

Craniomandibular osteology of *Manidens condorensis* (Ornithischia:
Heterodontosauridae) from the late Early Jurassic of Argentina

MARCOS G. BECERRA^{*1,2}, DIEGO POL^{1,3}, LAURA B. PORRO⁴, ARIANA
PAULINA-CARABAJAL^{1,5} and OLIVER W. M. RAUHUT^{6,7,8}

¹ Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET)

² Centro de Investigaciones en Ciencias de la Tierra (CICTERRA), Universidad Nacional
de Córdoba, Av. Vélez Sarsfield 1611, X5016GCA, Ciudad Universitaria, Córdoba,
Argentina; e-mail: marcosgbecerra@gmail.com, <https://orcid.org/0000-0002-1123-7236>

³ Museo Paleontológico Egidio Feruglio, Consejo Nacional de Investigaciones Científicas
and Técnicas (CONICET), Fontana 140, Trelew, Chubut 9100, Argentina; e-mail:

dpol@mef.org.ar, <https://orcid.org/0000-0002-9690-7517>

⁴ Centre for Integrative Anatomy, Department of Cell and Developmental Biology,
University College London, Gower Street, London, WC1E 6BT, UK; e-mail:

l.porro@ucl.ac.uk, <https://orcid.org/0000-0002-0546-2381>

⁵ Instituto de Investigaciones en Biodiversidad y Medioambiente (CONICET-UNCo), San
Carlos de Bariloche 8400, Río Negro, Argentina; email: premjisaurus@yahoo.com.ar,

<https://orcid.org/0000-0002-7820-4770>

⁶ Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Str. 10,
Munich 80333, Germany; email: rauhut@snsb.de, <https://orcid.org/0000-0003-3958-603X>

⁷ Department of Earth and Environmental Sciences, Ludwig-Maximilians-Universität
München

⁸ GeoBioCenter, Ludwig-Maximilians-Universität München

* Corresponding author

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CONDORENSIS

ABSTRACT— Heterodontosauridae is a lineage that appears early in the ornithischian fossil record, and clusters small-bodied, highly specialized species characterized by an unusual heterodont dentition. Although known from relatively few taxa, the early representation of the clade and the still unsolved phylogenetic relationships within heterodontosaurids and among ornithischians implies that novel information may better support a certain phylogenetic hypothesis and with this, affect the inferred diversification patterns in the early evolution of the highly diverse Ornithischia. This paper describes the cranial osteology of the heterodontosaurid *Manidens condorensis* based on computed microtomographic scans of MPEF-PV 3211 and MPEF-PV 3809. This enabled more detailed descriptions of previously recognized bones, corrections, and the identification of undescribed elements. We present a new skull reconstruction and propose an amended diagnosis in light of novel anatomical information. Areas of jaw muscle attachment were identified and compared with *Heterodontosaurus* and *Lesothosaurus*, and mandibular function among heterodontosaurids is discussed. Our results indicate a more diverse skull construction and functioning existed among early Jurassic ornithischians: with *Manidens* being intermediate between the generalized cranial condition and primitive functioning associated to a generalist diet present in early ornithischians (present in *Tianyulong* and basally branching members of other lineages as *Lesothosaurus*) and the more derived cranial construction and specialized functioning better adapted to herbivory identified in heterodontosaurids from South Africa such as *Heterodontosaurus*.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Ornithischian dinosaurs were important terrestrial herbivores of the late Mesozoic, evolving high taxonomic and morphological diversity (Serenó, 1997). Most ornithischians were herbivorous, although the absence of specialized craniomandibular and dental features among early members of the lineage indicates some early ornithischians may have been omnivorous (Barrett et al., 2011; Porro et al., 2015; Breeden et al., 2021). The transition to obligate herbivory in Ornithischia was independent of other dinosaur clades and occurred several times within the clade (e.g., Barrett and Rayfield, 2006; Barrett et al., 2011; Norman et al., 2011; Butler et al., 2012; Becerra and Pol, 2020; Button and Zanno, 2020). Previous studies of Early to Middle Jurassic faunal assemblages indicate ornithischians of that time were mostly small, bipedal species **grouped within** Neornithischia, Thyreophora and Heterodontosauridae, and there was a low global taxonomic diversity (Serenó, 1997; Benton, 2005; Barrett et al., 2009; Spencer, 2013; Boyd, 2015). Scarce fossil remains of ornithischians are known during the ~30 Myr time interval between the appearance of these clades (Hettangian–Sinemurian) and the more diverse ornithischians recorded **from** the Oxfordian onward (Butler, 2005; Barrett et al., 2005; Butler et al., 2007; Boyd, 2015). The sudden appearance of major successively nested clades **from the Middle–Late Jurassic boundary (e.g., ornithopodan and marginocephalian clades within Cerapoda; eurypodan clades within Thyreophora, neornithischian taxa at the base of Cerapoda)** after a long period of **poor** fossil representation demonstrates that our understanding of the early evolution of Neornithischia and the events that triggered the Late Jurassic–Early Cretaceous diversification of the major clades is incomplete (Boyd, 2015; Han et al., 2018; Madzia et al., 2018; Herne et al., 2019; Brown et al., 2021; Dieudonné et al., 2021; Černý et al., 2022; Norman et al., 2022). New evidence of ornithischian species from the Pliensbachian–Callovian interval is critical to

enhance phylogenetic resolution, and reveal evolutionary patterns in the appearance of cranial specializations and body plans that may have driven in the diversification of major ornithischian lineages.

The phylogenetic relation between species in Heterodontosauridae and among the latter clade with other ornithischians have been a matter of debate (see Sereno, 2012; Madzia et al., 2021; Norman et al., 2022; and references therein), with most recent analyses having them occupy different positions within Ornithischia: as an early branching monophyletic lineage of Ornithischia outside Genasauria (e.g., Boyd, 2015; Han et al., 2018; Herne et al., 2019; Yang et al., 2020); as a sister group of Marginocephalia (Xu et al., 2006), and as a paraphyletic group of basally branching pachycephalosaurians (Dieudonné et al., 2021). Heterodontosaurid remains were first recovered from the Hettangian–Sinemurian of the Elliot and Clarence formations of South Africa, including *Abriotosaurus consors* (Thulborn, 1974), *Lycorhinus angustidens* (Haughton, 1924; Thulborn, 1970), *Lanasaurus scalpridens* (Gow, 1975, 1990), and *Heterodontosaurus tucki* (Crompton and Charig, 1962; Santa Luca et al., 1976; Santa Luca, 1980; Butler et al., 2008b; Porro et al., 2011; Sereno, 2012; Radermacher et al., 2021). The diversity and temporal/geographic distribution of the family increased with confirmation of heterodontosaurid affinities for *Echinodon becklesii* (Berriasian, Middle Purbeck Beds of the Purbeck Formation, England; Owen, 1861; Galton, 1978; Norman and Barrett, 2002; Butler et al., 2008a), and the descriptions of *Fruitadens haagarorum* (Titonian, Morrison Formation, USA; Butler et al., 2010, 2012), *Tianyulong confuciusi* (Callovian, Lanqi Formation, Liaoning Province, China; Zheng et al., 2009; Liu et al., 2012), *Manidens condorensis* (Toarcian, Cañadón Asfalto Formation, Chubut Province, Argentina; Pol et al., 2011), and *Pegomastax africanus* (Hettangian–Sinemurian, Elliot Formation, South Africa; Sereno, 2012). Isolated fragmentary remains from the Elliot and Clarence Formations (Hettangian–Sinemurian, South Africa) were referred to either Heterodontosauridae indet.

(e.g., former *Geranosaurus atavus*, now considered as a nomen dubium; Norman et al., 2011) or known heterodontosaurid species (including NHMUK RU A100) (Butler et al., 2008a; Porro et al., 2011; Norman et al., 2011; Sereno, 2012; Radermacher et al., 2021). Additional heterodontosaurid specimens include the cf. *Heterodontosaurus* sp. from the Lower Jurassic of the Laguna Colorada Formation (El Tranquilo Group; Argentina; Báez and Marsicano, 2001; Pol et al., 2021), and undescribed heterodontosaurid remains from the Kayenta Formation (Sinemurian–Pliensbachian, Arizona; Sereno, 2012). **Regardless of the phylogenetic relation among heterodontosaurids, the clade groups taxa possessing a primitive craniodental anatomy, including *Echinodon*, *Fruitadens*, and *Tianyulong*; with taxa featuring specialized craniodental traits divergent from the primitive condition of early ornithischians, including *Abrictosaurus*, *Heterodontosaurus*, *Lycorhinus*, *Pegomastax* and *Manidens* (Pol et al., 2011; Butler et al., 2012; Sereno, 2012; Becerra et al., 2018).** The best-preserved skulls in Heterodontosauridae to date are known from *Heterodontosaurus* (Norman et al., 2011; Sereno, 2012; Porro et al., 2011; Radermacher et al., 2021). *Abrictosaurus* and published specimens of *Tianyulong* have relatively complete skulls, but only one side is exposed and both lack a well-preserved braincase (e.g., Thulborn, 1974; Zheng et al., 2009; Sereno, 2012). The remaining species (excluding *Manidens*) comprise fragmentary remains.

Heterodontosauridae contains relatively few species but represents a significant part of early ornithischian diversity. In this context, anatomical information from new species could: (1) determine the ancestral state for certain characters and affect optimization at the node Ornithischia; (2) affect the known succession of anatomical, functional, and ecological changes that occurred through the evolution of the lineage; and (3) reduce the overall uncertainty in the early evolution of Ornithischia prior to the latest Middle Jurassic.

The heterodontosaurid *Manidens condorensis*, known from one relatively complete individual and other fragmentary remains, represents the most complete ornithischian from

the Early Jurassic of South America (Pol et al., 2011). *Manidens* combines plesiomorphic (incipient development of wear in a vertical orientation) and derived (sub-hypsodont crowns closely packed in the mid-posterior dentition) craniodental features, as well as multiple autapomorphies (Pol et al., 2011; Becerra et al., 2018, 2020). Although the dentition of *Manidens* has been studied in detail (Becerra et al., 2014, 2018, 2020; Becerra and Pol, 2020), its craniomandibular anatomy has only briefly been described. In addition, *Manidens* comes from the Pliensbachian–Callovian gap in the worldwide ornithischian fossil record. This study describes the osteology of the skull of *Manidens condorensis* in detail, based on novel information obtained from 3D reconstructed skull bones from the holotype and referred specimens. A more accurate reconstruction of the skull and an amended diagnosis for the species are presented, and the cranial foramina and correlates of pneumatic recesses in the skull bone surfaces are addressed. Furthermore, this study describes the attachment regions for the cranial musculature and compares the jaw structure and function in several taxa.

Institutional Abbreviations—**EPI**, Evolutionary Studies Institute, Johannesburg, South Africa; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China; **MB**, Museum für Naturkunde, Berlin, Germany; **MPEF**, Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina; **MUCPv**, Museo de la Universidad Nacional del Comahue, Neuquén, Argentina; **NHMUK**, Natural History Museum, London, United Kingdom; **SAM**, Iziko South African Museum, Cape Town, South Africa.

