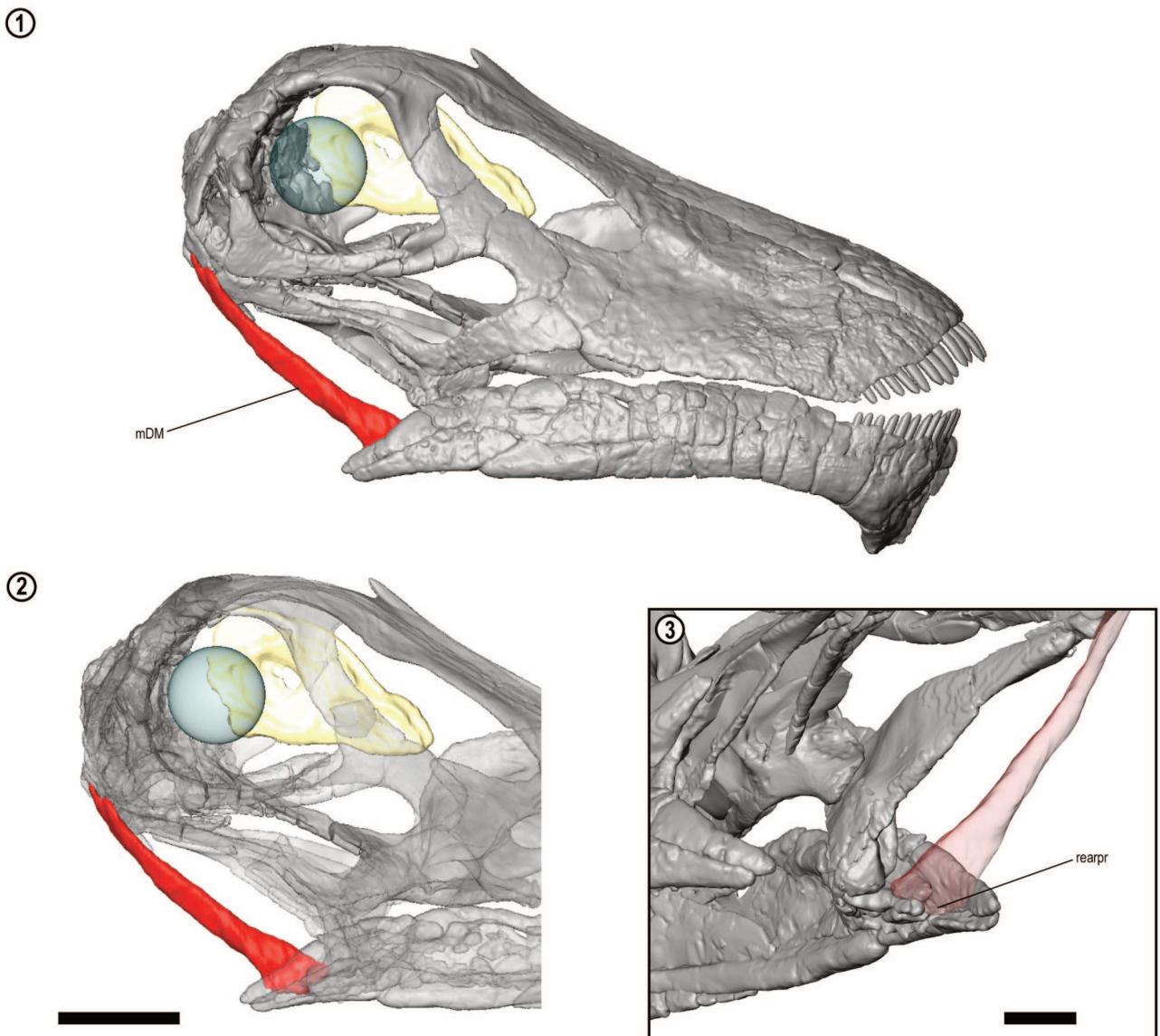

Figure 8. Depressor musculature. 1, general display in lateral view; 2, muscle *depressor mandibulae* (mDM); 3, insertion on the retroarticular process in detail. Abbreviations: mDM, muscle *depressor mandibulae*; rearp, retroarticular process. Colour pattern: grey, skull; light blue (in transparency), inferred eye; light yellow, interorbitary septum; red (opaque and in transparency), muscle. Scale= 5 cm for 1–2 and 2 cm for 3.

eyeball and the orbit length parallel to the plane containing the skull roof is similar to that of *Diplodocus* (CM 11161) and *Nemegtosaurus* (Z.PAL MgD-I/9), and; b) the size of the eye skeleton formed by the scleral ossicles is a proper indicator of the size of the eyeball (Martínez et al., 2016; Franz-Odendaal, 2018 and references therein).

Muscle *rectus dorsalis* (CN III). The origin of mRd in Crocodylia attaches to the basisphenoid, surrounding the foramen for CN II (Smith-Paredes & Bullar, 2019; Lessner & Holliday, 2020). In Aves, it originates on the interorbitary cartilage (Smith-Paredes & Bullar, 2019), although it sometimes degenerates (*Buteo buteo*, Lautenschlager et al., 2013; *Coragyps atratus* CFA-OR-1793, JPG pers. obs.). In both clades, it inserts on the dorsal surface of the eyeball
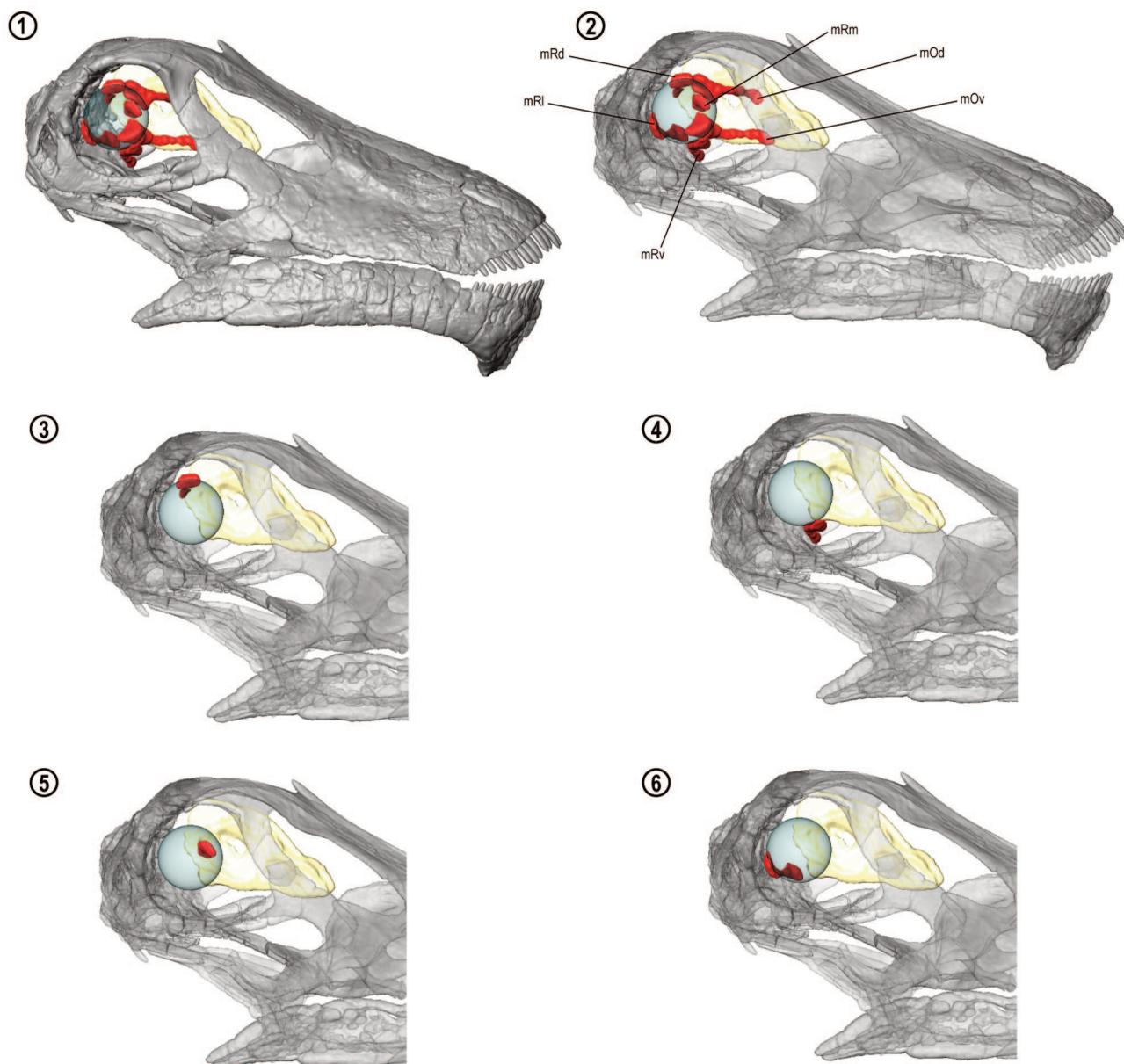

Figure 9. Extrinsic eye musculature, *rectum* muscles. 1, general display in lateral view; 2, general display in lateral view (with muscles indicated); 3, muscle *rectus dorsalis* (mRd); 4, muscle *rectus ventralis* (mRv); 5, muscle *rectus medialis* (mRm); 6, muscle *rectus lateralis* (mRl). Abbreviations: mOd, muscle *obliquus dorsalis*; mOv, muscle *obliquus ventralis*. Colour pattern: grey, skull; light blue (in transparency), inferred eye; light yellow, interorbitary septum; red, muscle. Scale= 5 cm.

(Lautenschlager et al., 2013; Smith-Paredes & Bullar, 2019; Lessner & Holliday, 2020).

The inferred mRd of *Bajadasaurus* originates on the area where the orbitosphenoid and the basisphenoid tentatively contact, dorsal to the foramen for CN II (Fig. 9.2), leaving a smooth osteological correlate as a shallow concavity, observable as a change of the inclination of the ventral surface of the orbitosphenoid. As this muscle originates from different areas in extant related taxa, the presence of a mRd with this configuration in *Bajadasaurus* represents a level II inference for its origin, while it represents a level I one for its presence. An insertion on the dorsal surface of the eyeball is also inferred.

Muscle *rectus ventralis* (CN III). The origin of mRv in Aves generally attaches to the interorbitary septum (Smith-Paredes & Bullar, 2019), although in *Buteo* it originates caudolaterally to the foramen for CN II (Lautenschlager et al., 2013). In Crocodylia, this muscle originates on the dorsal area of the basisphenoid, ventral to the foramen for CN II (Smith-Paredes & Bullar, 2019; Lessner & Holliday, 2020). In both clades, the mRv inserts on the ventral area of the eyeball (Lautenschlager et al., 2013; Smith-Paredes & Bullar, 2019; Lessner & Holliday, 2020).

The origin of mRv in *Bajadasaurus* attaches to the dorsal area of the basisphenoid, onto a shallowly depressed osteological correlate ventral the foramen for CN II (Fig. 9.3). The presence of mRv in *Bajadasaurus* represents a level I inference, given its ubiquity in Aves and Crocodylia (Smith-Paredes & Bullar, 2019). The insertion of this muscle on the eyeball is inferred to attach onto its ventral surface.

Muscle *rectus medialis* (CN III). The origin of mRm attaches to the interorbitary septum in both Aves and Crocodylia (Lautenschlager et al., 2013; Smith-Paredes & Bullar, 2019; Lessner & Holliday, 2020). This muscle inserts onto the rostral surface of the eyeball (Smith-Paredes & Bullar, 2019; Lessner & Holliday, 2020), although it shifts its position to the medial surface in taxa with binocular eyesight (*e.g.*, Lautenschlager et al., 2013).

The mRm is inferred to originate on the interorbitary septum in *Bajadasaurus*, immediately rostral to the foramen of the conjoined CN II (Fig. 9.4). As this cartilage is not preserved in the specimens assigned to *Bajadasaurus*, the presence and morphology of an osteological correlate for this attachment cannot be assessed. This, with the presence of the muscle in Aves and Crocodylia, results in that the presence of mRm in *Bajadasaurus* represents a level I' inference. An insertion onto the rostral surface of the eyeball for the mRm in *Bajadasaurus* is inferred.