MATERIALS AND METHODS

The holotype of *Manidens condorensis*, MPEF-PV 3211, is composed of 11 separated pieces (Pol et al., 2011) that are partially articulated and belong to a single individual. Some of the preserved bones were isolated during preparation: the right quadrate (MPEF-PV 3211-5); right quadratojugal (MPEF-PV 3211-6); right postorbital (MPEF-PV 3211-7); complete pelvic girdle and sacral region comprised of six sacral vertebrae (MPEF-PV 3211-1); one cervical vertebra (MPEF-PV 3211-8); two dorsal vertebrae (MPEF-PV 3211-2 and MPEF-PV 3211-4); and a caudal vertebra (MPEF-PV 3211-3). The overlapping of many of the remaining bones precluded their complete separation during mechanical preparation, and these were left as three blocks of associated remains (MPEF-PV 3211-9, MPEF-PV 3211-10 and MPEF-PV 3211-11). MPEF-PV 3211-11 comprises the nasals, prefrontals, supraorbitals, lacrimals, a fragment of the left maxilla, frontals, parietals, the right squamosal, and most of the left laterosphenoid, together with the left pectoral girdle (scapula and coracoid), a cervical vertebra, three dorsal vertebrae, a caudal vertebra, and several associated and fragmented ribs (Fig. 1). MPEF-PV 3211-10 comprises both lower jaws (dentaries with their complete dentitions, coronoids, surangulars, angulars, splenials, prearticulars, articulars), the right jugal, the right maxilla with teeth, the right ectopterygoid, the condylar region of the left quadrate, a fragment of the left pterygoid, a dorsal vertebra, isolated teeth, and rib fragments (Fig. 2). MPEF-PV 3211-9 comprises part of the left side of the orbital and temporal regions of the skull (left postorbital, jugal, squamosal, quadratojugal and most of the left quadrate), occipital region (supraoccipital, basioccipital, both prootics, and both opisthotic-exoccipital complexes), sphenoidal region (basisphenoid, parasphenoid, and possible fragments of both laterosphenoids), and pterygoid region (left pterygoid and left ectopterygoid) (Fig. 3). The following description is based on the type specimen as well as the referred specimens MPEF-PV 3808 and MPEF-PV 3809 (Becerra et al., 2018, 2020) that complement the information provided by MPEF-PV 3211.

Pictures of MPEF-PV 3819 were taken using a camera with digital display (Nikon SMZ 1000), assisted by a binocular microscope equipped with an optic fiber point light. Scanning Electron Microscope (SEM) images of MPEF-PV 3819 were taken in the industrial plant ALUAR Aluminio Argentino SAIC (Puerto Madryn, Chubut province), using a Jeol JSM-6460 with backscattered electron detector. Micro-computed tomographic scanning (μ CT scan) of MPEF-PV 3211 and MPEF-PV 3809 was conducted using a GE phoenix nanotom® at the Staatliche Naturwissenschaftliche Sammlungen Bayerns (Munich, Germany). Segmentation and 3D reconstructions were carried out in 3DSlicer 4.3.0 (Fedorov et al., 2012). Minor modelling of damaged bones and the cranial reconstruction of *Manidens* were carried out in Blender 2.8 (Community, 2018).

To assist the comparison of cranial functional morphology between heterodontosaurids, two methodologies were used (Greaves, 1974; Butler et al., 2012) and these were compared with the results of Butler et al. (2012) on *Heterodontosaurus* and *Tianyulong*. In the first approach, the upper dentition in the 2D skull reconstruction of *Manidens* in lateral view was set in the horizontal plane, and the lower jaw was rotated to a gape of 15° along the lower dentition, and the perpendicular distances between the line parallel to each dentition and the center of the quadrate-articular joint were measured (following Greaves, 1974). In the second approach, the 2D skull reconstruction of *Manidens* in lateral view was used to map the vectors of the jaw muscle resultants separated to Group 1 (the three portions of the m. adductor mandibulae externus, m. adductor mandibulae posterior, and the two portions of the m. adductor pseudotemporalis) and Group 2 (m. pterygoideus dorsalis and m. pterygoideus ventralis). To ease comparisons, the origin and end of each vector was set following Butler et al. (2012) (for Group 1 between the highest point of the coronoid process and the center of the supratemporal bar, and for Group 2 between the posteroventral margin of the lower jaw and the dorsal surface of the palate), and the moment arm was divided by mandible length. In the

first case, the measure of the difference in distance between upper and lower dentitions allows understanding of how the tooth rows came together during jaw closure: if the measures are equal, then teeth occlude simultaneously, while if these differ in value, a single occlusion point occurs and moves anteriorly while the jaws are closing in a scissor-like shearing action (Greaves, 1974). In the second case, the lengths of the moment arms of the Group 1 and Group 2 muscle resultants are compared in proportional value, with higher values indicating greater mechanical advantage (Butler et al., 2012). Additional relative measures were obtained from 2D skull reconstructions of *Manidens*, *Heterodontosaurus* and *Tianyulong* (Butler et al., 2012) based on the lowering of the jaw joint relative to the dentition occlusal line, height of the coronoid eminence to the jaw joint, quadrate shaft height and length of the retroarticular process, expressed relative to the jaw length (based on Nabavizadeh, 2016).

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842

ORNITHISCHIA Seeley, 1887

HETERODONTOSAURIDAE Kuhn, 1966

MANIDENS Pol, Rauhut and Becerra 2011

MANIDENS CONDORENSIS Pol, Rauhut and Becerra 2011

(Figs. 1–22)

Holotype—MPEF-PV 3211, partial skeleton including approximately 80% of the skull and mandibles preserved in articulation or association, isolated vertebrae representing all regions of the column, most of the left pectoral girdle, and both pelvic girdles (Pol et al., 2011; Becerra et al., 2014).

Referred Specimens—Pol et al. (2011) referred five isolated teeth (MPEF-PV 1719, MPEF-PV 1786, MPEF-PV 1718, MPEF-PV 3810 and MPEF-PV 3811). Subsequently, Becerra et al. (2014) referred five additional isolated teeth (MPEF-PV 3812, MPEF-PV 3813, MPEF-PV 3814, MPEF-PV 3815 and MPEF-PV 3816). Additional material has recently been referred, including an isolated left maxilla (MPEF-PV 3809), cranial and postcranial remains of a larger specimen from the Frenguelli fossil site (MPEF-PV 3808), and multiple isolated teeth (MPEF-PV 3818, MPEF-PV 3820, MPEF-PV 3825, MPEF-PV 10861, MPEF-PV 10866, MPEF-PV 10862, MPEF-PV 10863, MPEF-PV 10865, MPEF-PV 3821, MPEF-PV 10823, MPEF-PV 10864) (Becerra and Pol, 2020; Becerra et al., 2018, 2020). Finally, a possible premaxillary tooth, MPEF-PV 3819 is here referred to *Manidens condorensis* based on its overall morphology.

Locality, Horizon, and Age—The type and all the referred specimens of *Manidens condorensis* were found at the same site and horizon, the Queso Rallado locality (Pol et al., 2011; Becerra et al., 2018, 2020). The sole exception is MPEF-PV 3808 that was found at a different locality, the Frenguelli fossil site (Becerra et al., 2020). All fossil remains come from basal levels of the Cañadón Asfalto Formation, a unit recently dated as mid–late Toarcian (179.170±0.120–178.070±0.210 Mya; Pol et al., 2020). Information regarding the geologic setting, paleoflora, and paleofauna of this Lower Jurassic unit can be found in Escapa et al. (2008), Cuneo et al. (2013), Figari et al. (2015), Pol et al. (2020), and references therein.

DESCRIPTION

Snout, Frontoparietal, Orbital, and Temporal Regions

Maxilla—The maxilla in MPEF-PV 3211-10 is almost complete and was correctly identified by Pol et al. (2011), but the original description of this bone was based on a

mistaken orientation (Becerra et al., 2018). The anterior process of the maxilla is almost complete, but this is fractured at its base and is anteriorly displaced. The anterior third of the main body of the maxilla is well preserved and bears four tooth positions and three teeth in situ, whereas the posterior two-thirds of the maxilla are damaged. This region includes a posteroventrally displaced ascending process of the maxilla, a mediolaterally thin vertical lamina posterior to the antorbital fenestra (the posterodorsal process), and the posterior process of the maxilla (which contacted the jugal), the latter two are anterodorsally displaced. There are further four posterior teeth displaced from their alveoli (Fig. 4A–B). The maxilla of MPEF-PV 3211-10 is mainly exposed medially, and only the anterior third and the first four tooth positions are also exposed laterally (Becerra et al., 2018; Fig. 4A–B). Becerra et al. (2018, 2020) reinterpreted the lateral face of the maxilla described by Pol et al. (2011) as the medial face. The medial face has a dorsoventrally wide, longitudinal maxillary shelf that divides the main body of the maxilla from the alveolar margin. This ridge was originally misinterpreted by Pol et al. (2011) as the maxillary ridge, a lateral horizontal ridge that separates the emarginated dentition from the antorbital fossa (supra-alveolar lamina; Witmer, 1997a), a feature common in Heterodontosauridae (Zheng et al., 2009; Norman et al., 2011; Sereno, 2012). However, Becerra et al. (2018, 2020) identified a similarly developed shelf on the medial face of a more complete maxilla referred to *Manidens condorensis* (MPEF-PV 3809), in which it divides the main body of the maxilla into dorsal (facing the nasal cavity) and ventral regions (facing the buccal cavity), and forms the lateral boundary of the choana (Fig. 4C–D). The dental morphology and identification of the maxillary shelf in MPEF-PV 3809 (nasopalatine ridge; Becerra et al., 2018, 2020) confirms that what was previously considered the lateral face of the maxilla of MPEF-PV-3211-10 actually corresponds to its medial face, and that the preserved maxilla corresponds to the right side instead of the left as

Pol et al. (2011) interpreted. Additionally, we interpret the preserved dorsal margin of MPEF-PV 3211-10 as collapsed region instead of the internal antorbital fenestra.

The description of the maxilla is based in that of MPEF-PV 3809, which is better preserved than that of MPEF-PV 3211-10 (Becerra et al., 2018). The maxilla is sub-triangular in outline (32.31 mm in length), with a dorsoventrally high main body (alveolar ramus) of the maxilla (minimum 6.58 mm dorsoventral height measured below the external antorbital fenestra), a posterior (jugal) process, and two dorsally projecting laminae: the ascending process of the maxilla (13.97 mm maximum height), and the posterodorsal process (10.28 mm height), which **borders** the external antorbital fenestra. Within the antorbital region, the medial dorsal lamina is as high as the ascending process of the maxilla and borders the internal antorbital fenestra. The maxilla tapers anteriorly along its anterior process to contact the premaxilla and posteriorly to the posterior process, which has a dorsal contact for the jugal and a medial contact for the ectopterygoid. The height-width relation of the main body of the maxilla indicates a tall maxilla and a short snout, similar to other heterodontosaurids, *Hypsilophodon*, and *Gasparinisaura*, but different from the condition in derived ornithischians (Galton, 1974; Coria and Salgado, 1996; Sereno, 2012). Medially, the maxillary shelf (medial lamina in *Heterodontosaurus*; Norman et al., 2011) is low and robust. The maxillary shelf expands medially along the anterior process of the maxilla to form the medial articulation region of the anterior process of the maxilla, and a ventrally concave contribution to the palatal roof. The medial articulation of the anterior process (complete in MPEF-PV 3809) is lenticular in shape, bears three narrow sulci separated by three conspicuous, anteroposteriorly oriented crests, and faces medially in its middle portion and posteromedially in its posterior third (Fig. 4D, K). Is here interpreted that the anterior third of this region articulated with the medial posterior process of the premaxilla (as in *Hypsilophodon* and *Heterodontosaurus*; Galton, 1974; Norman et al., 2011), whereas the

remainder of the anteromedial process contacted the opposite maxilla at its midpoint, and the fused vomers posteriorly (Fig. 4D, K). The anterior process widens dorsoventrally at its base and bears a concave face laterally, indicating the region that is overlapped by the posterior margin of the premaxilla (Fig. 4A, C).

Dorsal to the base of the anterior process and at the anterior margin of the ascending process of the maxilla three distinct features are found: a ventrally directed notch, a small opening confluent with this notch (neurovascular foramen, see below), and a spindle-shaped opening included within the lateral lamina of the ascending process of the maxilla. The ventrally directed notch is limited posteriorly by an anterolaterally directed concave surface and anteriorly by a posteromedially directed convex face, both subparallel to each other, and identified in MPEF-PV 3211-10 also. A similarly positioned anterior notch was described by Galton (1974) in a juvenile specimen of *Hypsilophodon* (NHMUK-PV R2477), but it is completely overlapped by the premaxilla in a larger specimen (NHMUK-PV R197), interpreted as ontogenetic variation. Similarly, an anterior notch was identified in *Changchunsaurus parvus* and *Thescelosaurus neglectus*, but associated with a subnarial fossa (Jin et al., 2010; Boyd, 2014). For *Manidens*, the subparallel configuration of the boundaries of this notch with the concavity that accommodates laterally the posterior edge of the premaxilla indicates that this feature might represent a second articulation for the premaxilla. If a partial premaxilla-maxilla overlap existed in this region, it might form an anterior fossa, as also present in *Hypsilophodon*, *Thescelosaurus*, and *Changchunsaurus* (Galton, 1974; Jin et al., 2010; Boyd, 2014). The dorsoventrally oriented and spindle-shaped opening forms a wide fossa near the premaxilla-maxilla articulation, which is located outside the antorbital fenestra. This passage is evident in MPEF-PV 3809, but not recognized in MPEF-PV 3211-10. This anteriorly placed opening is interpreted as a subnarial foramen, a feature repeatedly identified in specimens of *Jeholosaurus shangyuanensis* (Barrett and Han, 2009), and

possibly present in *Haya griva* (maxillary fenestra; Makovicky et al., 2011; Barta and Norell, 2021), *Kulindadromeus* (Godefroit et al., 2014), and widely present in ceratopsians theropods and sauropodomorphs (e.g., Dodson et al., 2004; Langer and Benton, 2006).

Anterior to the tooth row there is a small depression limited posterodorsally by a low, arched crest, a feature more evident in MPEF-PV 3809, and covered in MPEF-PV 3211-10. This depression, which corresponds in position to the opposing enlarged dentary caniniform (e.g., Pol et al., 2011; Becerra et al., 2014, 2018), is here interpreted as the maxillary component of the arched diastema (Fig. 4C, I), a feature present in most heterodontosaurids (Crompton and Charig 1962; Gow 1975; Zheng et al., 2009; Butler et al., 2010; Sereno, 2012). The arched diastema forms an incipient medial wall, which is more developed than that in *Goyocephale lattimorei* and *Homalocephale calanthoceros* (Maryanska and Osmólska, 1974; Perle et al., 1982), but not completely enclosing this space as in *Heterodontosaurus* (e.g., Norman et al., 2011; Sereno, 2012). The previous interpretation of an absent diastema in *Manidens* (Pol et al., 2011), was due to their mistaken orientation of the maxilla.

The alveolar region bears 10 tooth positions and eight teeth in MPEF-PV 3809, and at least eight tooth positions with seven teeth in MPEF-PV 3211-10, although it is likely that this tooth row is incomplete (Becerra et al., 2020). In occlusal view, the alveolar region and the tooth row form a slightly concave outline facing medially, and the opposite occurs in the dentary (tooth row curved slightly medially in occlusal view), as in *Heterodontosaurus* (Norman et al., 2011). The ventral boundary of the external antorbital fenestra does not form a laterally prominent horizontal ridge of the maxilla, instead the lateral face of the maxilla is levelled with the boundary of the external antorbital fenestra, which forms a smooth unevenness with the antorbital fossa (Fig. 4C). The absence of a maxillary ridge ventrally limiting the external antorbital fenestra in *Manidens* characterizes an alveolar region laterally positioned instead of medially inset (contra Pol et al., 2011). This morphology is more similar

to that in the **basally branching** heterodontosaurids *Fruitadens*, *Tianyulong* and *Echinodon* (Norman and Barrett, 2002; Zheng et al., 2009; Butler et al., 2012; Sereno, 2012) **than the medially inset tooth row of** *Heterodontosaurus* (Norman et al., 2011), *Lanasaurus scalpridens* (EPI/1/4244 and EPI/1/5253, Gow, 1975; = *Lycorhinus angustidens*, Sereno 2012), and *Abriktosaurus* (Sereno, 2012) (Fig. 4C, I).

The ascending process of the maxilla is formed by two laminae: the lateral and medial dorsal laminae. **The medial dorsal lamina of the maxilla is a dorsal continuation of the medial wall of the maxilla, extends dorsally to reach the premaxilla-lacrimal-maxilla articulation and also forms part of the ascending process of the maxilla, enclosing the antorbital region at least in its anterior half (Fig. 4C, I).** The anterodorsal portion of the antorbital fossa is fractured, thus the presence **or absence** of an accessory opening –a feature present in *Heterodontosaurus*– cannot be confirmed (Norman et al., 2011). The antorbital fossa is positioned anteriorly and does not develop posteroventrally as in other heterodontosaurids (Norman et al., 2011; Sereno, 2012), **and is** more similar to **that in** *Orodromeus*, *Gasparinisaura*, and *Hypsilophodon* (e.g., Norman et al., 2004b). In dorsal view of the antorbital region of MPEF-PV 3809, the medial and lateral walls of the maxilla meet each other at the base of the antorbital region forming a narrow slit with interdigitated margins that extends anterodorsally **separating the** lateral and medial laminae of the ascending process of the maxilla. This narrow slit opens to an internal empty space within the main body of the maxilla; possibly a pneumatic space (Fig. 4L; Witmer, 1997a). Posteriorly, the medial and lateral walls form a narrow and long sulcus along the posterodorsal process of the maxilla that widens mediolaterally while reaching the posterior process of the maxilla. The narrow region of this depression articulates with the anterior process of the jugal, and its posterior widening **articulates** with the ectopterygoid and possibly part of the jugal (Fig. 4D, E-H, J). The internal antorbital fenestra **locates in the posterior half of the antorbital region and** is enclosed

anteriorly and posteroventrally by the medial lamina of the maxilla, and posterodorsally by the lacrimal (as seen in the right lacrimal of specimen MPEF-PV 3211-11). The jugal is excluded from the boundaries of the internal antorbital fenestra (Fig. 4C, E, I). The posterior process of the maxilla bears a small, anteroposteriorly extending, slightly prominent lateral crest near its contact with the jugal. The lateral flaring of the posterior process of the maxilla in MPEF-PV 3809 might create a slight emargination of the posterior tooth row, as in *Hypsilophodon*, *Orodromeus*, *Gasparinisaura*, and early ornithopods (Galton, 1974; Coria and Salgado, 1996; Scheetz, 1999; Norman et al., 2004b). The lateral wall of the main body of the maxilla is depressed below the level of the external antorbital fenestra, and pierced by numerous neurovascular foramina. Three neurovascular foramina are identified in MPEF-PV 3211-10 (Fig. 4A), while at least eight large foramina forming a dorsally concave row below the external antorbital fenestra are identified in MPEF-PV 3809 (Fig. 4I). In both specimens, the anteriormost foramen is confluent with the anteriorly positioned, dorsoventrally concave notch for the premaxilla (Fig. 4). This laterally depressed region of the maxilla continues posteriorly along the lateral face of the jugal and below the “jugal boss” (see below). These neurovascular foramina more closely resemble those of *Hypsilophodon* than other heterodontosaurids principally in their large size (Galton, 1974; Norman et al., 2011; Sereno, 2012). Together with the depressed region in the maxilla-jugal, these indicate that a soft-tissue cheek covered the entire maxillary tooth row, as assumed in *Heterodontosaurus*, *Lycorhinus*, *Abrictosaurus*, *Echinodon* (Sereno, 2012) and *Fruitadens* (Butler et al., 2012) and argued to be the common condition in Ornithischia (Galton, 1973a; Knoll, 2008; Morhardt, 2009; but see Nabavizadeh, 2020). Alveolar foramina that open directly to the developing replacement teeth were recognized medially and above the maxillary shelf in MPEF-PV 3809 (tooth positions M8 and M10; Fig. 4J) and MPEF-PV 3211-10 (tooth positions M3 and M4; Becerra et al., 2018, fig. 2, tooth crypts tcM3-tcM4). The presence of

alveolar foramina is **widespread** in Ornithischia (e.g., *Scutellosaurus* [Colbert, 1981], *Lesothosaurus* [Porro et al., 2015], *Jeholosaurus* [Barrett and Han, 2009], *Psittacosaurus* [Serenó, 2010]), but has only recently been identified in *Heterodontosaurus*, being possibly **less common** in heterodontosaurids than in other lineages due to their low rate of tooth replacement (Norman et al., 2011; Becerra et al., 2020).

Nasal—Both nasals are present and exposed dorsally in MPEF-PV 3211-11 and are **slightly** deformed (Fig. 5). They are fractured **in** the premaxillary and prefrontal regions, and the ventrolateral processes were diagenetically displaced in a hinge-like motion, preserving their position with the rest of each nasal and the contact with the lacrimal **on** the left side (Fig. 5A–B). The nasals are medially fused to each other, and contact the lacrimal laterally in a butt joint, the prefrontal posterolaterally in a **bevelled** articulation, and the frontals form an oblique anterior edge with four anterior projections that **form an overlapping** and interdigitated articulation with the nasals, as commonly observed in Ornithischia (Fig. 5). Although the premaxilla is not preserved, the ventrolateral process of the nasal seems to preserve an arched/depressed region that contacted the premaxilla. The contact between the nasal and the lacrimal **on** both sides of the skull prevents the premaxilla from contacting the prefrontal in lateral view, while it is assumed that these bones contact each other in *Heterodontosaurus* (Norman et al., 2011). In dorsal view, the suture line at the nasal-frontal contact is laterally and posteriorly directed from the internasal suture to the nasal-prefrontal-frontal contact and forms a V-shaped suture with its apex directed anteriorly that almost reaches the level of the anterior third of the orbit, as in *Heterodontosaurus* (Norman et al., 2011). The nasal-prefrontal suture line is more concave laterally than that in *Heterodontosaurus*. At the nasal-lacrimal-prefrontal junction at both sides of the skull, there is a small foramen with a shallow fossa that goes through the snout and reaches the cavity within the nasal bones (Fig. 5T).

In dorsal view, the nasals form the main roof of the snout (29.2 mm long). They taper anteriorly after widening slightly at the snout end (8.41 mm), and are constricted medially at the level the arched diastema (6.25 mm), before reaching their greatest width above the articulation with the lacrimals (13.2 mm), and tapering posteriorly to the nasal-frontal suture (4.57 mm). The dorsal view of the nasals is similar to that of *Heterodontosaurus* (Norman et al., 2011), although the snout constriction is more conspicuous in *Manidens*. The anterior tip of the nasals is not complete, which is also the case for the borders of the external nares (Fig. 5E–F, S). Anteriorly, the lateral margin of each nasal flexes dorsally, forming a bulbous crest that extends posteriorly to reach the conspicuously thickened sides of the snout and to the nasal-prefrontal contact, forming a V-shaped thickened region in dorsal view (Fig. 5C). This structure continues over the anterior portion of the prefrontals and extends along the lateral face of the supraorbitals. These thickened edges of the snout are wider and more prominent anteriorly and taper posteriorly. They mark an abrupt change between the roof and the lateral wall of the snout, and limit a medial depression dorsally, a feature named the medial or internasal sulcus by Norman et al. (2011) in *Heterodontosaurus*, but apparently absent in other heterodontosaurids. This internasal sulcus is similar to the nasal fossa present in *Yinlong* (Han et al., 2015), *Liaoceratops* (Xu et al., 2002), *Agilisaurus* (Peng, 1992), *Jeholosaurus* (Xu et al., 2000; Barrett and Han, 2009), *Haya* (Barta and Norell, 2021) and *Changchunsaurus* (Jin et al., 2010); however, the raised lateral rims of the snout in the skull of heterodontosaurids enhance this feature, developing an even deeper and narrower internasal sulcus. The thickening of the dorsal crests and the depth of the internasal sulcus in *Manidens* are developed to a lesser extent than in *Heterodontosaurus*, and is bounded posteriorly by an anteriorly facing concave crest entirely formed by the nasals at the nasal-frontal contact.