Muscle *obliquus ventralis* (CN III). The origin for mOv differs in Aves and Crocodylia. In the former, this muscle attaches onto the rostroventral surface of the interorbitary septum (Lautenschlager et al., 2013; Smith-Paredes & Bullar, 2019), while in Crocodylia, its attachment is located on the rostroventral surface of the descending surface of the frontal (Smith-Paredes & Bullar, 2019; Lessner & Holliday, 2020). In both clades, the mOv inserts on the rostroventral surface of the eyeball, between the insertions for mRv and mRm (Lautenschlager et al., 2013; Lessner & Holliday, 2020).

The mOv in *Bajadasaurus* is inferred to originate on the interorbitary cartilage as in Aves, on its rostroventral surface (Fig. 10.1). A tentative origin on the frontal (Fig. 10.2), as in Crocodylia, is considered implausible here based on the position of the frontal, which would imply the fibers of the mOv crossing over with those of other extrinsic eye muscles, potentially hampering the lines of actions of this muscle. An origin on the interorbitary septum implies a straighter line of action for this muscle, without crossing with other muscles. The insertion of mOv is inferred as identical to that in Crocodylia and Aves, placed on the rostroventral surface of the eyeball, between those of mRv and mRm. The presence of a mOv with this configuration in *Bajadasaurus* represents a level II' inference for its origin.

Muscle *obliquus dorsalis* (CN IV). Similar to mOv, the origin for mOd in Aves and Crocodylia attaches to different areas. In Aves, the attachment surface is the dorsorostral area of the interorbitary septum, dorsal to that of mOv (Lautenschlager et al., 2013; Smith-Paredes & Bullar, 2019), while in Crocodylia the mOv originates on the descending surface of the frontal (Smith-Paredes & Bullar, 2019; Lessner & Holliday, 2020). In both clades, the mOd inserts onto the dorsorostral surface of the eyeball, placed between the insertion surfaces for mRm and mRd (Lautenschlager et al., 2013; Lessner & Holliday, 2020).

The reconstructed mOd in *Bajadasaurus* originates on the interorbitary septum as in Aves, on its rostrodorsal area,
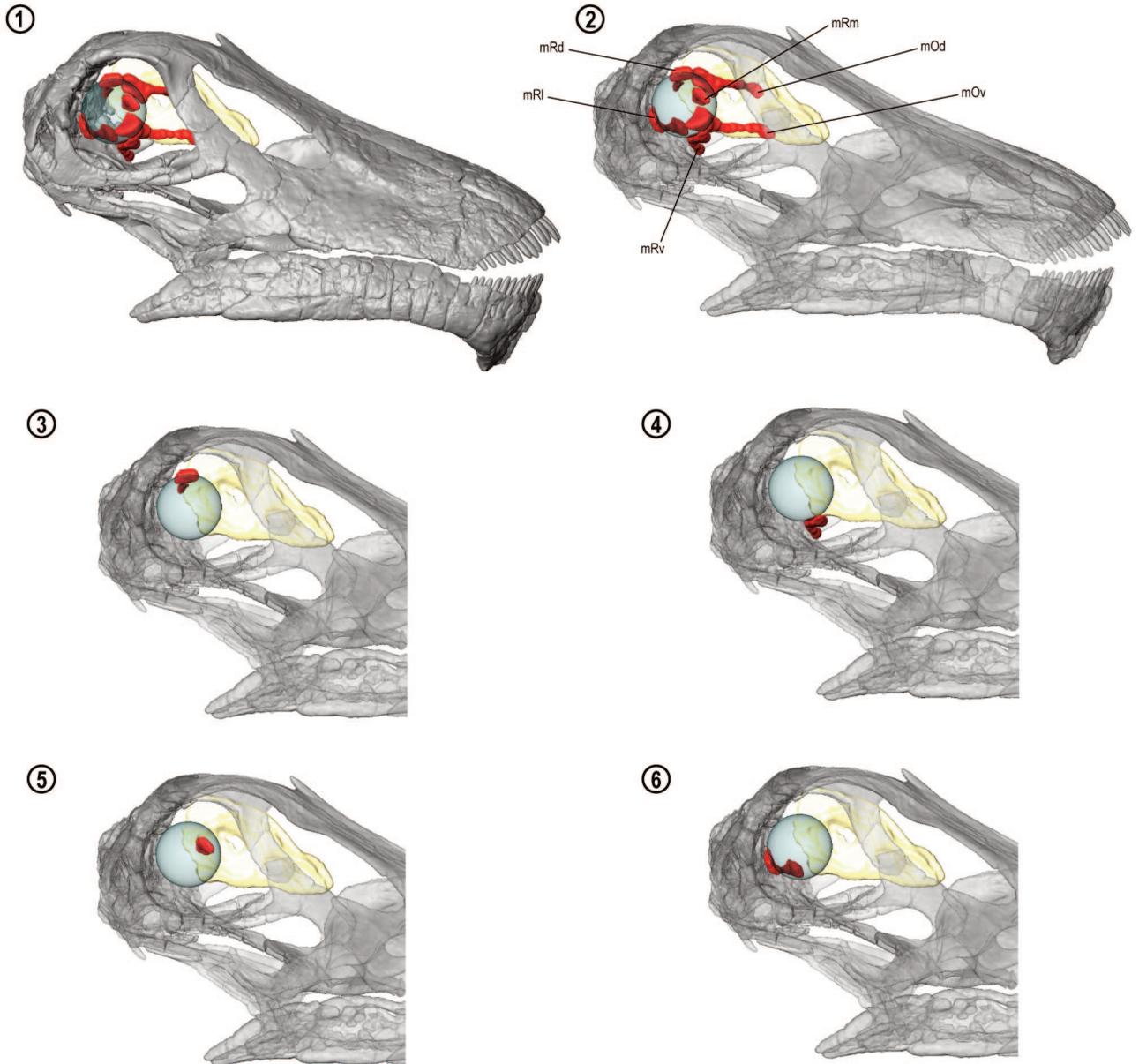
Figure 10. Extrinsic eye musculature, oblique muscles. 1, muscle *obliquus ventralis* (mOv); 2, alternative reconstruction for mOv; 3, muscle *obliquus dorsalis* (mOd); 4, alternative reconstruction for mOd. The arrows indicate the line of action of the muscle, indicating the direction of rotation of the eye. Colour pattern: grey, skull; light blue (in transparency), inferred eye; light yellow, interorbitary septum; red, muscle. Scale= 5 cm.

dorsal to the origin for mOv (Fig. 10.3). In the same way as for mOv, an origin for mOd on the frontal (Fig. 10.4) would imply a crossover with other extrinsic eye muscles, being the most affected the mRd. Even though this crossover cannot be strictly ruled out, given the laminar morphology of these muscles, the fact that the lines of action of mOd have the same issues than those of mOv, given the retraction of the frontal, suggests a more plausible origin

on the interorbitary septum. The insertion of mOd attaches to the rostrodorsal surface of the eyeball, between the insertions of mRm and mRd. The presence of this muscle represents a level I' inference, while the configuration of the inferred origin represents a level II' inference.

Muscle *rectus lateralis* (CN VI). The mRl originates on the basisphenoid in Crocodylia (Smith-Paredes & Bullar, 2019; Lessner & Holliday, 2020), while in Aves, the origin places

either in the interorbitary cartilage (Smith-Paredes & Bullar, 2019) or the basisphenoid (Lautenschlager et al., 2013). It inserts onto the caudal surface of the eyeball (Lautenschlager et al., 2013; Smith-Paredes & Bullar, 2019; Lessner & Holliday, 2020).

The mRI in *Bajadasaurus* originates onto the basisphenoid, caudal to the foramen for CN II and the attachment surface for the origin of mRv, leaving no clear osteological correlate (Fig. 9.5). As this muscle is ubiquitous in Aves and Crocodylia, its presence represents a level I' inference. The insertion of mRI of *Bajadasaurus* is inferred to attach at the caudal area of the eyeball.

Cervicocranial musculature

The cervicocranial (= craniocervical; Snively & Russell, 2007a; Tsuihiji, 2010) musculature relates to the skull only by the attachments representing the insertions of these muscular groups (Figs. 11.1–4). Even though the holotype of *Bajadasaurus* (MMCh-PV 75) preserves vertebral elements—proatlantal apophyses, atlas, axis, and an anterior cervical vertebra—from where the origin of the muscles described below can be recognized, this analysis is focused exclusively on the skull.

Dorsiflexion

Muscle *transversospinalis capitis*: Muscle *transversospinalis capitis medialis*. Epaxial muscle. Nomenclature= *spinalis capitis* (Tsuihiji, 2010; Button et al., 2014). Part of the *transversospinalis* group (Smith-Paredes & Bullar, 2019). The insertion of mTspCm extends along the dorsomedial surface of the parietal and a lateral depression of the supraoccipital in sauropods (Button et al., 2014). In derived Dicraeosauridae, the parietal is deeply depressed dorsally, showing a conspicuous rostral scar, as in *Amargasaurus* (Salgado & Calvo, 1992; Paulina-Carabajal et al., 2014) and *Dicraeosaurus* (Janensch, 1935–1936). The mTspCm inserts onto the dorsal surface of the supraoccipital and part of the adjacent parietal in non-avian dinosaurs (Tsuihiji, 2010). As in other non-avian dinosaurs (*Diplodocus*, *Camarasaurus*—Button et al., 2014—, Ceratopsia, Pachycephalosauria and Tyrannosauridae—Tsuihiji, 2010), extant Aves, and Crocodylia, this muscle inserts lateral to the sagittal crest (Snively & Russell, 2007a; Tsuihiji, 2010).

The mTspCm in *Bajadasaurus* inserts along the rostro-lateral surface of the sagittal crest and the caudomedial surface of the parietal, caudolateral to the postparietal fenestra, leaving a clear osteological correlate as a smooth depression (Fig. 11). It probably invaded the medial portion of the post-temporal fenestra laterally. The proposed osteological correlate and insertion differ from that suggested for *Amargasaurus* (Salgado & Calvo, 1992; Paulina-Carabajal et al., 2014) and *Dicraeosaurus* (Janensch, 1935–1936), although the dorsal concave surface of the parietal, where this attachment was suggested for these Dicraeosauridae, is present in *Bajadasaurus* (Fig. 6.6). The presence of the mTspCm in *Bajadasaurus* represents a level I inference.

Muscle *transversospinalis capitis*: Muscle *transversospinalis capitis lateralis*. Epaxial muscle. Nomenclature= *longissimus capitis pars articuloparietalis* (Tsuihiji, 2010); muscle *complexus* (Button et al., 2014). Part of the l*ongissimus* group (Smith-Paredes & Bullar, 2019). The insertion of mTspCl places on the distal dorsal surface of the parietal, lateral to the post-parietal fenestra in Sauropoda (Button et al., 2014), or on the caudal surface of the parietal, extending up to the squamosal in Marginocephalia (Tsuihiji, 2010). This muscle is present in Aves as an individual muscle (Snively & Russell, 2007a; Tsuihiji, 2010; Smith-Paredes & Bullar, 2019), while in Crocodylia and Lepidosauria is considered as part of the *longissimus* muscle group (as part of the *longissimus capitis pars articuloparietalis*; Tsuihiji, 2007, 2010; Smith-Paredes & Bullar, 2019).

The mTspCl in *Bajadasaurus* attaches onto the caudodorsal surface of the distal wing of the parietal, caudolateral to the insertion of mTspCm (Fig. 11.2). This represents a condition similar to the observed in *Camarasaurus* and *Diplodocus* (Button et al., 2014; in this study, the mTspCl is named as *muscle complexus* and expands rostrally along the dorsal surface of the parietal), leaving a clear but smooth osteological correlate, along the dorsal margin of the post-temporal fenestra. The presence of mTspCl in *Bajadasaurus* represents a level I inference (considering it homologue to the portions of the *longissimus capitis pars articuloparietalis*).