Only part of the margin of the external nares is preserved at the anterior end and along the ventral processes of the nasals. In this region, the left nasal preserves a free tip that is anteroventrally directed; however, the premaxilla-nasal contact at this point is not preserved. Thus, it cannot be confirmed that the anterior tip of the nasals formed a median projection that overhangs the external nares as in *Heterodontosaurus* (Norman et al., 2011) or if they contacted the anterodorsal (narial) process of the premaxilla as in the primitive heterodontosaurid *Tianyulong* (Zheng et al., 2009). The left ventrolateral process of the nasal is less damaged than the right one. This process narrows abruptly toward its wedge-shaped termination between the posterior border of the external nares and the lacrimal (Fig. 5E–F). The ventrolateral process of the nasal is assumed to articulate posteriorly with the anterior margin of the anterodorsal process of the maxilla before reaching the lacrimal, a feature evidenced by a vertically oriented depression at the anterior region of the maxilla, and shared with *Heterodontosaurus* and *Tianyulong* (Norman et al., 2011; Sereno, 2012). The ventrolateral process of the nasal prevents the premaxilla from contacting the lacrimal, as also in *Lesothosaurus* (Porro et al., 2015), *Agilisaurus* (Peng, 1992), *Hypsilophodon* (Galton, 1974), *Yinlong downsi* (Xu et al., 2006, Han et al., 2015; contra Dieudonné et al., 2021), *Archaeoceratops oshimai* (You and Dodson, 2003), the jeholosaurid *Haya griva*, and pachycephalosaurids as *Dracorex*, *Prenocephale*, and *Stegoceras* (Bakker et al., 2006; Makovicky et al., 2011; Barta and Norell, 2021). The premaxilla-lacrimal contact is present in *Jeholosaurus shangyuanensis*, basally branching iguanodontians (e.g., *Tenontosaurus*, *Dryosaurus*, *Iguanodon*, *Ouranosaurus*; Galton, 1983; Norman, 2004; Barrett and Han, 2009), *Auroraceratops*, *Liaoceratops*, and psittacosaurids (Xu et al., 2002; You et al., 2005; Sereno, 2010). In addition, given the dimensions of the ventrolateral process of the nasals and their assumed contact with the posterodorsal process of the premaxilla, is likely that the latter do not reach the prefrontal, unlike in *Heterodontosaurus* (Norman et al., 2011).

The ventrolateral process of the nasal bears a depression with a sub-oval shape on its anterior margin, which opens into the external nares, forming a conspicuous narial fossa (Fig. 5S). A common feature among dinosaurs is that the anterolateral border of the nasal flexes ventrolaterally to form the posterior border of the external nares with its corresponding narial fossa. The nasal in *Heterodontosaurus* does not form a ventrolateral process: the posterodorsal process of the premaxilla extends further dorsally to limit the posterior margin of the naris, and a posterior narial fossa was absent (Norman et al., 2011). The presence/absence of this feature cannot be confirmed in *Abrictosaurus* or *Tianyulong*, or any other heterodontosaurid due to the nature of their remains (e.g., Thulborn, 1974; Zheng et al., 2009; Sereno, 2012). Thus, the presence of a ventrolateral process of the nasals with a posterior narial fossa is a feature shared between *Manidens* and other dinosaurs, and contrast at least with *Heterodontosaurus* among heterodontosaurids (Norman et al., 2011; Sereno, 2012).

The impression of the nasal cavity forms a lobe-like depression on the ventral surface of each nasal, separated by a medial and short low rim that does not reach the palate, indicating that the remaining separation between left and right nasal cavities is either not preserved or was possibly cartilaginous (Fig. 5D). The rostralateral bones of the snout limit the lateral boundaries of the nasal cavity, and the absence of any other internal structures precludes further partitioning of the nasal cavity. Posteriorly, the inner face of both nasals thickens before reaching the nasal-frontal articulation, marking a conspicuous posterior boundary between the nasal cavity and the olfactory lobes at the inner face of the frontals.

Prefrontal—In MPEF-PV 3211-11, both prefrontals are preserved and exposed in dorsal view, with only the right element exposed ventrally. The bones articulate with the nasals anteromedially along a scarf joint, with the frontals posteromedially via an overlapping joint, and with the lacrimals anteroventrally through a butt joint, and together with the lacrimals

they form a flat, posterolaterally oriented articular region for the supraorbital. The prefrontals are dorsally flat, except for the continuation of the dorsal crests of the nasals that form rounded and low crests anteriorly, and continue posteriorly over the lateral face of the supraorbital (Fig. 5G, K). In dorsal view, the suture line formed by the nasals-prefrontals and prefrontals-frontals articulations curve forming a laterally concave line from the posterior half of the nasals to the midpoint of the orbit as in *Heterodontosaurus*. However, the suture line in *Manidens* turns abruptly anterolaterally to end in the orbital margin. The ventral crest of the prefrontals contributes to the posterodorsal boundary of the posterior nasal cavity in its anterior half, while its posterior half contributes to the anterodorsal wall of the eye socket. The crests are concave, shaping the corresponding cavity. The medial face of the prefrontals extends obliquely forming a bevelled articulation with the frontals. The ventral extension of this medial face forms the posterior portion of the ventral crest of the prefrontals, a crest that contacts the ventral crests of the frontals that shape the lateral walls of the olfactory bulbs posteriorly (Fig. 5H–J, L–N). In the transverse section, the prefrontals are anteriorly flat, with a tri-radiate cross-section due to the ventral crest in their mid-section, and form a rather subtriangular shape posteriorly. The lateral margin of the prefrontal, forming the anterodorsal limit of the orbit, is sharp-edged, instead of rugose as in *Heterodontosaurus* (Norman et al., 2011). The overall morphology of the prefrontals is more similar to that in *Heterodontosaurus* than to the plate-like prefrontals of *Lesothosaurus* (Norman et al., 2011; Porro et al., 2015).

Frontal—As mentioned by Pol et al. (2011), the frontals are medially fused and their suture is hard to recognize. The interfrontal suture is interpreted as a butt joint that fused early during ontogeny, as is common in early Ornithischia (Currie, 1997; Norman et al., 2004a, 2011; Porro et al., 2015). In dorsal view, the frontals are shorter in anteroposterior length than the nasals (23.95 mm). The fused frontals form a straight contact with the nasals in dorsal view, and their narrowed anterior region is bounded laterally by the prefrontals. Posterior to

the prefrontal-frontal contact, the frontals widen laterally to border the orbit and reach their widest point just before the frontal-postorbital contact (17.05 mm). Posteriorly, the fused frontals become narrower firstly forming a laterally sinuous-concave facet for their contact with the postorbitals and then **bordering** the supratemporal fenestra (11.77 mm). Each frontal contacts the nasal anteriorly **along** an interdigitated and underlapping articulation (common in Ornithischia; **Weishampel, 1984**), **with** the prefrontal in an underlapping articulation **anterolaterally** (Fig. 6A–D), and the anterior process of the fused parietals insert into a groove formed by the fused frontals in an interdigitated articulation posteriorly (Fig. 6J–L, see **Parietal**). Laterally, the frontal-postorbital articulation **on** the frontals is formed by a narrow notch anteriorly and a crest-like facet posteriorly to receive a similarly configured articulation facet **on** the medial process of the postorbital (Fig. 6J, see **Postorbital**). The boundaries of the frontal-postorbital articulation and the posterior **positioning** of the parietal confirm that the parietal does not contact the postorbital.

Slightly posterior to the orbit, there is a rounded, shallow fossa in the dorsal surface of each frontal, which marks the dorsal **apex** of the margin of the orbit and medially **delimits** a dorsally low, dome-like structure. In this view, the nasal-frontal articulation forms a wedged, but more open suture line **than that in *Heterodontosaurus*** (Norman et al., 2011). The mediolateral path of the nasal-frontal suture is interrupted by the prefrontal facet, whereas in *Heterodontosaurus* and *Lesothosaurus* this contact forms a curved line in dorsal view that deviates from the nasal-frontal suture to the prefrontal-frontal suture line (**Norman et al., 2011; Porro et al., 2015**).

Posteriorly, the frontals bear an anterior continuation of the sagittal crest, which is 5.2 mm long and 1mm high, similar to that developed on the parietals of *Heterodontosaurus*, *Lesothosaurus*, *Jeholosaurus*, and other ornithischians. Posteromedial to the frontal-postorbital articulation, there is a smooth, posterolaterally and dorsally oriented fossa in the

frontal that continues onto the parietal and opens in the supratemporal region. The difference in orientation between this fossa and the rest of the frontal is not as marked as in *Heterodontosaurus* (Norman et al., 2011), and although its boundaries are not easily delimited, this fossa does not reach the sagittal crest or the region of the postorbitals facing the supratemporal region (Fig. 6J–K). The classic interpretation for the anterior portion of the dorsotemporal fossa of the frontals, and in some cases the parietals, was related to the attachment of the *m. pseudotemporalis superficialis* (e.g., Holliday, 2009). However, recent observations on extant and extinct archosaurs and archosauriforms identify this anterior region as the frontoparietal fossa, a distinctive region within the dorsotemporal fossa that housed a large vascular structure, and possibly adipose tissue, instead of an attachment site for the mandibular musculature (Holliday et al., 2020, see Discussion). In *Manidens*, a differently oriented smooth surface located anteriorly within the dorsotemporal fossa but separated from the sagittal crest may represent the interpreted frontoparietal fossa by Holliday et al. (2020), being here regarded as such. In dorsal view, the sagittal crest of the frontals reaches further anteriorly than the anterior boundary of the aforementioned frontoparietal fossa.

Ventrally, each frontal has a well-developed crista cranii (as identified for *Lesothosaurus*; Porro et al., 2015). This crest contacts a similarly oriented crest on the prefrontals anteriorly. It is sagittally oriented anteriorly and then curves in an S-shape posteriorly, forms a concave orbital vault contributing to the eye socket laterally and the endocranial cavity medially. It delimits the olfactory bulb and tracts cavities anteriorly, and the cavity for the cerebral hemisphere posteriorly (Fig. 6D). The crista cranii extends posterolaterally and reaches the anteroventral margin of the postorbital-frontal articulation ventrally, forming an anteriorly facing concavity at the posterior end of the eye socket that continues onto the postorbital. At the same level, a medial longitudinal crest on the ventral process of the postorbital forms a boundary between the eye socket and the temporal cavity (see Postorbital). After reaching its

widest point at the level of the cerebral hemispheres (6.42 mm wide), the *crista cranii* flex medially, possibly shaping the posterior portion of the cerebellum (Hopson, 1979). The orbital rim formed by the frontals is pierced by small foramina, but its surface is not as rugose as in *Heterodontosaurus* (Norman et al., 2011) and ornithopods such as *Zephyrosaurus* (Sues, 1980). The ventral surfaces of the frontals roofing the intracranial space form well marked forebrain osteological correlates with raised margins, although these are less marked than previously thought (Pol et al., 2011). An oblique fracture across the forebrain region and a dorsoventral displacement of the halves results in the impression of an increased depth for the endocast. When reconstructing the divided halves of the fused frontals in a more natural position, this depth decreases, and the forebrain facets with raised margins become less developed.

Parietal—Both parietals are preserved in MPEF-PV 3211-11. As in other ornithischians, these are fused medially forming a single element in the skull roof. This region of the skull is preserved in four fragments: the anterior portion of the fused parietals, the interparietal region bearing a damaged sagittal crest, the mid-posterior portion of the left parietal, and the posterior portion of the right parietal. The contacts of these fragments with the laterosphenoids and prootics ventrally, the bases of the paroccipital processes of the opisthotic posterolaterally, the supraoccipital posteriorly, and the squamosal posterolaterally, are not preserved; nevertheless, they are assumed to be similar to the condition seen in *Heterodontosaurus* (Norman et al., 2011). The anterior portion articulates tightly with the frontals medially, whereas the lateral half of the frontal-parietal articulation is not preserved. The parietals articulate with the frontals via an interdigitated articulation in which an anterior process from the parietals enters a groove formed by the frontals medially; laterally, a posterior projection of the frontals passes lateral to the sagittal crest and fits into a notch in the parietals. A similar anterior process of the parietal that fits between the frontals is present in

Dysalotosaurus (MB-R 1372, MGB pers obs), *Hypsilophodon* (Galton, 1974), possibly *Zephyrosaurus* (Sues, 1980), some hadrosaurid species (e.g., Horner et al., 2004), and *Yinlong* (Han et al., 2015). Contrastingly, the frontal-parietal contact forms a straight suture finely interdigitating in *Lesothosaurus* (Porro et al., 2015). Thus, the frontal-parietal contact in *Manidens* is more similar to that in derived ornithopods than to *Lesothosaurus*.