Muscle *splenius capitis*: Muscle *splenius capitis medialis*. Epaxial muscle. The insertion of mSpCm extends along the lateral surface of the supraoccipital, lateral to the sagittal crest and caudal to the insertion of mTspCm in sauropods
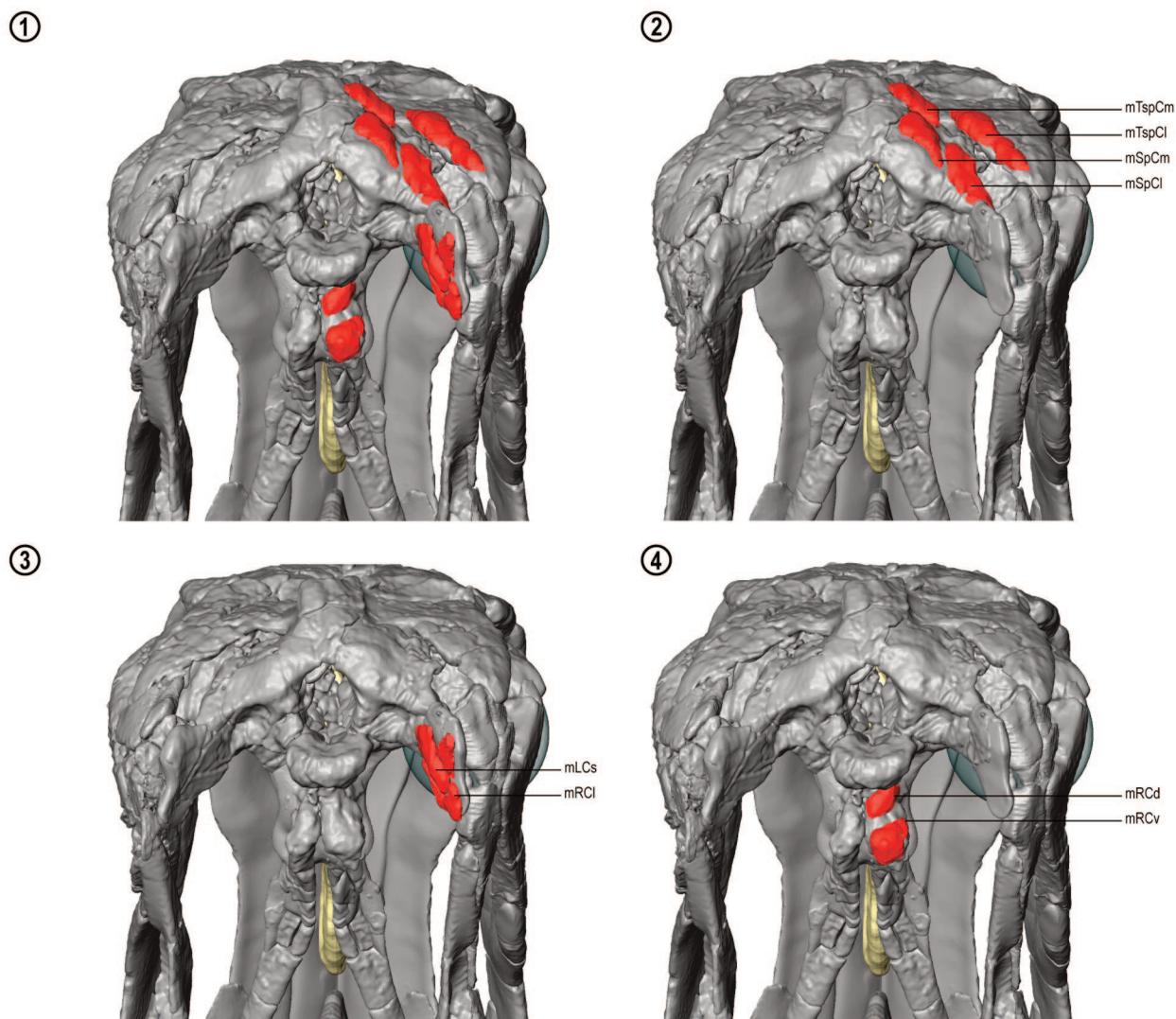
Figure 11. Cervicocranial musculature. 1, general display in caudal view; 2, dorsiflexor musculature (*transversospinalis* and *splenius capitis* groups); 3, lateroflexor musculature (*longissimus capitis* group and lateral part of the *rectus capitis*); 4, ventroflexor musculature (parts of the *rectus capitis* group). Abbreviations: mLCs, muscle *longissimus capitis superficialis*; mRCd, muscle *rectus capitis dorsalis*; mRCl, muscle *rectus capitis lateralis*; mRCv, muscle *rectus capitis ventralis*; mSpCl, muscle *splenius capitis lateralis*; mSpCm, muscle *splenius capitis medialis*; mTspCl, muscle *transversospinalis capitis lateralis*; mTspCm, muscle *transversospinalis capitis medialis*. Colour pattern: grey, skull; light blue (in transparency), inferred eye; light yellow, interorbitary septum; red, muscle. Scale= 3 cm.

(Button et al., 2014), or along the caudal surface of the supraoccipital in other non-avian dinosaurs (Tsuihiji, 2010). In Crocodylia and Aves this muscle inserts along the lateral surface of the supraoccipital (with alternative nomenclature in both taxonomic groups; Tsuihiji, 2007, 2010; Snively & Russell, 2007a).

The inferred mSpCm in *Bajadasaurus* inserts along the caudolateral surface of the sagittal crest and the dorsal area of the supraoccipital (Fig. 11.2). In the holotype of *Bajadasaurus*, this surface is better preserved on the right half of the skull, where a smooth osteological correlate can be recognized, medial to a projection of the supraoccipital on the putative limit with the otooccipital. This correlate is similar, although less concave, to a structure observed in *Amargasaurus* and *Lingwulong*, and is placed on an area similar to the correlate for mSpCm in *Diplodocus*, *Camarasaurus* (Button et al., 2014), Ceratopsia, Pachycephalosauria, basal Ornithopoda (Tsuihiji, 2010) and Tyrannosauridae (Snively

& Russell, 2007a; Tsuihiji, 2010). The presence of mSpCm in *Bajadasaurus* represents a level I inference.

Muscle *splenius capitis*: Muscle *splenius capitis lateralis*. Epaxial muscle. Nomenclature= *obliquus capitis magnus* (Tsuihiji, 2010; Button et al., 2014). Part of the *transversospinalis* group (Smith-Paredes & Bullar, 2019). The insertion of the mSpCl attaches to the caudal surface of the supraoccipital, lateral to the insertion of mSpCm in non-avian dinosaurs (Tsuihiji, 2010).

In *Bajadasaurus* the mSpCl inserts on the dorsal surface of the paroccipital process of the otooccipital, extending along half of the total lateral extension of the process in a distal direction (Fig. 11.2). It probably expanded rostrally entering the post-temporal fenestra. The medial extension of this attachment is limited by the proatlantal facets on the occipital region. The mSpCl leaves a smooth osteological correlate in the dorsal surface of the paroccipital process, from the proatlantal facet up to the distal dorsal projection of the paroccipital process, as in Pachycephalosauria, Ceratopsia, Tyrannosauridae, Aves, Crocodylia, Lepidosauria (Snively & Russell, 2007a; Tsuihiji, 2010) and *Sphenodon* (Jones et al., 2009). Tsuihiji (2010) considers that the inferential reconstruction of this muscle in non-avian dinosaurs represents a level I/I' inference under the EPB, and, similarly, the results of the inference in *Bajadasaurus* for mSpCl represent a level I for its insertion.

Lateroflexion

Muscle *longissimus capitis superficialis*. Epaxial muscle. Nomenclature= *longissimus capitis pars transversalis capitis* (Tsuihiji, 2010). Part of the *longissimus* group (Smith-Paredes & Bullar, 2019). The attachment surface for the insertion of mLCs extends along the caudal surface of the paroccipital process, along a sub-rectangular and dorsoventrally elongate surface, with a dorsomedial projection along the dorsal surface of the paroccipital process in Sauropoda (Button et al., 2014). In Lepidosauria the mLCs inserts onto the ventral margin of the distal extreme of the paroccipital process, whereas in Aves this muscle is absent (Tsuihiji, 2010). However, the ventral portion of *muscle complexus* in the cervicocranial musculature in Aves might be homologue to the mLCs of Crocodylia (Snively & Russell, 2007a).

The mLCs in *Bajadasaurus* is inferred to insert along the caudolateral surface of the distal portion of the paroccipital process (Fig. 11.3), as in *Diplodocus* and *Camarasaurus* (Button et al., 2014), dorsal and medial to mRCl (below). This muscle does not leave a clear osteological correlate on the paroccipital process. The mLCs is present as a distinguishable muscle in Lepidosauria and Crocodylia (Snively & Russell, 2007a; Tsuihiji, 2010), but its absence in Aves (excluding putative homologies), suggests that the presence of mLCs in *Bajadasaurus* represents a level II' inference.

Muscle *rectus capitis lateralis*. Hypaxial muscle. The mRCl inserts on the distal area of the paroccipital process, medial to mDM, in non-avian dinosaurs (Tsuihiji, 2010). The inferential mRCl in *Bajadasaurus* inserts onto the ventral and lateral edges of the paroccipital process, surrounding the mLCs, leaving a clear osteological correlate as a scar along the ventral edge of the process (Fig. 11.3). This muscle was not inferred in previous muscular reconstructions for Sauropoda (Button et al., 2014), but it was inferred on the same area in Tyrannosauridae (Snively & Russell, 2007a) and Marginocephalia (Tsuihiji, 2010). Moreover, mRCl is present in Aves and Crocodylia, inserting on the ventral surface of the paroccipital process (Snively & Russell, 2007a; Tsuihiji, 2010), albeit in Crocodylia it merges with the surrounding musculature (Tsuihiji, 2010). As a consequence, the presence of the insertion of mRCl in *Bajadasaurus* represents a level I inference.

Ventroflexion

Muscle *rectus capitis*: Muscle *rectus capitis dorsalis*. Epaxial muscle. Nomenclature= muscle *episternocleidomastoideus* in Lepidosauria (Tsuihiji, 2010); muscle *iliocostalis capitis* + muscle *longissimus capitis profundus* in Aves (Tsuihiji, 2010); in Crocodylia includes a portion unrelated to the hypaxial or epaxial musculature (Tsuihiji, 2010). Part of the *iliocostalis* group (Smith-Paredes & Bullar, 2019). The mRCd inserts to the skull at the ventrocaudal surface of the paroccipital process and its attachment surface places lateral to the foramen magnum, dorsal to the base of the occipital condyle (Button et al., 2014). In Crocodylia, Aves and other non-avian dinosaurs, the mRCd inserts onto the caudal surface of the basal tubera, fused to mRCl and muscle *episternocleidomastoideus* in Crocodylia, and, alternatively, with muscle *longissimus capitis profundus* in Aves and non-

avian dinosaurs (Tsuihiji, 2010).