The sagittal crest on the anterior fragment of the parietals is prominent but fractured, and the interparietal articulation is obscured by fusion, which probably occurred during the early stages of ontogeny (Currie, 1997). The parietals do not contact the postorbitals anterolaterally, differing from *Lesothosaurus*, *Hypsilophodon*, *Jeholosaurus*, *Agilisaurus*, *Dysalotosaurus*, and other ornithopods, but resembling *Heterodontosaurus* and *Yinlong* (Galton, 1974; Peng, 1992; Barrett and Han, 2009; Norman et al., 2011; Han et al., 2015; Porro et al., 2015). The interparietal fragment preserves the sagittal crest up to its posterior bifurcation, which forms the occiput and nuchal crest. The sagittal and nuchal crests are prominent, as in *Heterodontosaurus* (Norman et al., 2011), and the nuchal crest is at least as prominent as the same preserved along the posterodorsal border of the squamosal.

Among the remaining posterior fragments, the overall shape of the left parietal fragment shows little deformation compared with the right posterior fragment, and its ventral margin is complete. The left parietal fragment is dorsally arched in transverse section, and laterally concave anteroposteriorly in dorsal view. It has a posterior process that projects laterally at about 40° from its main axis for contact with the squamosal, and a ventral notch for its articulation with the opisthotic. The right parietal fragment was identified based on the aforementioned ventral notch, but due to its damage this fragment is not informative.

Lacrimal—Both lacrimals are preserved in MPEF-PV 3211-11; however, only the right element is informative. MPEF-PV 3809 preserves a small fragment of the left anterior process

of the lacrimal in articulation with a fragment of the posterolateral process of the premaxilla anteriorly, and with the medial dorsal lamina of the maxilla medially.

In lateral view, the lacrimal consists of a long and thin anterior process and a short ventral process with a wide base, which gives it a sub-triangular shape (Fig. 50–R). Contrary to the condition observed in most ornithischians, in *Manidens* the anterior process is longer than the ventral process of the lacrimal (Norman et al., 2011; Porro et al., 2015; Galton, 1974, Barrett and Han, 2009). The lacrimal separates the orbit and the external antorbital fenestra, and its boundary with the latter is an anteroventrally concave edge. The posterior margin of the ventral process of the lacrimal flares medially forming a dorsoventrally oriented crest that walls the orbit anteriorly. The lacrimal bears a shallow groove on its dorsal aspect into which the posterolateral process of the premaxilla, the nasal and the prefrontal fit. The medial edge limiting this groove forms a longitudinal crest in a bevelled articulation with the ventral aspect of the nasal and the anterior portion of the prefrontal, but not the premaxilla. The lacrimal contributes only slightly to the articulation facet for the supraorbital, where the lacrimal overlaps the prefrontal. There is a longitudinal groove on the ventral margin of the anterior process of the left lacrimal that meets the lamina of the maxilla in a butt joint, with its medial limit forming a thin, ventrally-projecting crest, which corresponds to the only known contribution of the lacrimal to the antorbital fossa. In medial view, this longitudinal groove opens to a medial depression along the anterior half of the ventral process of the lacrimal, which is bounded by a dorsoventrally oriented low ridge. The maxilla-lacrimal butt joint continues posteriorly to form a tight bevelled joint with the ventral process of the lacrimal along this depressed medial region. The lateral edge of this longitudinal groove partially overhangs the antorbital region. In medial view, a small space remains between the ventral groove of the lacrimal and the maxillary lamina, which is interpreted as the articular region for the anterodorsal process of the jugal (see Jugal).

The opening of the nasolacrimal canal (Porro et al., 2015; *canalis nasolacrimalis* in Witmer, 1997b) is preserved in MPEF-PV 3809 and MPEF-PV 3211-11 (Fig. 4C–D, 5O, Q). The nasolacrimal canal opens laterally in the anterodorsal corner of a sub-triangular and dorsoventrally oriented fossa that occupies most of the ventral process of the lacrimal, goes through the anterior process of the lacrimal longitudinally, and opens medially into a fossa *delimited* laterally by the premaxilla and ventrally by the anterior process of the lacrimal. A second small foramen opens laterally in the lacrimal fragment of MPEF-PV 3809 but not in MPEF-PV 3211-11. The lateral opening of the nasolacrimal canal and presence of the triangular fossa is more similar to *Heterodontosaurus* than to *either Hypsilophodon or other heterodontosaurids* (Witmer, 1997b; Norman et al., 2011).

Supraorbital/Palpebral—Pol et al. (2011) mistook a rib fragment associated with the left postorbital for the supraorbital. Correcting this misinterpretation, both supraorbitals were identified in MPEF-PV 3211-11, with the right supraorbital in its natural position and the left one posteriorly displaced and fractured (Fig. 6A–B). The *planar* articulation facet for the supraorbital *is oriented* anteromedially and occupies mostly part of the prefrontal and a slight portion of the lacrimal. As in *Heterodontosaurus* and other ornithischians, the supraorbital is robust and proximally expanded and distally is rod-like and conical, tapering posteriorly (Fig. 7). *The articular (medial) face of the supraorbital is sub-triangular in shape*, anteroposteriorly longer than dorsoventrally high and slightly concave anteroposteriorly (Fig. 7D). In dorsal view, the rod-shaped portion forms an angle of approximately 32° from its expanded foot, curves medially, and diverges from the snout outline (Fig. 7A–B, E–F). In lateral view, the supraorbital is straight dorsally and curved ventrally, following the contour of the orbit (Fig. 7C). The supraorbital reaches the posterior half of the orbit but does not completely span it, as *also occurs in Heterodontosaurus and Gasparinisaura* (Norman et al., 2011; Coria and Salgado, 1996), *but* differing from *Agilisaurus* and *Thescelosaurus* (Peng, 1992; Barrett et al.,

2005; Boyd, 2014; *contra* Pol et al., 2011). A small foramen pierces the supraorbital in a dorsoventral direction, opening dorsally into a depression at the angle formed between the base and the rod-like portion, and is bounded anteromedially by a slight crest that limits posterodorsally the articulation of the supraorbital (Fig. 7).

Postorbital—Both postorbitals are complete. The right one is isolated and its ventral (jugal) process is fractured and slightly displaced (MPEF-PV 3211-7). The left postorbital is in association with the left temporal region and lacks any taphonomic alteration (MPEF-PV 3211-9). The postorbital is a triradiate element in lateral view, with a short anterior process and long posterior and ventral processes (Pol et al., 2011). This bone limits the posterodorsal vertex of the orbit, the anterodorsal portion of the infratemporal fenestra, and the anterolateral portion of the supraorbital fenestra, as in other ornithischians. The postorbital shows a lateral protuberance as a rounded swelling with its most prominent region positioned ventrally, which occupies the posterodorsal margin of the orbit below the junction between the anterior and ventral branches of the postorbital. In *Manidens*, this lateral “boss” becomes more prominent ventrally, reaching its maximum near the midpoint of the postorbital ventral process, where it is abruptly truncated. The only heterodontosaurid preserving a complete postorbital is *Heterodontosaurus tucki* (the postorbital in *Pegomastax africanus* is partially covered). *Heterodontosaurus* has a lateral ridge of the postorbital (lateral “boss”) at the main body of the postorbital, whereas the same in *Manidens* is comparatively located ventrally on the base of the ventral process of the postorbital. The anterior half of the lateral process, the region facing the orbit, is rugose and made up of highly vascularized periosteal bone (outer 0.2 mm), as evident in the micro-CT scans (Fig. 8I–J). This rugose region faces the posterior end of the supraorbital, indicating that it was covered by connective tissue that possibly reached the supraorbital (Maidment and Porro, 2010). A similarly rugose anterior margin can be identified in *Heterodontosaurus* (Norman et al., 2011), *Orodromeus* (Scheetz, 1999), and

Dysalotosaurus (MB.R 1375; MGB, pers obs), but it is anteriorly developed within the orbit in lateral view **in these taxa**, instead of laterally as in *Manidens*.

The base of the median process is as wide as the main body of the postorbital, as in *Orodromeus* (Scheetz, 1999) and *Agilisaurus* (Peng, 1992), while this process is narrower than the latter in *Heterodontosaurus* (Norman et al., 2011), *Jeholosaurus* (Barrett and Han, 2009), *Hypsilophodon* (Galton, 1974), *Lesothosaurus* (Sereni, 1991), **and** *Gasparinisaura* (Coria and Salgado, 1996; MUCPv-208, MGB pers obs). In dorsal view, the anterior corner of the supratemporal fenestra is narrower than in *Heterodontosaurus*, but the dorsotemporal fossa does not reach the medial process of the postorbital as in *Heterodontosaurus* (Fig. 8G, N). The intertemporal bar formed by the squamosal and the postorbital is at least twice as high dorsoventrally as its mediolateral width. There is a lateral fossa in the main body of the postorbital, which is bounded anteriorly by the lateral “boss” and posteriorly reaches the base of the posterior process of the postorbital. Exists a similar fossa in the lateral aspect of the postorbital in *Heterodontosaurus* (SAM-PK-K337), but the same is located posteroventral to the lateral “boss” instead of posteriorly as occurs in *Manidens*. The base of the lateral “boss” does not form a pocket-like recess as the lateral ridge does in *Heterodontosaurus*, **in which it is considered to be part of the attachment site for the m. adductor mandibulae externus superficialis** (Norman et al., 2011).

In medial view, the postorbital-frontal suture is above and slightly posterior to the eye socket, and involves the entire anterior process of the postorbital and its dorsal border **with** the margin of the supratemporal fenestra. This suture is complex and includes two well-defined regions: a medially prominent longitudinal ridge anteriorly; and a dorsoventrally and anteroposteriorly wide concave region excavated into the postorbital, located posteriorly (Fig. 8D, K). The anterior region fits into an embayment in the frontal with dorsal and ventral margins that firmly enclose this region, and the posterior concavity embraces a convex

surface on the frontal. In dorsal view, the frontal-postorbital contact forms a laterally concave sinuous suture. In *Manidens*, the postorbital does not contact the parietals, whereas the postorbital-parietal contact is present in *Heterodontosaurus* (Norman et al., 2011), *Lesothosaurus* (Serenó, 1991; Porro et al., 2015), *Agilisaurus* (Peng, 1992), *Orodromeus* (Scheetz, 1999; fig. 7, c-par, c-f), and *Jeholosaurus* (Han et al., 2009), among others.

In medial view, a medially prominent crest bounds the posteroventral and posterior limits of the frontal-postorbital contact. The ventral postorbital process bears a longitudinal ridge from the ventral boundary of the postorbital- frontal joint to its distal end. This medial ridge is continuous proximally with the *crista cranii* of the frontals, anteriorly bounds the eye socket, and distally is included in the postorbital-jugal articulation. The ventral process of the postorbital is markedly depressed medially with an oblique step-like boundary, oriented from distally to the process and anterior to the medial ridge, to the base of the process and the posterior to the medial ridge, ending at the base of the process in a sharp tongue-like depression. The postorbital and jugal bones meet *along* a scarf joint where the ventral process of the postorbital fits into a rounded fossa in the dorsal process of the jugal, which posteriorly embraces the postorbital (Fig. 8D, K). The synovial socket for the anterolateral (capitated) process of the laterosphenoid is present on the medial surface of the postorbital as a subcircular depression limited anteriorly by the medial ridge of the postorbital, dorsally by the frontal-postorbital articulation and posteriorly by a faint ridge (Fig. 8D, K). *This facet is evident on the left postorbital, identified in Heterodontosaurus* (Norman et al., 2011; fig. 10, pos), and likely widespread among heterodontosaurids as it is for ornithomorphs as *Orodromeus* (Scheetz, 1999), *Hypsilophodon* (Galton, 1974), *Thescelosaurus* (Boyd, 2014), *Tenontosaurus tilleti* (Thomas, 2015), among others.

The posterior process of the postorbital bears a U-shaped depressed region on its medial surface with crested boundaries for the bevelled postorbital-squamosal articulation, which

comprises at least the medial half of the posterior process of the postorbital. At the postorbital-squamosal articulation, the posterior process of the former forms a concavity and turns to face slightly dorsally to receive the anterior process of the latter, which turns slightly ventrally before they meet (Fig. 8H, P, W). Anterior to the postorbital-squamosal articulation facet, a slight longitudinal groove extends anteriorly on the medial aspect of the postorbital, becoming faint near the socket for the laterosphenoid. This groove corresponds to the attachment region for **the m. adductor mandibulae externus medialis**, as in *Heterodontosaurus* (Norman et al., 2011; Sereno, 2012).

Squamosal—Only the left squamosal is preserved, in articulation with the quadrate and the quadratojugal, and contacting the postorbital in MPEF-PV 3211-9 (Fig. 8A–B). The squamosal is a tetraradiate element that connects the temporal region with the skull table and the orbital region, and **delimits** the supraorbital fenestra posterodorsally and the infratemporal fenestra posterolaterally, as in *Heterodontosaurus* (Norman et al., 2011), other **ornithischians** (Weishampel et al., 2004), and other diapsids. Regardless of being partially disarticulated, the main body of the squamosal is slightly displaced dorsally in lateral view (Pol et al., 2011). This is evidenced by the uneven angle of contact between the posterior process of the postorbital and the anterior process of the squamosal (Fig. 8Q, S). The base of the anterior (postorbital) process of the squamosal is robust whereas its distal portion, including most of the overlapping region with the postorbital, is missing. As with the postorbital, there is a longitudinally developed groove on the medial surface of the anterior process of the squamosal, with its dorsal boundary as a conspicuous crest, forming the attachment site for **the m. adductor mandibulae externus medialis** (Norman et al., 2011).

In dorsal view, the post-temporal crest of the squamosal increases in prominence as it approaches the squamosal-parietal contact that delimits the posterolateral corner of the supratemporal fenestra. This crest corresponds to the posterior bifurcation of the sagittal crest

of the parietals that extends over the posteromedial margin of the supratemporal fenestra delimited by the squamosal, as in *Heterodontosaurus* (Norman et al., 2004b, 2011). Although the wing-shaped medial process is mostly preserved and forms a flat region oriented anteriorly, the squamosal-parietal contact region is missing. At the vertex formed by the medial process of the squamosal, a medially-facing, deep depression acted as an additional reinforcement for the squamosal-parietal articulation (Fig. 8S). The main body of the squamosal, with its lateral rim and its medial wing-shaped process, form a posterodorsally facing plane divided into two halves by an oblique faint unevenness: the dorsal region contributes to the occiput, and the ventral and slightly depressed region forms the face overlapped by the paroccipital process of the opisthotic, with the faint unevenness marking the suture line (Fig. 8R, T, V). The lateral thickening of the paroccipital process contributes to the lateral rim of the squamosal. More than half of the posterior face of the squamosal is obscured posteriorly by the paroccipital process of the opisthotic (Fig. 8V). The anteriorly facing aspects of the medial process of the squamosal formed part of the origin of the *m. adductor mandibulae externus medialis*, or at least limited this muscle posteriorly together with the paroccipital process.

In lateral view, the lateral rim of the squamosal reaches the level of the posterolateral corner of the supratemporal fenestra, then curves ventrally to delimit the infratemporal fenestra, and then extends laterally and posteroventrally further than the ventral (prequadratic) process of the squamosal, enclosing the postquadratic process (Fig. 8Q). As Pol et al. (2011) mentions, the lateral rim in *Manidens* is more laterally prominent than that of *Heterodontosaurus* (Norman et al., 2011). However, the smaller skull size of the former than the latter precludes relating the difference in prominence and robustness of the lateral rim of the squamosal to size differences, being more likely related to their muscular attachment function. Together with the deep fossa of the main body of the postorbital and its posterior

continuation as a longitudinal fossa along the upper temporal bar, this lateral crest gives an attachment surface for the *m. adductor mandibulae externus superficialis*. In *Heterodontosaurus*, a faint oblique ridge on the upper temporal bar was interpreted as dividing this muscle into anterior and posterior portions (Norman et al., 2011). A similar ridge at the beginning of the lateral crest of the squamosal might indicate a similar division of this muscle in *Manidens*. The postquadratic process contributed to the attachment site of the *m. depressor mandibulae* (Holliday, 2009; Norman et al., 2011).

The prequadratic process extends posteroventrally from the main body of the squamosal, is anteroventrally directed and tapers distally. The lateral aspect of this process bears a shallow depression that receives the quadratojugal in a bevelled articulation, and posteromedially exhibits a deep cotylus that articulates with the head of the quadrate. The prequadratic process has fossa on its anterior half, limited dorsally by the lateral rim of the squamosal, and posteriorly by a dorsoventrally oriented crest that continues ventrally over the lateral face of the quadrate shaft. The cotylus for the quadrate is dorsally incised within the main body of the squamosal, posteriorly limited by the postquadratic process, and anteriorly bounded by the formerly mentioned dorsoventrally oriented crest. This crest separates the squamosal-quadrate articulation from the temporal muscle chamber, and corresponds also to the most important boundary for the socket that houses the quadrate head within the squamosal (Fig. 8S). The quadrate head fits loosely in this socket, possibly involving a fibrous/cartilaginous covering of this head in a synovial articulation, a common inference in ornithopods (Weishampel, 1984; Norman, 1984; Norman and Weishampel, 1985; Holliday and Witmer, 2008). The squamosal-quadrate articulation faces medially and the squamosal-quadratojugal contact excludes quadrate from the border of the infratemporal fenestra, as in *Heterodontosaurus*.

Jugal—In addition to the left jugal identified by Pol et al. (2011) in MPEF-PV 3211-9 (Fig. 9A–B), here we report the presence of the right jugal in MPEF-PV 3211-10. The left jugal is mostly complete but fractured, its anterodorsal and dorsal processes are displaced, and the ventral margin is incomplete anteriorly and posteriorly (Fig. 9C–G). The right jugal is crushed, its anterior half is fractured and dorsally displaced, the anterodorsal process is incomplete distally, and the posterodorsal process is fractured and its distal half is displaced (Fig. 9C). Nevertheless, both elements allow **reconstruction of** the morphology of the jugal as composed of a main body with five processes: the anterior, dorsal, posterior, and ventral processes, and the lateral process or “**jugal boss**”. As in other ornithischians, the jugal forms the ventral limit of the orbit and the anteroventral corner of the infratemporal fenestra (Norman et al., 2004b).

The anterior process of the jugal divides into an anterodorsally tapering process and a lateromedially thin anteroventral rounded edge. The anterodorsal portion of the process forms part of the margin of the orbit anteroventrally. Distally, this process bears a posterolaterally facing fossa that fits between the ventral process of the lacrimal and the medial fossa of the maxilla in a bevelled articulation. The maxilla-jugal articulation continues along the lateromedially thin ventral margin of this process, a bevelled **articular** region with its dorsal boundary marked by a step-like unevenness at both sides of the process. The ventral margin of this **jugal process** fits into a narrow and long sulcus in the posterodorsal region of the maxilla, covering most of the lateral aspect of this process, as in *Zephyrosaurus* (Sues, 1980). In medial view, the medial depression of the jugal and the posterior widening of the narrow sulcus of the maxilla form a depressed articulation face with raised margins for the ectopterygoid, a depression limited posteriorly and laterally by the jugal (which ends into a ventral medial process), and anteriorly by the medial lamina of the maxilla. A similar jugal-maxilla-ectopterygoid contact is present in *Hypsilophodon* (Galton, 1974), *Dryosaurus*

(Galton, 1983), and *Heterodontosaurus* (Norman et al., 2011). Enclosed in this depression, a broad subcircular passage goes through the jugal from the lateral side of the skull to the articular face for the ectopterygoid, and does not open to the medullary cavity of the jugal (Fig. 9C, F, H, J). This foramen corresponds to a neurovascular passage and may not be related to an incipient jugal sinus (as in *Tyrannosaurus*; Witmer and Ridgely, 2008).

Additional passages go through the jugal; these were related to blood vessels that passed through the floor of the orbit.

The dorsal process of the jugal was previously interpreted as posteriorly twisted, an autapomorphy mainly interpreted from the left jugal (Pol et al., 2011). However, the dorsal process of the right jugal extends straight upwards and is slightly posteriorly oriented in lateral view (Fig. 9B), and this process in the left jugal is fractured with the distal fragment posteriorly displaced (Fig. 9A), both features indicating a rather straight and distally tapering dorsal process of the jugal (Fig. 9B–J). As in *Heterodontosaurus*, the dorsal process of the jugal contacts the ventral process of the postorbital along a long suture. The articular surface for the postorbital is marked by a deep groove at the base of the dorsal process into which the ventral postorbital process fits. The distal half of the dorsal process of the jugal rotates to embrace the ventral process of the postorbital in its posterior aspect, consistent with the anatomy of its counterpart in the postorbital. The dorsal process of the jugal, unlike *Heterodontosaurus* (Norman et al., 2011) and contrary to previous reconstructions of *Manidens* (Pol et al., 2011; Sereno, 2012), is located posterior to the postorbital and excluded from the posteroventral margin of the orbit, which is completely delimited by the postorbital. Medially, there is a dorsoventrally oriented crest on the dorsal process of the jugal, a continuation of the crest on the ventral process of the postorbital, which outlines the eye socket and continues ventrally as the anterior boundary of the jugal-maxilla-ectopterygoid

articulation. An additional crest parallel to the former extends downwards to the base of the process and deviates posteriorly, marking the anteroventral limit of the infratemporal fenestra.

The posterior half of the jugal divides into a posterior process and a ventral process, a novel feature shared with *Heterodontosaurus* (e.g., Norman et al., 2011; Sereno, 2012). **Note that the ventral process of the jugal is independent of the jugal-quadratojugal articulation.** Some taxa show a distally bifurcated posterior process of the jugal, but both ends participate in the jugal-quadratojugal articulation, such as *Herrerasaurus* and other saurischians (e.g., Sereno and Novas, 1994), *Jeholosaurus*, psittacosaurids, and early ornithischians (e.g., Barrett and Han, 2009). The region posterior to the dorsal process is lateromedially thin and dorsoventrally expanded. Pol et al. (2011; fig. 2a, b) and Sereno (2012; fig. 81) considered that the region bearing the posterior and posteroventral processes was ventrally deflected, and that the posterior process was dorsally oriented along its contact with the quadratojugal. A more detailed observation **indicates** that rather **than** being dorsally oriented, the dorsal and ventral borders of the posterior region of the left jugal are damaged. The better preserved posterior region at the right jugal, and the overall morphology of the depressed jugal-quadratojugal articulation limited by a slight unevenness in both quadratojugals indicate that the posterior process is horizontally disposed and at least twice the length than that preserved (Fig. 9). As in *Heterodontosaurus* and other ornithischians (Norman et al., 2004b, 2011), the jugal had a posteriorly tapering process directed upwards towards the temporal bar, forming an extensive overlap with the anterior process of the quadratojugal. In this new interpretation, the posterior process is larger than the ventral process (**contra** Pol et al., 2011) unlike *Heterodontosaurus* (Norman et al., 2011). The overlapping jugal-quadratojugal suture lacks **evidence** of interdigitations **such as reported in** *Heterodontosaurus* (Norman et al., 2011), being more similar **to the condition found in** some euornithopods **instead** (Norman et al., 2004b).