In *Bajadasaurus*, the inferred insertion for mRCd attaches onto the caudal surface of the basal tubera (Fig. 11.4), as in other non-avian dinosaurs, Aves and Crocodylia (Tsuihiji, 2010), Plesiosauria (Nagesan, 2017) and *Sphenodon* (Jones et al., 2009). This muscle probably includes two fused muscles (muscle *iliocostalis capitis* and muscle *longissimus capitis profundus*), as it was inferred for Marginocephalia, Ornithopoda and Tyrannosauridae (Tsuihiji, 2010), based on the absence of osteological correlates dividing the general attachment surface, something also observed in extant Aves and Lepidosauria. Under this interpretation, and due to the lack of a clear osteological correlate, the inference of mRCd—isolated and homologue to the mRCd in extant taxa—represents a level II' inference. However, considering mRCd (*sensu lato*) as the triptych formed by the mRCd *sensu stricto*, muscle *iliocostalis capitis* and muscle *longissimus capitis profundus*, the level of the inference changes. Regarding the fibers primarily homologue to muscle *iliocostalis capitis* in other taxa, the suggested inference in *Bajadasaurus* differs from that inferred in other Sauropoda (Button et al., 2014), where the muscle *iliocostalis capitis* attaches to the base of the paroccipital process as in Crocodylia (Snively & Russell, 2007a; Tsuihiji, 2010; Button et al., 2014). Regarding the fibers tentatively homologue to those of muscle *longissimus capitis profundus*, the insertion in *Bajadasaurus* is common in other non-avian dinosaurs such as *Camarasaurus*, *Diplodocus*, Tyrannosauridae, Ceratopsia, Pachycephalosauria and basal Ornithopoda (Snively & Russell, 2007a; Tsuihiji, 2010), the insertion suggested for the dicraeosaurid taxon represents a level I' inference. Overall, as mRCd *sensu lato* did not leave a clear osteological correlate in *Bajadasaurus*, and as at least part of this muscle inserts on the same area than in extant related taxa—on the caudal surface of the basal tubera—, the insertion of this muscle represents a level I' inference.

Muscle *rectus capitis ventralis*. Hypaxial muscle. Nomenclature= *rectus capitis anterior* (Tsuihiji, 2010). The insertion for mRCv attaches to the distal and caudoventral surface of the basal tubera, ventral to the insertion of mRCd, extending in rostral direction along the ventral surface of the tubera in Sauropoda (Button et al., 2014) and other non-avian dinosaurs (Tsuihiji, 2010).

The inferential reconstruction of mRCv in *Bajadasaurus* attaches onto the caudoventral surface of the basal tubera, ventral to the insertion for mRCd (Fig. 11.4), as in *Diplodocus* and *Camarasaurus* (Button et al., 2014), and other non-avian dinosaurs (Snively & Russell, 2007a; Tsuihiji, 2010). Mimicking the condition for mRCd, mRCv does not leave any clear osteological correlate on its attachment surface. Considering its ubiquitous presence in extant Aves and Crocodylia (Snively & Russell, 2007a; Tsuihiji, 2010; Smith-Paredes & Bullar, 2019—although in Crocodylia it is debated), the presence of mRCv in *Bajadasaurus* represents a level I' inference.

Relative distribution of the cervicocranial musculature

The muscles of the neck of *Bajadasaurus*, as well as those of any taxon in which the skull-neck complex is mobile, can be divided on their dorsoventral and lateromedial components of the moment arms of the muscles, with the center on the pivot of the movement, therefore, the occipital condyle. In *Bajadasaurus*, the lateromedial components of the muscles are 1.46 times greater than those dorsoventral components. When dividing the dorsoventral component into dorsal and ventral components, the former representing 0.76 of the latter.

DISCUSSION
Cranial musculature in Dicraeosauridae

In the previous reconstructions of cranial musculature in Dicraeosauridae, the main focus was to understand the muscles originating from the supratemporal fossa, as in *Amargasaurus* (Salgado & Calvo, 1992), and the cervicocranial musculature (Harris, 2006; Tschopp & Mateus, 2013; Paulina-Carabajal et al., 2014).

The most comprehensive and detailed inference for Dicraeosauridae in terms of craniomandibular musculature (temporal, palatal and orbitotemporal muscle groups), suggested morphological and functional similarities to those of Diplodocidae (Nabavizadeh, 2020). Nevertheless, a greater mechanical advantage was suggested for the temporal muscles for Dicraeosauridae based on the insertion of this musculature onto the inferred expanded coronoid eminence, according to reconstructions on specimens originally lacking postdentary elements (Nabavizadeh, 2020).

The craniomandibular musculature of *Bajadasaurus* shows similarities with previous inferential reconstructions. Its general configuration shows voluminous palatal muscles, with inferred lines of action (regarding the orthal plane and in occlusion) being more vertically-oriented than those of the temporal musculature (Fig. 7). The latter muscular group is divided into four clearly delimited muscles occupying almost completely the supratemporal fossa, and inserting on the lower jaw, rostral to the temporomandibular joint, without extending further than the dentary-postdentary limits rostrally. The dorsal area of the postdentary elements in *Bajadasaurus* is simple, not expanded by a triangular and well-developed coronoid eminence in the surangular or the dentary, slightly contrasting with previous inferences on the morphology of this portion of the skull in Dicraeosauridae (Nabavizadeh, 2020). It is noteworthy, however, that within the same analysis, a low coronoid eminence was also suggested to be likely in dicraeosaurids (*e.g.*, Nabavizadeh, 2020, table 4). Therefore, if this was the original inter-pretation on the clade, dicraeosaurids would have been considered similar to other diplodocoids in Nabavizadeh (2020), with low coronoid eminences and lower mechanical advantages. The temporal musculature of *Bajadasaurus* resembles that of Diplodocidae, attaching onto the medial surface of the surangular and the adductor mandibular fossa distally. The fibers of all temporal muscles are inclined in a low angle regarding the orthal plane (Fig. 7), as in other Diplodocoidea and titanosaurs (Nabavizadeh, 2020), although these bundles shift ventrally after passing through the ITW, resulting in a more vertical orientation. Among the palatal muscles, as in other Sauropoda (Holliday, 2009; Button et al., 2014, 2016; Nabavizadeh, 2020), the mPt divides in a dorsal (mPtd) and a ventral belly (mPtv); the origin of the ventral volume is rostrally-limited by a rugose shelf, which is caudal to the base of the transverse process of the pterygoid. Its insertion, attaching along the lateral surface of the lower jaw, displays along a slightly-depressed surface of the angular, with a reduced extension when com-pared to the expanded insertion in other sauropodomorphs like *Diplodocus*, *Camarasaurus* and *Massospondylus* (Holliday, 2009; Young et al., 2012; Nabavizadeh, 2020). The cau-dalmost palatal muscle in *Bajadasaurus*—mAMP—has an origin limited to the rostroventral surface of the quadrate.

This contrasts with the typical—caudally-expanded along the lateral surface of the quadrate—condition in other Sauropoda (Holliday & Witmer, 2008; Holliday, 2009; Button et al., 2014, 2016). This rostroventrally-restricted origin of the mAMP is based on the orientation of the quadrate—whose major axis parallel to the same of the temporal muscles—, implying a reduced space for a dorsocaudal extension of the mAMP, and on the presence of the laminar expansion of the quadrate between the articular and pterygoid processes of the element, a tentatively apomorphic trait in *Bajadasaurus* (Garderes et al., 2023), from where this muscle attaches. This reduction in the length of the fibers of the mAMP implies a greater percentage in the exertion of muscular forces among the total muscle forces in *Bajadasaurus* (about a 30% of the total mandibular forces; Garderes, 2024) when compared to its contribution in other sauropodomorphs (Young et al., 2012; Button et al., 2014, 2016; Lautenschlager et al., 2016).

The orbitotemporal musculature, derived from the divi-sion of the mCID (Holliday & Witmer, 2007; Holliday, 2009), has been usually avoided in previous muscular reconstruc-tions of dinosaur taxa, albeit the presence of clear osteo-logical correlates in several specimens (Holliday, 2009). These muscles are mainly related to the movement of the palatal complex, a complex usually considered akinetic in non-avian dinosaurs, although potentially kinetic—partially kinetic competent—in several clades, among others, Sauropoda (Holliday & Witmer, 2008). The mPPt is a key muscle for the protraction of the pterygoid, usually origi-nating on the lateral portions of both the laterosphenoid and the basisphenoid. These areas are charac-teristically expanded in Dicraeosauridae as a lateral projection of the ventral end of the prootic crista, in a leaf-like process (Salgado & Calvo, 1992; Tschopp et al., 2015; Whitlock & Wilson Mantilla, 2020). Salgado & Calvo (1992) suggested an origin for mPPt attaching to this expanded process in *Amargasaurus*, configuration coincident with the proposed in this study for *Bajadasaurus*. This condition suggests a plausible occurrence of some degree of palatal kinesis in Dicraeosauridae, and mostly, in *Bajadasaurus*, where this condition could be also assisted by the wide morphological disparity between the two elements contacting on the

palatobasal joint (the pterygoid and the basipterygoid process; Garderes et al., 2023) with a high potential movement range, and an otic articulation (quadrate and neurocranium) not restricting a rostrocaudal displacement along the joint (Figs. 12.1–4). If such kinesis existed, it would have allowed a rostrocaudal displacement of the temporomandibular joint, triggered by the orbitotemporal musculature, allowing slight palinal movements in the feeding process of *Bajadasaurus* (Figs. 12.5–9) and, potentially, in Dicraeosauridae. Cranial kinesis and masticatory movements in non-avian dinosaurs, however, have been topics of debate. In particular, these movements were discussed for Sauropoda (Nabavizadeh, 2020) and tested in the diplodocid *Diplodocus*, with both favorable (Barrett & Upchurch, 1994; Upchurch & Barrett, 2000) and unfavorable stances (Holliday & Witmer, 2008; Whitlock, 2017). Of the criteria suggested by Holliday & Witmer (2008) for cranial kinesis, *Bajadasaurus* presents several of them. Its palatobasal joint—synovial in extant taxa (Holliday & Witmer, 2008), and *a priori* synovial in *Bajadasaurus*—does not present a tight relation between the basipterygoid process and the pterygoid—allowing great movement potential—, unlike in non-dicraeosaurid sauropods. Its pterygoid is not tightly linked to the braincase via a bony epipterygoid (traits shared with other sauropods), like in non-dicraeosaurid sauropods. Moreover, *Bajadasaurus* has a well-developed mPPt, compared to non-dicraeosaurid eusauropods (Holliday & Witmer, 2008), but expected for potentially kinetic taxa. Finally, in the otic joint of *Bajadasaurus*—also synovial in extant taxa (Holliday & Witmer, 2008), and *a priori* synovial in *Bajadasaurus*—the quadrate contacts the squamosal through a long surface oriented parallel to the longest axis of the mPPt, having a caudal limit on the hook-like process of the latter (synapomorphy of Dicraeosauridae; *e.g.*, Whitlock & Wilson Mantilla, 2020). The absence of thinned flexion zones in *Bajadasaurus* hampers the idea of this taxon having cranial kinesis as that in extant taxa (*e.g.*, rhynchokinesis), but the presence of several kinesis-related traits on the latter might have allowed accommodation movements, most likely, of the palate during the feeding process. Regarding the masticatory movements, orthal movements have been suggested to be the only possible movements in diplodocoid sauropods based on the mor-

phology of the temporomandibular joint (Whitlock, 2017). In *Bajadasaurus*, the morphologies and dimensions of both articular facets of this joint (that of the articular for the quadrate, and *vice versa*) are similar (supplemental information in Garderes et al., 2023), suggesting only orthal movements within the temporomandibular joint, as in other sauropods. Overall, the musculoskeletal configuration could have allowed movements resulting in slight intracranial accommodation of the location, in particular, of the temporomandibular joint. However, these movements would not have been triggered by the displacement of the quadrate along the rostrocaudal axis of the articular (as proper palinal movements), but by a pseudo-palinal movement triggered by the rostrocaudal displacement of the palate via loose palatal links and strong orbitotemporal muscles.

As for the orbitotemporal musculature, the extrinsic eye musculature is a scarcely explored muscular group in fossil taxa in Dinosauria. This inferred musculature in *Bajadasaurus* shows a configuration similar to that of Aves, with a great proportion of the muscles originating from the interorbitary septum. In Crocodylia (Wedin, 1953; Lessner & Holliday, 2020) most of the rectus muscles originate from the rostral elements of the lateral wall of the neurocranium, while the oblique muscles originate from the rostrally-placed descending frontals. A crocodilian configuration of the extrinsic eye muscles in *Bajadasaurus* would result in a dorsal position, regarding the eye, of the origin of both oblique muscles (Figs. 10.2, 10.4), implying a dorsally-directed movement of the eye when the mOd is activated, instead of the usual, rostrodorsally-directed movement (Fig. 10). The inferential reconstruction based on the avian configuration for this musculature in *Bajadasaurus* (Figs. 10.1, 10.3) shows oblique muscles with lines of actions directed rostrodorsally (for mOd) and rostroventrally (for mOv), without crossovers with the lines of action of the other extrinsic eye muscles. The rectus musculature attaching on the lateral wall of the neurocranium of *Bajadasaurus*, with an exception in mRl, leave smooth osteological correlates evidenced as slight changes of deepness on the bone surface.