The ventral process, or jugal flange, has been characterized as unique to *Heterodontosaurus* (e.g., Charig and Crompton, 1974; Norman et al., 2004b, 2011; Sereno, 2012), but both its presence and its posteroventral orientation are shared with *Manidens* (Pol et al., 2011). Both jugals preserve a ventral process, although the margins are more complete in the right jugal. In lateral view, the anterior edge of the ventral process is anteroventrally concave and the posterior edge is strongly concave, forming a rounded wing-shaped distal end directed posteriorly. This process is thickened along its anteroventral edge and is transversely flattened posteriorly at its tip, is directed ventrally (not ventrolaterally), and oriented posteriorly to a lesser degree than previously thought (Pol et al., 2011).

One of the most prominent features of the jugal is the presence of a lateral process or “jugal boss”, a condition shared with *Heterodontosaurus* in Heterodontosauridae (Norman et al., 2011), *Orodromeus* (Scheetz, 1999), *Zephyrosaurus* (Sues, 1980; Norman et al., 2004b), *Jeholosaurus* (Barrett and Han, 2009), *Changchunsaurus* (Jin et al., 2010), and ceratopsians (You and Dodson, 2004). The “jugal boss” begins as a shallow rim at the base of the anterodorsal process of the jugal, increases progressively its lateral prominence posteriorly and is directed slightly dorsally, and ends abruptly in a brief crest directed posteroventrally. Anatomically speaking, this “boss” differs from that in *Heterodontosaurus* in its progressive development in an anteroposterior direction along the main body of the jugal - not as a laterally oriented bulging process - and in its location along the dorsal half of the main body of the jugal (Norman et al., 2011). The “jugal boss” is ventrally depressed. This depressed region is a posterior continuation of the laterally depressed face of the maxilla below the antorbital fenestra, instead of being a posterior extension of the antorbital fossa along the jugal as previously thought (contra Becerra et al., 2014). As interpreted for the maxilla, this laterally depressed face along the body of the jugal contributed to the attachment of soft tissue cheeks posteriorly. The jugal does not participate in the boundary of the external antorbital

fenestra and the antorbital fossa does not extend further posteriorly along the main body of the jugal as previously thought (*contra* Becerra et al., 2014), and does not participate in the posterior limit of the antorbital fossa, all of which are features present in *Heterodontosaurus* (Norman et al., 2011).

In cross-section, there is altered cortical bone at the posterodorsal portion of the “jugal boss”: a thickened region with growing bone over old cortical bone, and intruding within the medullary bone of the jugal (Supplemental Data 1). This bone arrangement is uneven but present in both jugals, and resembles the type of tissue observed in broken and healed bones (Supplemental Data 1). Considering previous hypotheses on sexual dimorphism, sexual display, and agonistic behavior in heterodontosaurids based on their prominent tusks, the presence of crushed and remodeled bone tissue in the “jugal boss” may suggest a likely lateral head-butting behavior for *Manidens* (e.g., Becerra et al., 2020 and references therein). Lateral head-butting behavior has never been proposed for Heterodontosauridae, however it might be a convergent behavior within Ornithischia, common in pachycephalosaurids and ceratopsids, and described outside Ornithischia in synapsids (Carpenter, 1997; Farke, 2004; Snively and Cox, 2008; Snively and Theodor, 2011; Peterson et al., 2013; Benoit et al., 2016, 2017).

Quadratojugal—The holotype preserves both quadratojugals (Fig. 9): the right quadratojugal is isolated (MPEF-PV 3211-6, Fig. 9M–N), and the left quadratojugal is articulated with the quadrate and the squamosal, and in association with other elements of the left temporal region (MPEF-PV 3211-9, Fig. 9A, K–L). The quadratojugal is a triradiate and mediolaterally thin element that forms the posteroventral corner of the infratemporal fenestra and bounds the temporal adductor chamber laterally (Fig. 9A). The angle between the anterior and posterodorsal processes is 138°, that between the posterodorsal and posteroventral processes is 121°, and that separating the posteroventral and anterior processes is 101°. The anterior process of the quadratojugal is dorsoventrally constricted at its middle region and

widens distally into a rounded end. The anterior process is thickened at its base and mediolaterally flattened **in the region where it articulates** with the jugal. The jugal-quadratojugal contact is a well-defined depressed region on the lateral aspect of the anterior process that tapers posteriorly and reaches the main body of the quadratojugal (Fig. 9K, N). The medial aspect of the base of the anterior process has thickened dorsal and ventral margins, reinforcing the thin lower temporal bar (Fig. 9L–M).

The posterodorsal process of the quadratojugal has sub-parallel sides in lateral view and a rounded distal end. This process laterally overlaps the prequadratic process and fits into a “cuff”, with a dorsally convex outline in lateral view. The prequadratic process of the squamosal extends ventrally and overlaps the quadratojugal along its posterior edge up to the midpoint of the main body in medial view. This **overlapping** contact and the exclusion of the quadrate from the infratemporal fenestra are features shared with *Heterodontosaurus* (Norman et al., 2011). Both the posterodorsal and posteroventral processes of the quadratojugal contact the quadrate along its posterior edge, while the main body of the quadratojugal is separated from the quadrate. The posterior edge of the posterodorsal process of the quadratojugal and the ventral extension of the prequadratic process of the squamosal are bound by a laterally prominent crest on the lateral aspect of the quadrate shaft that curves anteriorly along its edge. Ventral to this quadratojugal-squamosal-quadrate contact, the ventralmost portion of this crest **on** the quadrate turns abruptly posteriorly, separating from the quadratojugal and merging with the shaft of the quadrate in lateral view, resulting in a spindle-shaped groove facing posteroventrally. In posterolateral view, this opening is bounded anteriorly by the posterior margin of the quadratojugal and mediolaterally by the quadrate. In *Heterodontosaurus*, this opening is **termed the** paraquadratic foramen (Norman et al., 2011), and **this feature is** interpreted as such in *Manidens*, although in the latter it opens posterolaterally instead of posteriorly.

In lateral view, the posteroventral process of the quadratojugal shows an anteriorly concave anterior edge and a posteriorly convex posterior edge, and bends anteriorly before terminating in a rounded end (similar to *Heterodontosaurus*: Norman et al., 2011). The posteroventral process is medially reinforced by a dorsoventrally oriented crest. The distal half of the posteroventral process contacts the anteriorly directed and thin lateral process of the quadrate in an overlapping articulation, at the anterolateral margin of the quadrate condylar process. The close relationship between the quadratojugal and the quadrate would direct stress related to chewing from the quadrate to the temporal region and skull roof; furthermore, it is possible that the quadratojugal-quadrate joint was reinforced by ligamentous fibers, as suggested for *Heterodontosaurus* (Norman et al., 2011). In medial view, the medial crest of the posteroventral process and the thickened ventral margin of the anterior process meet in the main body and dorsally bound a groove, located at the anteroventral corner of the quadratojugal. The quadratojugal is separated from the pterygoid wing of the quadrate, which together with the quadrate wing of the pterygoid medially bounds the space for the mandibular adductor musculature.

Among heterodontosaurids, the anatomy of the quadratojugal is unknown in *Lycorhinus* (Serenó, 2012), *Lanasaurus* (Gow, 1975, 1990), *Fruitadens* (Butler et al., 2010, 2012), *Echinodon* (Norman and Barrett, 2002; Sereno, 2012), and *Tianyulong* (Zheng et al., 2009; Sereno, 2012); it is damaged in *Abriktosaurus* (Thulborn 1974; Sereno, 2012), and is complete in *Heterodontosaurus* (Norman et al., 2011; Sereno, 2012). Sereno (2012) mentions the preservation of a postorbital in SAM-PK-K10488 (fig.82); however, the overall shape of this element is similar to the anatomy of the quadratojugal described here, but its brief description prevents discussion of its identity. Most descriptions and reconstructions represent the quadratojugal in Heterodontosauridae (*Abriktosaurus*, and *Heterodontosaurus*) as a triradiate element, an uncommon condition compared with other ornithischians such as

Lesothosaurus, *Gasparinisaura*, *Parksosaurus*, *Hypsilophodon*, and *Jeholosaurus*, where these elements are V-shaped in lateral view, or plate-like elements as in Iguanodontia and Psittacosauridae (Galton, 1973b, 1974; Sereno, 1991; Coria and Salgado, 1996; Norman, 2004; You and Dodson, 2004; Barrett and Han, 2009).

Quadrate—The right quadrate of MPEF-PV 3211-5 is complete but disarticulated (Pol et al., 2011), whereas the left quadrate is preserved in articulation with the left quadratojugal and squamosal in MPEF-PV 3211-9 although its condylar region was separated from its shaft and preserved in articulation with the lower jaw of MPEF-PV 3211-10. If the condyles of the complete right quadrate are positioned as those in the articulated left quadrate (nearly 90° to the skull sagittal plane), the dorsal half of the right quadrate is twisted due to deformation, the pterygoid wing is broken across the base and displaced medially, and the lateral process of the quadrate is slightly deflected laterally (Fig. 10I–N). Although in articulation, the left quadrate is damaged at its condyles, all features along the anterolateral margin of the quadrate (including the lateral process) up to the region of the paraquadratic foramen are missing, and its pterygoid wing is not deformed but broken in its base and displaced laterally.

The quadrate of *Manidens* is elongate and posteriorly curved in lateral view, slender in its dorsal half, and more robust and column-like in its condylar shaft (Pol et al., 2011). The quadrate head fits into a medioventrally oriented cotylus in the squamosal forming a synovial joint, an assumption supported by its loose fit and its rugose and striated periosteal texture (Holliday and Witmer, 2008), a feature common in Ornithopoda (Fig. 10A–B). These features indicate that a fibrous/cartilaginous covering was present, functioning to dissipate feeding forces transmitted to the skull (Norman 1984; Weishampel, 1984; Holliday and Witmer, 2008). As in *Heterodontosaurus* and *Zephyrosaurus* (Sues, 1980; Norman et al., 2011) and contrasting with *Hypsilophodon* and more derived ornithopods (Galton, 1974, 1983), the quadrate head is separated from the pterygoid wing of the quadrate.

Along the anteromedial margin of the dorsal half of the shaft, the pterygoid wing of the quadrate extends anteromedially as a sub-triangular sheet of bone (Fig. 10C, F, J–K). Despite this breakage, the dorsalmost portion of the left element preserves its angle with respect to the condyles (Fig. 10G–H). In dorsal view, the pterygoid wing of the right quadrate is twisted counter clockwise about 10° if compared to the condylar region (Fig. 10M–N), while in the left quadrate this measure is 65–70° (Fig. 10G–H), indicating that the pterygoid wing is altered in the right element. In medial view, the posteromedial margin of the quadrate forms a robust rim that divides the medial wing from the posterior face of the quadrate (Fig. 10F, K). This posteromedial rim begins at the quadrate head and disappears at the base of the quadrate condylar shaft. **This feature is hard to assess for other heterodontosaurids given that few quadrates are preserved in the clade and was not described for *Heterodontosaurus* (Norman et al., 2011), as for *Lesothosaurus* and *Thescelosaurus* outside Heterodontosauridae (Boyd 2014; Porro et al., 2015), although a similar structure is present in *Dysalotosaurus* (MB.R 1320, MGB pers obs).** The extent of the overlapping quadrate-ptyergoid articulation is not easy to elucidate, although it is likely that this articulation **did** not reach the posteromedial rim of the quadrate (Fig. 10F).

Contrary to *Heterodontosaurus* (Norman et al., 2011), no groove **representing potential cranial pneumaticity** is identified on the posterior face of the condylar process. The anterolateral margin of the quadrate receives the posterior edges of the quadratojugal and the prequadratic process of the squamosal dorsally within a narrow and anteriorly facing sulcus enclosed laterally by the laterodorsal crest of the quadrate and medially by the pterygoid wing of the quadrate, and dorsally limits the paraquadratic foramen. Both the pterygoid wing of the quadrate and its counterpart in the pterygoid form the medial boundary of the infratemporal fossa and **bound the m. adductor mandibulae externus superficialis** (Norman et al., 2011; Sereno, 2012). The slender dorsal half of the quadrate features an anteriorly concave space,

which together with the pterygoid wing (medially) and the anterolateral margin contacting the quadratojugal formed a bony wall posteriorly enclosing the *m. adductor mandibulae externus medialis and externus profundus*. Ventrally, the lateral process of the quadrate extends anterodorsally and bears a lateral depression that underlaps the posteroventral process of the quadratojugal. Its subcircular dorsal outline indicates that ventrally bounds the posterolateral exit of the paraquadratic foramen. A similarly positioned lateral process is described in *Dysalotosaurus* and *Dryosaurus* (Galton, 1983), although this crest forms a butt joint instead of an overlap suture with the quadrate as in *Manidens*; a similar feature has not been identified in *Heterodontosaurus* or other *heterodontosaurids*.