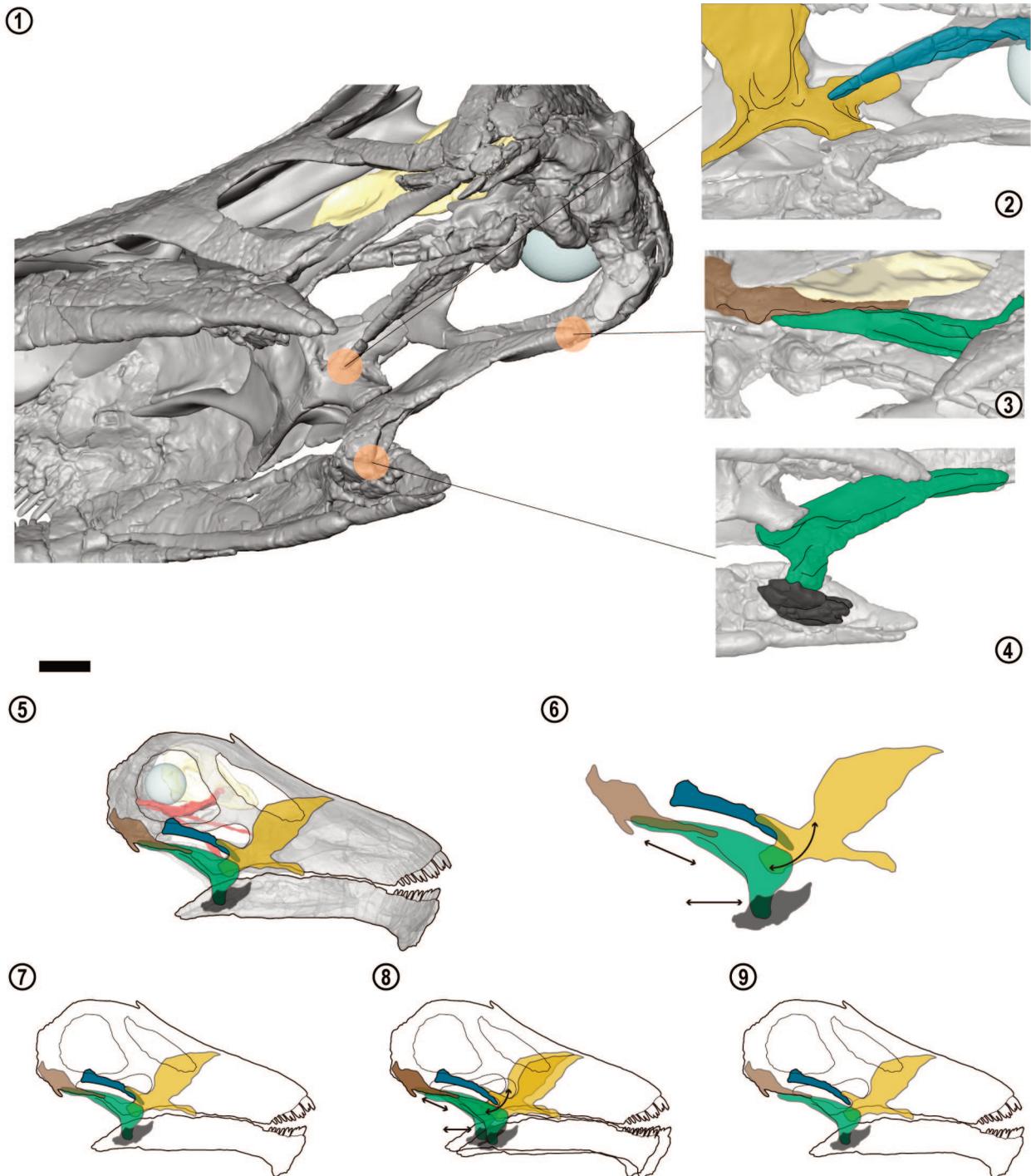The cervicocranial musculature has been consistently mentioned in Dicraeosauridae (Harris, 2006; Tschopp &

Figure 12. Potentially kinetic joints. 1, location; 2, palatobasal joint; 3, otic joint; 4, temporomandibular joint; 5–9, potential cranial kinesis. 1 shows the three potential kinetic joints detailed in 2–4. The palatobasal joint (2) shows a mortar-and-pestle morphology, with a pestle several times wider than the mortar, potentially allowing a rotation of the pterygoid (yellow) regarding the basipterygoid process (blue). The articulation along the otic joint (3) has a planar morphology, potentially allowing a displacement of the quadrate (green) regarding the neurocranium along the squamosal (in brown). The mandibular joint (4), between the quadrate (green) and the articular (black), shows a morphology similar to that of other taxa with orthal bite. The sequence 5 to 9 shows a hypothetical mechanism of pseudo-palinity based on the potential displacements along the basal, otic and temporomandibular joints. 6 shows the kind of movements tentatively allowed by the potential kinetic joints; 7 shows the resting position of the system; 8 shows the overlap between resting and action positions of the system; 9 shows the results of the potential kinetic movements (action position), allowing a forward-directed movement of the lower jaw (palinity) not related to a change inside the temporomandibular joint (between the quadrate and the articular). Colour pattern: black, articular; brown, squamosal; green, quadrate; grey, skull; light blue (in transparency), inferred eye; light yellow, interorbitary septum; pale yellow, pterygoid; red, muscle. Scale= 3 cm for 1–4.

Mateus, 2013; Paulina-Carabajal et al., 2014), albeit with a lower level of analysis when compared to the inferences in other groups of non-avian dinosaurs, either Sauropoda (Button et al., 2014) or non-sauropods (Snively & Russell, 2007a, b, c; Tsuihiji, 2010; Snively et al., 2013a, b). The *transversospinalis* musculature, rostrodorsally placed along the caudal wall of the skull and attaching to the parietals, has been previously reconstructed showing an extended insertion in Dicraeosauridae (*e.g.*, Paulina-Carabajal et al., 2014), attaching to wide depressions on the dorsal surface of the parietals, similar to the inferred in other Sauropoda (Button et al., 2014). These reconstructions, however, imply an elliptic insertion for muscles that in extant taxa have attachments and physiological cross-sections with a laminar outline (Snively & Russell, 2007b; Jones et al., 2009; MM. pers. obs.). An alternative interpretation for the dorsal parietal depressions, assigned in its fullness to the *transversospinalis* musculature insertion in other Dicraeosauridae, assigns part of the depression as osteological correlates related to other soft tissues (see Discussion: Sheltered neck), and that the *transversospinalis* group attached only to the edges of these depressions (Fig. 11.2). The deep dorsiflexor musculature (mSpCl and mSpCm) in Dicraeosauridae extends along almost the total dorsal extension of the paroccipital process. These muscles are ventrally limited by ridges and variations in inclination of the surface of the paroccipital process on its dorsal surface, similar to the observed in the theropod *Daspletosaurus* (Snively & Russell, 2007a), and among Pachycephalosauria and Ornithopoda (Tsuihiji, 2010), but contrasting with the inferred for *Diplodocus* and *Camarasaurus* (Button et al., 2014). In the two latter taxa, this muscular tandem is restricted to the vicinity of the sagittal crest, without extending significantly through the paroccipital processes. Moreover, in *Diplodocus* and *Camarasaurus*, the primarily lateroflexor musculature inserts along the total extension of the caudal surface of the paroccipital process, including the proximal-most area, surrounding the base of the neck of the occipital condyle (Button et al., 2014). In *Bajadasaurus*, this lateroflexor musculature does not extend proximally, and is restricted to the distal third portion of the paroccipital process. The area at the base of the processes, where the proximal-most muscles are inferred to attach in *Diplodocus* and *Camarasaurus*

(muscle *iliocostalis capitis*; Button et al., 2014), and where a deep depression lateral to the base of the neck of the condyle develops, is present in *Bajadasaurus*. This depression, however, is interpreted as the osteological correlate for the presence of an atlanto-occipital capsule, also inferred for other non-avian dinosaurs (Tsuihiji, 2010). The rostrally-directed tilting of the occipital region dorsal to the occipital condyle, a widely spread trait among dicraeosaurids, results in a reduced dorsal component of moment arms when compared to other sauropods in caudal view (Fig. 13). In this view, the ratio between the maximum horizontal and vertical distances, dorsal to the condyle, is 1.46 in *Bajadasaurus*, greater than the 1.2 ratio in *Diplodocus* and *Camarasaurus*, suggesting a more important role in the lateral movements of the skull in *Bajadasaurus* compared to other sauropods. The ratio between the maximal dorsal and ventral moment arm components is 0.76 in *Bajadasaurus* (being the ventral component the greatest), much lower than these ratios in *Diplodocus* (1.8) and *Camarasaurus* (3.11). This suggests less preponderant skull dorsiflexive movements in diplodocoids compared to *Camarasaurus*, more drastically in *Bajadasaurus*, and, probably, Dicraeosauridae. Unfortunately, these ratios do not include derived Macronaria, given the lack of detailed cervicocranial musculature reconstructions in that clade. A plausible explanation for these differences between *Camarasaurus* and diplodocoids may include that these are related to differences in feeding habits, rather than a phylogenetic constraint. Taxa with reduced dorsiflexive movements might have been foraging at the lower canopies, as it was suggested for Diplodocoidea (*e.g.*, Whitlock, 2011). Alternatively, taxa with enhanced dorsiflexive movements, such as *Camarasaurus* and probably *Giraffatitan*, might have fed on the upper canopy (Whitlock, 2011).

Variability in Dicraeosauridae

Temporal musculature. The osteological correlates for the temporal musculature observed in *Bajadasaurus* (MMCh-PV 75) are similar, but less concave (Fig. 6.2), to those of *Amargasaurus* (MACN-Pv N15 –previously referred to as MACN-N) and *Dicraeosaurus* (M.BR 2378, M.BR 2379). In these taxa, a clear osteological correlate for the mPsTs is observed on the caudal face of the crista antotica. The

correlate dividing the origins for mAMEM and mAMEP in *Bajadasaurus*, observed in the ventral surface of the parietal and the proximal area of the rostral surface of the paroccipital process (Fig. 6.1) is shared with *Dicraeosaurus*, but not with *Amargasaurus*, where this correlate is only observed on the paroccipital process. The correlates for the mAMES in *Amargasaurus* and *Bajadasaurus* are similar, being a poorly developed ridge on the medial face of the upper temporal bar. **Orbitotemporal musculature.** The osteological correlate for mTP in archosaurs is the ventral edge of the crista antotica
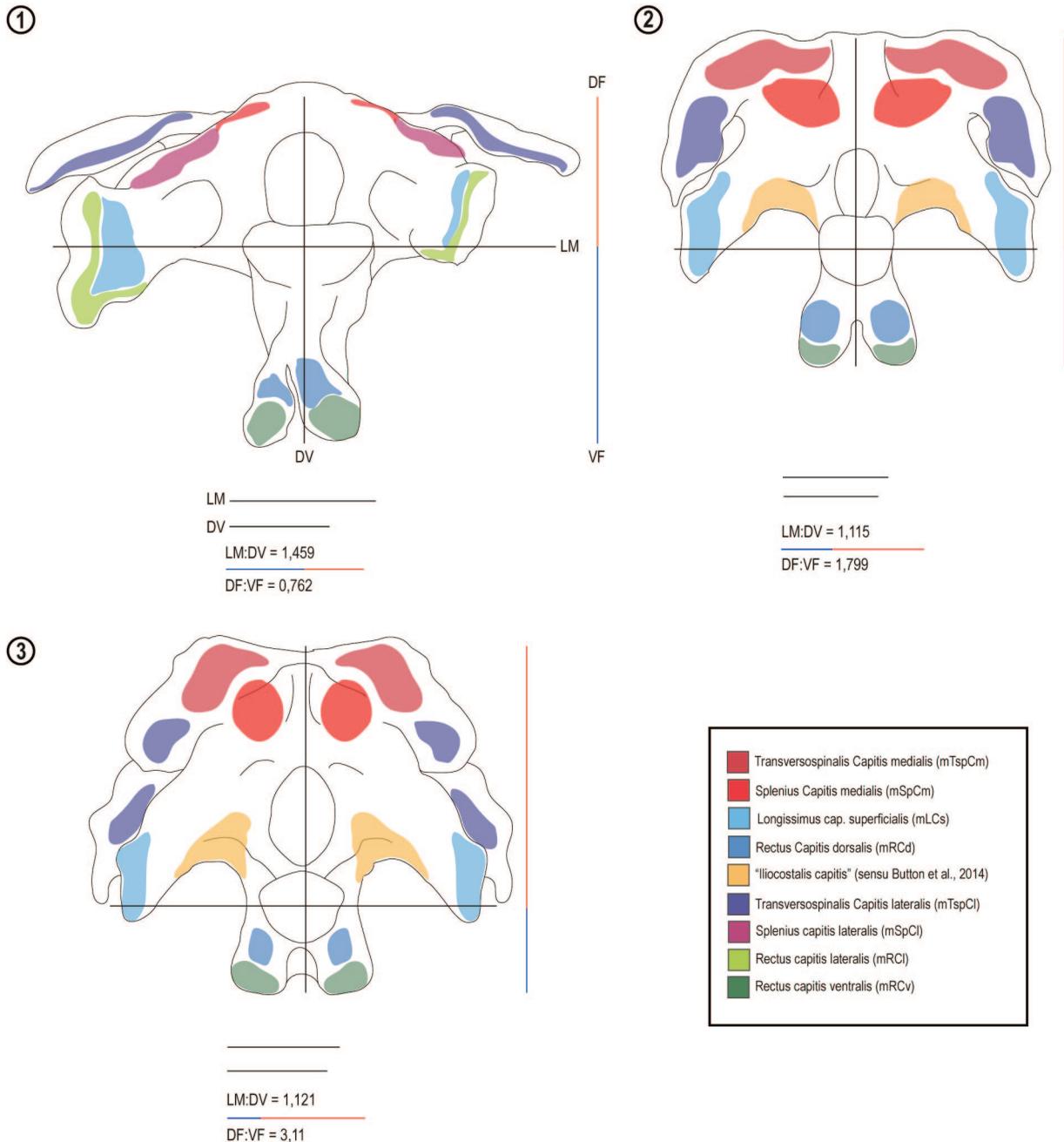

Figure 13. Moment arms of the cervicocranial musculature in Sauropoda. 1, *Bajadasaurus*; 2, *Diplodocus*; 3, *Camarasaurus*. Figures 2–3 based on Button et al. (2014). Abbreviations: DF, dorsiflexion; DV, dorsoventral; LM, lateromedial; VF, ventroflexion. In a view perpendicular to the plane including the maximum surface of the circumference of the foramen magnum, the cervicocranial musculature of *Bajadasaurus* differs from that of *Diplodocus* and *Camarasaurus*, even considering the differences among the reconstructions performed in this study and those from Button et al. (2014).

(Holliday, 2009), a structure spread among Dicraeosauridae. Both in *Bajadasaurus* and *Amargasaurus* the attachment surface for the origin of this muscle is exclusively the ventral edge of the crista; however, these taxa might differ from *Dicraeosaurus*, a taxon that bears a concavity on the rostral surface of the crista, probably indicating a wider attachment for the mTP. The mLPt in *Bajadasaurus* originates on a small osteological correlate placed caudal to the foramen for CN V (Fig. 6.3). This correlate is not shared with other Dicraeosauridae, but it is placed in a similar area as the crest of the laterosphenoid dorsally surrounding the foramen for CN V in other Dicraeosauridae (Whitlock & Wilson Mantilla, 2020). Regarding the mPPt, if the leaf-like process of the crista prootica is effectively where this muscle originated on (Fig. 6.4), this osteological correlate and the muscle were ubiquitous among Dicraeosauridae, with a considerable development albeit the lack of epipterygoid—which was considered as an indicator of the reduction of this muscle (Holliday, 2009).

Extrinsic eye musculature. The smooth osteological correlates for mRv and mRd in *Bajadasaurus* (Fig. 6.5) can be also observed in *Amargasaurus*, although more deeply depressed in the latter. Specifically, the correlate for mRv extends up to the cultriform process in these taxa, contrasting with the condition in *Dicraeosaurus*, where no clear osteological correlate is distinguishable. The correlate for mRd in *Bajadasaurus* resembles a concavity on the orbitosphenoid of *Dicraeosaurus*, located below the foramen for the olfactory tract, although the former is more dorsally displayed.

Cervicocranial musculature. The configuration for the *transversospinalis* musculature in Dicraeosauridae along the complete dorsal surface of the parietal (Fig. 6.6) is controversial, based on the morphology of these muscles in extant related taxa (Snively & Russell, 2007b; Button et al., 2014). Reconsidering the mTspCl and mTspCm in Dicraeosauridae under the morphology suggested for *Bajadasaurus*, in which these muscles attach to the dorsocaudal surface of the parietal (dorsal to the post-temporal fenestra), shows a high degree of variability within the clade. Under this scenario, in *Bajadasaurus* the mTspCm would have been invading the post-temporal fossa, as this fossa extends medially (autapomorphic trait; Gallina et al., 2019). This would contrast with the plausible, medially restricted, attachment in *Amargasaurus* and *Dicraeosaurus*, where it would only extend up to the medial edge of the post-temporal fenestra. In derived dicraeosaurids, the mTspCl shows a lesser development compared to that of *Bajadasaurus*, based on the lateral extension of the parietal; in *Bajadasaurus*, this extends further than the lateral extension of the paroccipital process, an inverted relationship in *Amargasaurus* and *Dicraeosaurus*. The *splenius capitis* muscles are more voluminous in derived dicraeosaurids than in *Bajadasaurus*. The mSpCm in *Amargasaurus* and *Dicraeosaurus* would insert on a deeply depressed osteological correlate on the lateral surface of the sagittal crest, along the tentative supraoccipital-otooccipital contact, which in *Bajadasaurus* is reduced by the medial expansion of the post-temporal fossa. Besides, the two derived taxa show a mSpCl attaching to a triangular, laterally-acute correlate, which differs from the flattened attachment in *Bajadasaurus*. Among the primarily lateroflexor muscles, the correlate-based division between mRCl and mLCs observed in *Bajadasaurus* is shared with *Dicraeosaurus*, while in *Amargasaurus* no correlate is observed for any of these muscles. The ventroflexor musculature does not leave clear osteological correlates in *Bajadasaurus*, as in derived dicraeosaurids, notwithstanding the great variability along the caudal surface of the basal tubera in these taxa.

Support-related soft tissues

The presence of support soft tissues for the temporal muscles in non-avian dinosaurs is a relatively poorly explored topic, mainly because of the preservation bias in cartilage and tendons. However, these tissues are widely extended among extant taxa, both closely related (Holliday & Witmer, 2007; Bona & Desojo, 2011; Smith-Paredes & Bullar, 2019; Lessner & Holliday, 2020) and less phylogenetically related Sauropsida (Jones et al., 2009; Daza et al., 2011). Moreover, specific intra-clade soft tissues have been inferred for dinosaurs, such as the buccal exoparia connecting the zigoma (attaching to the lateral surface of the jugal) and the mandible (Sharpe et al., 2025). Two specific soft tissues are fundamental for the transmission of forces of the temporal musculature. One is the bodenaponeurosis, or its tentatively homologues in Crocodylia (mandibular adductor tendon) and Aves (paracoronoid aponeurosis;

Holliday & Witmer, 2007), related the division and insertion of the muscle bundles of the mAME in Lepidosauria (Holliday & Witmer, 2007; Gröning et al., 2013). The other one is the *transiliens* cartilage, present in Crocodylia, and homologue to a minor tendon in several Aves (Holliday & Witmer, 2007), which connects to the origin of the muscle *intramandibularis* and to the insertion of mPsTs (Holliday & Witmer, 2007; Smith-Paredes & Bullar, 2019). This includes part of the insertion of different bundles of the mAME (Bona & Desojo, 2011). All of the aforementioned inferable elements affect the origin and insertion of the temporal muscles in extant taxa, as those are structures in which these muscles attach, and might have done so in non-avian dinosaurs, if present, affecting the mechanical advantage of the muscles.

The muscle direction shifting of the temporal musculature in *Bajadasaurus* suggests the presence of a structure that assisted such shifting (Figs. 14.1–3). As described above (see Results: Muscle inferential lines of action), the temporal muscles show a mean verticalization of 11.45° after passing through the ITW. Moreover, the dorsal portions of these muscles converge at an angle 14.6° up to the window, while the ventral portions diverge from this point at 48.5° (Fig. 14.2). If a structure, either analogue or homologue to a *transiliens* cartilage or the bodenaponeurosis, was present in *Bajadasaurus* assisting such change in muscle directions, it would represent a level II' inference, albeit this would utterly explain the angular variation and divergence of the temporal muscles at both sides of the ITW and the orthal plane. However, alternative ways and support tissues for angular shifting in muscle bundles are present in other muscles of both the skull (*e.g.*, the mPtv in *Bajadasaurus* itself) and the whole body (*e.g.*, the *trochlea fibularis* in the knee of birds and mammals), and cannot be discarded.

Sheltered neck

The depressions at the dorsal surface of the parietals (Fig. 6.6) in *Bajadasaurus*, previously suggested to be correlates for the *transversospinalis* muscles in *Dicraeosaurus* and *Amargasaurus* (Paulina-Carabajal et al., 2014), show, if working as the previously suggested correlates, completely different contours to the correlates in extant taxa (Snively & Russell, 2007b; Jones et al., 2009). Following a more con-

servative approach for muscular inferences, the possibility that these depressions were related to other, non-muscular, soft tissues cannot be ruled out. A highly speculative set of hypotheses imply that these depressions housed a dermal thickening, such as thickened skin or scales similar to those present in extant rhinoceros and hippopotamus (Hieronymus, 2009), an osteodermal pattern (Figs. 14.4–6) similar to the cartilage expansion of the palpebral in the dorsal area of the orbit (suggested for Sauropoda; Tschopp et al., 2018), or even subcutaneous tissues (Figs. 14.7–9) as the adipose concentrations in the hump of some camelids (Peters & Von Den Driesch, 1997; Martini et al., 2017).

CONCLUSIONS

Bajadasaurus pronuspinax shows a muscular arrangement similar to that of other Flagellicaudata. The craniomandibular musculature does not differ significantly from that of *Diplodocus*, with palatal muscles oriented more vertically than the temporal muscles. However, the temporal muscles show a directional shifting not previously reported, suggesting the presence of a support structure assisting this change in the muscle action line, either analogue or homologue to a *transiliens* cartilage or the bodenaponeurosis. The mPPt, attaching its origin to the expanded distal portion of the crista prootica as a leaf-like process, possibly triggered slight palatal movements that displaced the temporomandibular joint forwards and backwards as a complete unit, resulting in a pseudo-palinal displacement of the lower jaw. Regarding eye muscles, the first attempt to describe in detail the extrinsic musculature of a Sauropoda was performed, suggesting an avian-like configuration for the origin of the muscles. Finally, the cervicocranial musculature differs from that reconstructed for *Diplodocus* and *Camarasaurus*, with a *transversospinalis* group showing a planar outline in cross-section, and lateroflexor muscles restricted to the distal portions of the paroccipital processes. Overall, Dicraeosauridae taxa show patent osteological correlates for many of the muscles attaching to the cranium. One of these correlates, previously suggested to relate completely to the *transversospinalis* group, here is tentatively considered to be shared with other soft tissues, such as a thickened dermis or epidermis, or even subcutaneous deposits.
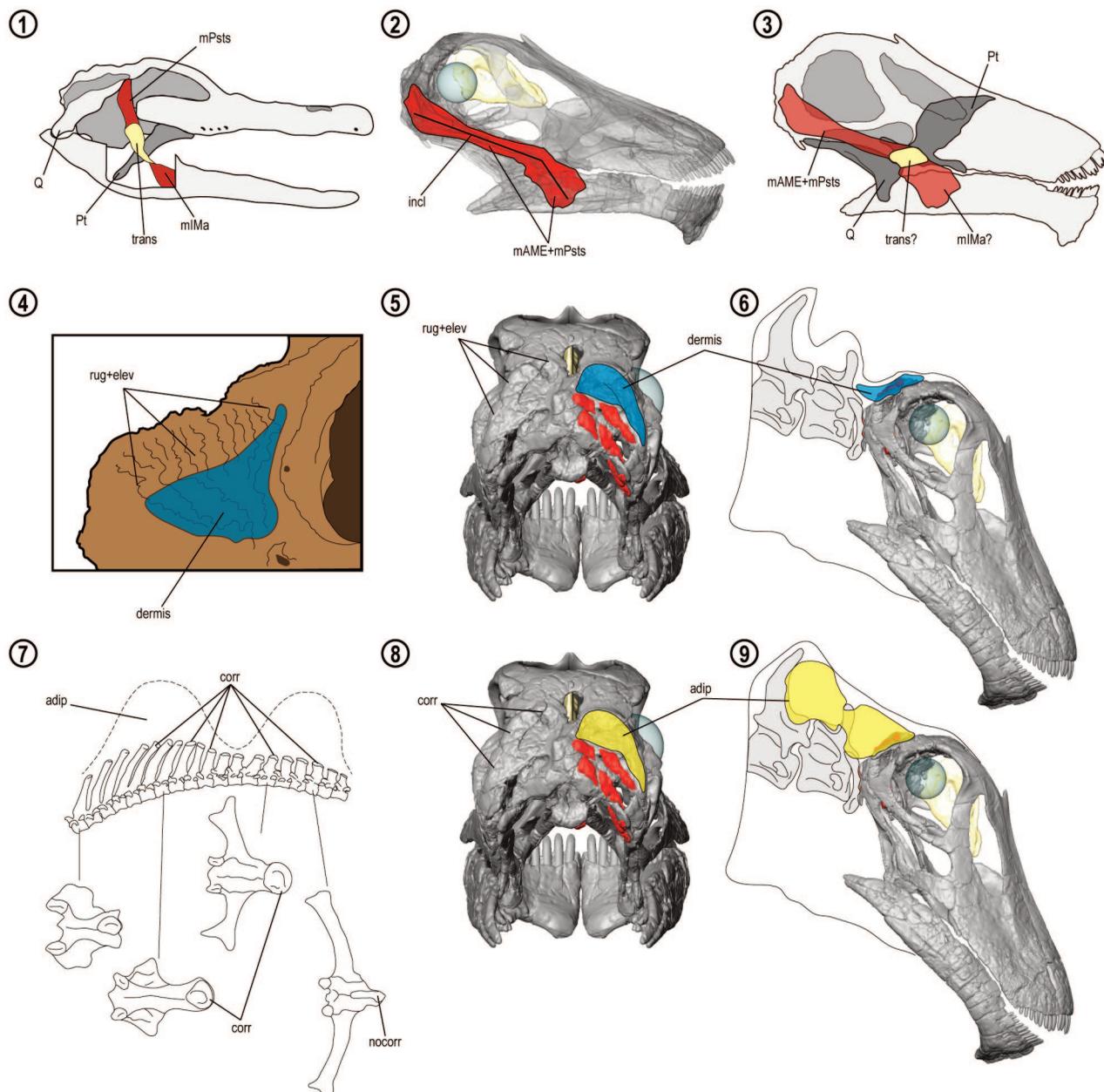
Figure 14. Inferential hypotheses in *Bajadasaurus*. 1, *transiliens* cartilage in Crocodylia (modified from fig. 10.5—c—in Smith-Paredes & Bullar, 2019); 2–3, hypothesis of an analogue for a *transiliens* cartilage in *Bajadasaurus*; 4, osteological correlates for a dermo-epidermal thickened tissue on the premaxilla of *Hippopotamus amphibius* (modified from fig. 5-7E in Hieronymus, 2009); 5–6, hypotheses of a dorsal osteodermal covering on the skull roof of *Bajadasaurus*; 7, osteological correlates for adipose-tissue deposits on the hip of *Camelus bactrianus* (modified from fig. 1A, B in Peters & Von Den Driesch, 1997); 8–9, hypothesis of subcutaneous adipose tissue housing in *Bajadasaurus*. Abbreviations: adip, adipose tissue; corr, osteological correlate for adipose tissue deposits; dermis, thickened dermal structure; inc, mean inclination of the muscle bundles; mAME, external mandibular adductor musculature; mIMa, *intramandibularis* muscle; mPsts, superficial *pseudotemporalis* muscle; nocorr, lack of osteological correlate for adipose tissue; Pt, pterygoid; Q, quadrate; rug+elev, correlate of epidermal structure where a combination of an osseous elevation and a rugose surface (Hieronymus, 2009); trans, *transiliens* cartilage. Colour pattern: blue (in transparency), dermal structure; grey, skull; light blue (in transparency), inferred eye; light yellow, cartilage; pale yellow, adipose tissue; red, muscle.

DATA AVAILABILITY STATEMENT

The digital models that support the present study are housed in the database Morphosource, within the link: https://www.morphosource.org/projects/000774438

REFERENCES

Al-Hassawi, A. M. (2007). *A comparative anatomy of the neck region in lizards: a research study*. Trafford Publishing.

Barrett, P. M., & Upchurch, P. (1994). Feeding mechanisms of *Diplodocus*. *Gaia*, *10*, 195–203.

Bona, P., & Desojo, J. B. (2011). Osteology and cranial musculature of *Caiman latirostris* (Crocodylia: Alligatoridae). *Journal of Morphology*, *272*(7), 780–795. https://doi.org/10.1002/jmor.10894

Button, D. J., Barrett, P. M., & Rayfield, E. J. (2016). Comparative cranial myology and biomechanics of *Plateosaurus* and *Camarasaurus* and evolution of the sauropod feeding apparatus. *Palaeontology*, *59*(6), 887–913. https://doi.org/10.1111/pala.12266

Button, D. J., Rayfield, E. J., & Barrett, P. M. (2014). Cranial biomechanics underpins high sauropod diversity in resource-poor environments. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1795), 20142114. https://doi.org/10.1098/rspb.2014.2114

Calvo, J. O. (1994). Jaw mechanics in sauropod dinosaurs. *Gaia*, *10*, 183–193.

Daza, J. D., Diogo, R., Johnston, P., & Abdala, V. (2011). Jaw adductor muscles across lepidosaurs: a reappraisal. *The Anatomical Record*, *294*(10), 1765–1782. https://doi.org/10.1002/ar.21467

Franz-Odendaal, T. A. (2018). Skeletons of the eye: An evolutionary and developmental perspective. *The Anatomical Record*, *303*(1), 100–109. https://doi.org/10.1002/ar.24043

Gallina, P. A., Apesteguía, S., Canale, J. I., & Haluza, A. (2019). A new long-spined dinosaur from Patagonia sheds light on sauropod defense system. *Scientific reports*, *9*(1), 1–10. https://doi.org/10.1038/s41598-018-37943-3

Garderes, J. P. (2024). *Anatomía y biomecánica craniodental de* Bajadasaurus pronuspinax *(Dinosauria, Sauropoda) y sus implicancias en el comportamiento alimentario de los diplodocoideos* [PhD Thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata]. Retrieved from https://doi.org/10.35537/10915/167625

Garderes, J. P., Gallina, P. A., Whitlock, J. A., & Toledo, N. (2023). Cranial osteology of *Bajadasaurus pronuspinax* (Sauropoda, Dicraeosauridae). *Historical Biology*, *36*(7), 1–25. https://doi.org/10.1080/08912963.2023.2212389

Garderes, J. P., Militello, M., Whitlock, J. A., Toledo, N., & Gallina, P. A. (2022). Retro- acupuncture: craniocervical musculature of the dicraeosaurid sauropod dinosaur *Bajadasaurus pronuspinax*. *Programs and Abstracts of the 82° Annual Meeting of the Society of Vertebrate Paleontology* (p. 154). Toronto.

Gorniak, G. C., Rosenberg, H. I., & Gans, C. (1982). Mastication in the tuatara, *Sphenodon punctatus* (Reptilia: Rhynchocephalia): structure and activity of the motor system. *Journal of Morphology*, *171*(3), 321–353. https://doi.org/10.1002/jmor.1051710307

Gröning, F., Jones, M. E., Curtis, N., Herrel, A., O'Higgins, P., Evans, S. E., & Fagan, M. J. (2013). The importance of accurate muscle modelling for biomechanical analyses: a case study with a lizard skull. *Journal of the Royal Society Interface*, *10*(84), 20130216. https://doi.org/10.1098/rsif.2013.0216

Haas, G. (1963). A proposed reconstruction of the jaw musculature of *Diplodocus*. *Annals of the Carnegie Museum*, *36*, 139–157.

Harris, J. D. (2006). Cranial osteology of *Suuwassea emilieae* (Sauropoda: Diplodocoidea: Flagellicaudata) from the Upper Jurassic Morrison Formation of Montana, USA. *Journal of Vertebrate Paleontology*, *26*, 88–102. https://doi.org/10.1671/0272-4634(2006)26[88:COOSES]2.0.CO;2

Harris, J. D., & Dodson, P. (2004). A new diplodocoid sauropod dinosaur from the Upper Jurassic Morrison Formation of Montana, USA. *Acta Palaeontologica Polonica*, *49*, 197–210.

Hieronymus, T. L. (2009). *Osteological correlates of cephalic skin structures in Amniota: documenting the evolution of display and feeding structures with fossil data* [PhD Thesis, Ohio University]. Retrieved from http://rave.ohiolink.edu/etdc/view?acc_num=ohiou1237491191

Holliday, C. M. (2009). New insights into dinosaur jaw muscle anatomy. *The Anatomical Record*, *292*(9), 1246–1265. https://doi.org/10.1002/ar.20982

Holliday, C. M., & Witmer, L. M. (2007). Archosaur adductor chamber evolution: integration of musculoskeletal and topological criteria in jaw muscle homology. *Journal of Morphology*, *268*(6), 457–484. https://doi.org/10.1002/jmor.10524

Holliday, C. M., & Witmer, L. M. (2008). Cranial kinesis in dinosaurs: intracranial joints, protractor muscles, and their significance for cranial evolution and function in diapsids. *Journal of Vertebrate Paleontology*, *28*(4), 1073–1088. https://doi.org/10.1671/0272-4634-28.4.1073

Holliday, C. M., Porter, W. R., Vliet, K. A., & Witmer, L. M. (2019). The frontoparietal fossa and dorsotemporal fenestra of archosaurs and their significance for interpretations of vascular and muscular anatomy in dinosaurs. *The Anatomical Record*, *303*(4), 1060–1074. https://doi.org/10.1002/ar.24218

Janensch, W. (1935–1936). Die Schädel der Sauropoden *Brachiosaurus*, *Barosaurus* und *Dicraeosaurus* aus den Tendaguruschichten Deutsch-Ostafrikas (Anfang). *Palaeontographica-Supplementbände*, *7(2)*, 145–248, *7(3)*, 249–298.

Jones, M. E., Curtis, N., O'Higgins, P., Fagan, M., & Evans, S. E. (2009). The head and neck muscles associated with feeding in *Sphenodon* (Reptilia: Lepidosauria: Rhynchocephalia). *Palaeontologia Electronica*, *12*(2), 7A.

Lautenschlager, S. (2013). Cranial myology and bite force performance of *Erlikosaurus andrewsi*: a novel approach for digital muscle reconstructions. *Journal of Anatomy*, *222*(2), 260–272. https://doi.org/10.1111/joa.12000

Lautenschlager, S., Brassey, C. A., Button, D. J., & Barrett, P. M. (2016). Decoupled form and function in disparate herbivorous dinosaur clades. *Scientific Reports*, *6*(1), 26495. https://doi.org/10.1038/srep26495

Lautenschlager, S., Bright, J. A., & Rayfield, E. J. (2013). Digital dissection–using contrast-enhanced computed tomography scanning to elucidate hard-and soft- tissue anatomy in the Common Buzzard *Buteo buteo*. *Journal of Anatomy*, *224*(4), 412–431. https://doi.org/10.1111/joa.12153

Lautenschlager, S., Witmer, L. M., Altangerel, P., Zanno, L. E., & Rayfield, E. J. (2014). Cranial anatomy of *Erlikosaurus andrewsi* (Dinosauria, Therizinosauria): new insights based on digital

reconstruction. *Journal of Vertebrate Paleontology*, *34*(6), 1263–1291. https://doi.org/10.1080/02724634.2014.874529

Lessner, E. J., & Holliday, C. M. (2020). A 3D ontogenetic atlas of *Alligator mississippiensis* cranial nerves and their significance for comparative neurology of reptiles. *The Anatomical Record*, *305*(10), 2854–2882. https://doi.org/10.1002/ar.24550

Martínez, R. D., Lamanna, M. C., Novas, F. E., Ridgely, R. C., Casal, G. A., Martínez, J. E., Vita, J. R., & Witmer, L. M. (2016). A basal lithostrotian titanosaur (Dinosauria: Sauropoda) with a complete skull: implications for the evolution and paleobiology of Titanosauria. *PLoS One*, *11*(4), e0151661. https://doi.org/10.1371/journal.pone.0151661

Martini, P., Schmid, P., & Costeur, L. (2017). Comparative morphometry of bactrian camel and dromedary. *Journal of Mammalian Evolution*, *25*(3), 407–425. https://doi.org/10.1007/s10914-017-9386-9

Militello, M., Otero, A., & Carballido, J. L. (2026). The occiput of *Amargasaurus* (Sauropoda, Dicraeosauridae): Reconstruction of the craniocervical muscular insertions with comments on feeding strategy. *Journal of Anatomy*, *248(2)*, 284–306. https://doi.org/10.1111/joa.70071

Nabavizadeh, A. (2020). Cranial musculature in herbivorous dinosaurs: a survey of reconstructed anatomical diversity and feeding mechanisms. *The Anatomical Record*, *303*(4), 1104–1145. https://doi.org/10.1002/ar.24283

Nagesan, R. (2017). *Neck Mobility of the Plesiosaur* Nichollsaura borealis [PhD Thesis, University of Calgary]. Retrieved from http://hdl.handle.net/11023/4042

Paulina-Carabajal, A., Carballido, J. L., & Currie, P. J. (2014). Braincase, neuroanatomy, and neck posture of *Amargasaurus cazaui* (Sauropoda, Dicraeosauridae) and its implications for understanding head posture in sauropods. *Journal of Vertebrate Paleontology*, *34*(4), 870–882. https://doi.org/10.1080/02724634.2014.838174

Peters, J., & Von Den Driesch, A. (1997). The two-humped camel (*Camelus bactrianus*): New light on its distribution, management and medical treatment in the past. *Journal of Zoology*, *242*(4), 651–679. https://doi.org/10.1111/j.1469- 7998.1997.tb05819.x

Rybczynski, N., Tirabasso, A., Bloskie, P., Cuthbertson, R., & Holliday, C. (2008). A three-dimensional animation model of *Edmontosaurus* (Hadrosauridae) for testing chewing hypotheses. *Palaeontologia Electronica*, *11*(2), 1–14.

Salgado, L., & Calvo, J. O. (1992). Cranial osteology of *Amargasaurus cazaui* Salgado & Bonaparte (Sauropoda, Dicraeosauridae) from the Neocomian of Patagonia. *Ameghiniana*, *29*(4), 337–346.

Schumacher, G. H. (1973). The head muscles and hyolaryngeal skeleton of turtles and crocodilians. In C. Gans, & T. S. Parsons (Eds.), *Biology of the Reptilia, 4* (pp. 101–199). Academic Press.

Sereno, P. C., Wilson, J. A., Witmer, L. M., Whitlock, J. A., Maga, A., Ide, O., & Rowe, T. A. (2007). Structural extremes in a Cretaceous dinosaur. *PLoS One*, *2*(11), e1230. https://doi.org/10.1371/journal.pone.0001230

Sharpe, H. S., Wang, Y. Y., Dudgeon, T. W., Powers, M. J., Whitebone, S. A., Coppock, C. C., Dyer, A. D., & Sullivan, C. (2025). Skull morphology and histology indicate the presence of an unexpected buccal soft tissue structure in dinosaurs. *Journal of Anatomy*, *247*, 790–818. https://doi.org/10.1111/joa.14242

Smith, D. K. (2015). Craniocervical myology and functional morphology of the small-headed therizinosaurian theropods *Falcarius utahensis* and *Nothronychus mckinleyi*. *PLoS One*, *10*(2), e0117281. https://doi.org/10.1371/journal.pone.0117281

Smith-Paredes, D., & Bullar, B. A. S. (2019). The skull and head muscles of archosauria. In J. Ziermann, Jr. R. Diaz, & R. Diogo (Eds.), *Heads, jaws, and muscles. Fascinating Life Sciences* (pp. 229–251). Springer. https://doi.org/10.1007/978-3-319-93560-7_10

Snively, E., & Russell, A. P. (2007a). Functional variation of neck muscles and their relation to feeding style in Tyrannosauridae and other large theropod dinosaurs. *The Anatomical Record*, *290*(8), 934–957. https://doi.org/10.1002/ar.20563

Snively, E., & Russell, A. P. (2007b). Functional morphology of neck musculature in the Tyrannosauridae (Dinosauria, Theropoda) as determined via a hierarchical inferential approach. *Zoological Journal of the Linnean Society*, *151*(4), 759–808. https://doi.org/10.1111/j.1096-3642.2007.00334.x

Snively, E., & Russell, A. P. (2007c). Craniocervical feeding dynamics of *Tyrannosaurus rex*. *Paleobiology*, *33*(4), 610–638. https://doi.org/10.1666/06059.1

Snively, E., Russell, A. P., Powell, G. L., Theodor, J. M., & Ryan, M. J. (2013a). The role of the neck in the feeding behaviour of the Tyrannosauridae: inference based on kinematics and muscle function of extant avians. *Journal of Zoology*, *292*(4), 290–303. https://doi.org/10.1111/jzo.12109

Snively, E., Cotton, J. R., Ridgely, R., & Witmer, L. M. (2013b). Multibody dynamics model of head and neck function in *Allosaurus* (Dinosauria, Theropoda). *Palaeontologia Electronica*, *16*(2), 1–29. https://doi.org/10.26879/338

Taylor, A. C., Lautenschlager, S., Qi, Z., & Rayfield, E. J. (2017). Biomechanical evaluation of different musculoskeletal arrangements in *Psittacosaurus* and implications for cranial function. *The Anatomical Record*, *300*(1), 49–61. https://doi.org/10.1002/ar.23489

Tschopp, E., & Mateus, O. (2013). The skull and neck of a new flagellicaudatan sauropod from the Morrison Formation and its implication for the evolution and ontogeny of diplodocid dinosaurs. *Journal of Systematic Palaeontology*, *11*(7), 853–888. https://doi.org/10.1080/14772019.2012.746589

Tschopp, E., Mateus, O., & Benson, R. B. J. (2015). A specimen-level phylogenetic analysis and taxonomic revision of Diplodocidae (Dinosauria, Sauropoda). *PeerJ*, *3*, e857. https://doi.org/10.7717/peerj.857

Tschopp, E., Mateus, O., Marzola, M., & Norell, M. (2018). Indications for a horny beak and extensive supraorbital connective tissue in diplodocid sauropods. *78th Annual Meeting of the Society of Vertebrate Paleontology* (p. 229). Albuquerque.

Tsuihiji, T. (2007). Homologies of the *longissimus*, *iliocostalis*, and hypaxial muscles in the anterior presacral region of extant Diapsida. *Journal of Morphology*, *268*(11), 986–1020. https://doi.org/10.1002/jmor.10565

Tsuihiji, T. (2010). Reconstructions of the axial muscle insertions in the occipital region of dinosaurs: evaluations of past hypotheses on Marginocephalia and Tyrannosauridae using the Extant Phylogenetic Bracket approach. *The Anatomical Record*, *293*(8), 1360–1386. https://doi.org/10.1002/ar.21191

Upchurch, P., & Barrett, P. M. (2000). The evolution of sauropod feeding mechanisms. In H. D Sues (Ed.), *Evolution of Herbivory in Terrestrial Vertebrates: Perspectives from the Fossil Record* (pp. 79–122). Cambridge University Press.

Van den Berge, C., & Zweers, G. A. (1993). Myologia. In J. J. Baumel, A. S. King, J. E. Breazile, H. E. Evans, & J. C. Vanden Berge (Eds.), *Handbook of avian anatomy: nomina anatomica avium* (pp. 189–247). Nuttall Ornithological Club.

Wedin, B. (1953). The origin and development of the extrinsic ocular muscles in the alligator. *Journal of Morphology*, *92*(2), 303–335.

Whitlock, J. A. (2011). Inferences of diplodocoid (Sauropoda: Dinosauria) feeding behavior from snout shape and microwear analyses. *PLoS One*, *6*(4), e18304. https://doi.org/10.1371/journal.pone.0018304

Whitlock, J. A. (2017). Was *Diplodocus* (Diplodocoidea, Sauropoda) capable of propalinal jaw motion? *Journal of Vertebrate Paleontology*, *37*(2), Article e1296457. https://doi.org/10.1080/02724634.2017.1296457

Whitlock, J. A., & Wilson Mantilla, J. A. (2020). The Late Jurassic sauropod dinosaur '*Morosaurus*' *agilis* Marsh, 1889 reexamined and reinterpreted as a dicraeosaurid. *Journal of Vertebrate Paleontology*, *40*(6), e1780600. https://doi.org/10.1080/02724634.2020.1780600

Whitlock, J. A., Wilson, J. A., & Lamanna, M. C. (2010). Description of a nearly complete juvenile skull of *Diplodocus* (Sauropoda: Diplodocoidea) from the Late Jurassic of North America. *Journal of Vertebrate Paleontology*, *30*(2), 442–457. https://doi.org/10.1080/02724631003617647

Witmer, L. M. (1995). The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. In J. J. Thomason (Ed.), *Functional Morphology in Vertebrate Paleontology* (pp. 19–33). Cambridge University Press.

Witzmann, F., Brainerd, E. L., & Konow, N. (2019). Eye movements in frogs and salamanders—testing the palatal buccal pump hypothesis. *Integrative Organismal Biology*, *1*(1), obz011. https://doi.org/10.1093/iob/obz011

Xu, X., Upchurch, P., Mannion, P. D., Barrett, P. M., Regalado-Fernandez, O. R., Mo, J., Ma, J., & Liu, H. (2018). A new Middle Jurassic diplodocoid suggests an earlier dispersal and diversification of sauropod dinosaurs. *Nature communications*, *9*(1), 1–9. https://doi.org/10.1038/s41467-018-05128-1

Young, M. T., Rayfield, E. J., Holliday, C. M., Witmer, L. M., Button, D. J., Upchurch, P., & Barrett, P. M. (2012). Cranial biomechanics of *Diplodocus* (Dinosauria, Sauropoda): testing hypotheses of feeding behaviour in an extinct megaherbivore. *Naturwissenschaften*, *99*(8), 637–643. https://doi.org/10.1007/s00114-012-0944-y

Zheng, Z. (1996). *Cranial anatomy of* Shunosaurus *and* Camarasaurus *(Dinosauria: Sauropoda) and the phylogeny of the Sauropoda*. [Unpublished PhD Thesis]. Texas Tech University.