The quadrate of *Manidens* is exceptionally tall, a feature shared with *Heterodontosaurus* (for which appropriate material is known) and that is uncommon in Ornithischia, which is associated with the ventral offsetting of the jaw articulation well below the level of the tooth row (Norman et al., 2011). However, the condylar process of the quadrate is 14% shorter than the dorsal half of the quadrate, whereas this difference is only 6% for *Heterodontosaurus* (SAM-PK-K337), being proportionately taller in the latter. The condylar process of the quadrate is wider mediolaterally than anteroposteriorly forming an ellipsoidal section that contrasts with the subcircular section of this process in *Heterodontosaurus*. The condylar shaft and the condyles are separated by a slight constriction in anterior view, outlining the rounded silhouette of the medial condyle and concave silhouette of the lateral condyle. In addition, the condylar shaft is divided from the condyles by a slight transverse ridge. The anteriorly concave surface of the quadrate shaft, from the ventral portion of the paraquadratic foramen to the slight transverse ridge above the condyles, forms the attachment site for the *m. adductor mandibulae posterior*. The smaller medial condyle is located slightly anterior and dorsally to the larger lateral condyle. A bicondylar jaw articulation is common in Ornithischia, with the larger condyle located laterally (Weishampel, 1984). In articular view,

the lateral condyle is wider anteroposteriorly than the medial condyle, and the intercondylar groove is oriented obliquely from the posterior portion of the lateral condyle to the anterior portion of the medial condyle (Fig. 10N). This intercondylar groove extends dorsally beyond the articular region onto the posterior aspect of the condylar process. The condylar surface has punctuations and open canaliculi near its edges, while the articular portion is smooth indicating a fibrous/cartilaginous covering, as expected for a condylar articulation (Holliday and Witmer, 2008).

The condyles in the left quadrate contact the articular at an angle close to 11° to the transverse plane of the skull in condylar view, less than the 40° present in *Heterodontosaurus* (Weishampel, 1984; Sereno, 2012, fig.92; contra Norman et al., 2011). The parallel orientation of the condyles to the transverse plane of the skull is plesiomorphic in Ornithischia and present in *Lesothosaurus* (Sereno, 1991; Porro et al., 2015); thus, the angle in *Manidens* is intermediate between the condition in *Lesothosaurus* and *Heterodontosaurus* (Sereno, 2012). The angle formed between the greater and the lesser condyles in the right quadrate goes up to 26° in *Manidens* with respect to the horizontal plane (with the lesser located dorsally), smaller than that reported in *Heterodontosaurus* (30° ; Sereno, 2012, fig.92). The orientation of both condyles at the same plane in posterior view is also plesiomorphic in Ornithischia and present in *Lesothosaurus*, *Hypsilophodon*, *Dysalotosaurus*, *Zephyrosaurus*, and *Dryosaurus*, although the orientation of the condyles in the sagittal plane of the skull in the above-mentioned ornithopods is nearly 45° (Weishampel, 1984). Similarly, the orientation of the quadrate condyles in *Manidens* is intermediate between the plesiomorphic and the derived conditions (greater condyle located more distally than the lesser condyle) present in *Heterodontosaurus*.

Pterygoid Region

Pterygoid—The left pterygoid is extensively fractured and slightly deformed, but most of its anatomy is preserved. Most of this element is in association with the left orbital-temporal region and the base of the neurocranium of MPEF-PV 3211-9, except for the distal portion of its pterygoid flange, which is preserved separately with MPEF-PV 3211-10 (Fig. 2, 11A). The overall anatomy of this bone does not differ significantly from that of *Heterodontosaurus* (Norman et al., 2011): it is formed by a main body that branches into an anterior process, a ventral pterygoid flange, and a posterior quadrate wing (Fig. 11C–F). The anterior process is incomplete, and its articulations with the vomer, palatine, and maxilla cannot be elucidated. The quadrate wing of the pterygoid is fractured at its base and offset from the main body. However, the preserved pterygoid wing is a lateromedially thin and dorsoventrally wide lamina, with the shape of its anterior/anterodorsal and ventral margins partially preserved in mediolateral view. Given the dimensions of the pterygoid wing of the quadrate, it is expected that the posterior part of the quadrate wing of the pterygoid widened dorsoventrally, although this is not preserved. The quadrate wing begins at the posterior end of the main body of the pterygoid, similar to other ornithischians (Norman et al., 2011; Boyd, 2014; Porro et al., 2015). In the ventral portion of the quadrate wing and in medial view, a brief peduncle-like process with a wide distal facet projects posteromedially, which is inferred to be the contact for the basiptyergoid process (forming the basal articulation, as in *Heterodontosaurus*; Norman et al., 2011).

The pterygoid flange is a long, rod-like process that is wider anteroposteriorly than mediolaterally and directed ventrolaterally. Its posterior edge is thickened compared to the anterior edge. The lengthening of the pterygoid flange and its triangular cross-section are proportionally similar to that in *Heterodontosaurus*. The thickened posterior edge of the pterygoid flange forms a slightly concave surface facing posterolaterally that functioned as the origin for the *m. pterygoideus dorsalis* (Holliday, 2009; *m. pterygoideus posterior* in

Heterodontosaurus, Norman et al., 2011). A bony callous on the anterolateral aspect of the base of the pterygoid flange represents part of the pterygoid-ectopterygoid butt joint, similar to its position in *Heterodontosaurus* (Norman et al., 2011); however, judging by the preservation of the ectopterygoid, this facet might be incomplete (see **Ectopterygoid**).

There is a triradiate medial rim at the main body of the pterygoid that reinforces the posteromedial edge of the pterygoid flange, the ventral edge of the quadrate wing, and the base of the anterior process of the pterygoid. As in *Heterodontosaurus* (Norman et al., 2011) this edge might correspond to the origin for **the m. pterygoideus ventralis** (Holliday, 2009; **m. pterygoideus posterior** in *Heterodontosaurus*: Norman et al., 2011). At the base of the pterygoid wing, this rim becomes prominent to form a ventromedially oriented crest with a ventral notch. Morphological homologies of the pterygoid with *Lesothosaurus* (Porro et al., 2015) indicate that this medial projection of the medial rim corresponds to the articulation surface for the opposing pterygoid, and its ventral notch may house a dorsal extension for the origin of **the m. pterygoideus ventralis** (Norman et al., 2011). The rim extends posteriorly to the peduncle that forms the basisphenoid-ptyerygoid contact. The rim continues on to the medial aspect of the pterygoid flange and the anterior process of the pterygoid, **delimiting** an anteromedially facing depression that may be an attachment site for **the m. pterygoideus anterior** as in *Heterodontosaurus* (Norman et al., 2011); however, its extension over the dorsal palate or the ectopterygoid cannot be confirmed. The medial face of the main body of the pterygoid, and the described medial crest, lack of any trace of a suture for the opposing pterygoid. These might have been bounded by connective tissue, as assumed in *Heterodontosaurus* (Norman et al., 2011), and the medial crest at the base of the pterygoid wing may be related to this attachment.

Ectopterygoid—Both ectopterygoids are preserved in disarticulation and complete. The left ectopterygoid was found in association with the left temporal/orbital region of MPEF-PV

3211-9 and the right ectopterygoid is associated with the right jugal and jaws of MPEF-PV 3211-10. The ectopterygoid is a curved bone formed by two halves that are oriented at 90° to each other and, based on their anatomy, firmly sutured with the maxilla-jugal laterally and the pterygoid medially. The posteroventral half of the left ectopterygoid is turned clockwise due to diagenetic processes, and the right element is covered by fractures but complete and undeformed (Fig. 11G–R). The morphology of this bone in *Heterodontosaurus* is only assumed (Norman et al., 2011), and is briefly described for *Echinodon becklesii* (Norman and Barrett, 2002; Sereno, 2012), in which it is medially exposed in specimen NHMUK OR 48210, but it can be compared with those of other small ornithischians.

The anterolateral half of the ectopterygoid is formed by a short base with a sub-triangular cross-section and rounded edges, and distally has an anteroposteriorly expanded wing and a depressed region facing mostly lateroventrally that houses a deep cavity. The convex depressed region forms a long and pit-like groove in the ectopterygoid that is blind at its medial end (preserved in the right ectopterygoid: Fig. 11O, Q). The expanded wing-like process contacts distally to the medial face of the jugal along its medial crest, and the pit-like blind groove faces laterally to the foramen piercing the jugal (see Jugal). The posteroventral edge of this wing forms the posteroventral boundary of the depressed region and closes posterolaterally the jugal-ectopterygoid articulation in its distal portion, while more medially this crest thickens first ventrally and then turns anteriorly and medially to form a robust anteroventral process. This thickened edge and the anteroventral process contact the posteriorly facing depressed region in the maxilla in a tight junction that envelopes this edge at most of the anterior aspect of this anterolateral half of the ectopterygoid (Fig. 4G–H, Fig. 11G). The overall shape and a similar laterally expanded half is shared with *Echinodon* (Norman and Barrett, 2002; Sereno, 2012).

The sharp dorsal, anterior, and ventral edges of the anterolateral half of the pterygoid are continuous with the posterolateral, medial, and ventrolateral edges of the posteroventral ectopterygoid. These sharp edges define three faces: a plane facing anterodorsally, an anteroposteriorly convex face that is anteromedially to medially oriented, and a dorsoventrally convex posterolateral face (Fig. 11). The concave medial face overlaps the pterygoid flange. The edges of the medially concave face are sharp, with the posterior edge more prominent and possibly homologous to the medial wing of the ectopterygoid described in *Hypsilophodon* (Galton, 1974). A laminar bone fragment with its anterior edge thickened ventrally was found in articulation with the right ectopterygoid in a butt joint. This laminar fragment is assumed to be a posterolateral fragment of the palatine that contacts the ectopterygoid (Fig. 11G–H).

Braincase

General Comments—Most of the bones in the braincase were found in articulation and associated with the left temporal region in MPEF-PV 3211-9. The basicranium preserves the complete parasphenoid, basisphenoid, and basioccipital, and other preserved bones include both prootics, both fused exoccipital-opisthotic complexes, the supraoccipital, and possible fragments of both laterosphenoids (Fig. 12). The orbitosphenoids of *Manidens* are missing or possibly did not ossify (as in *Hypsilophodon* and other dinosaur species; Galton, 1974; Paulina-Carabajal, 2015), as is probably the case with the ethmoidal elements also (sphenethmoid-mesethmoid): thus, their presence cannot be confirmed, as in *Heterodontosaurus* (Norman et al., 2011). The anterior half of the basicranium is deflected to the left, and the floor of the endocranial cavity has collapsed. In addition, the displacement of some features indicates that micro deformations occurred in the occiput. The contacts between the bones forming the base and walls of the neurocranium are difficult to recognize due to these being deeply fused but are inferred based on the surface morphology (Fig. 12).

Laterosphenoid—The left laterosphenoid was previously unknown for *Manidens* and here is described for the first time. It was found on the ventral aspect of the left frontal, disarticulated but near to its natural position (MPEF-PV 3211-11; Fig. 1E–F). The laterosphenoid is a laminar bone with a tapering anterodorsal end that curves laterally and widens forming the head of the laterosphenoid (postorbital process of the laterosphenoid), which contacts a small groove at the postorbital below the postorbital-frontal suture. The base of the head of the laterosphenoid extends **ventrally to form** a dorsoventrally oriented crest with a narrow anterior face on **its** lateral aspect. This crest, the laterosphenoid buttress or antotic crest (e.g., Holliday, 2009), may have been continuous with the medial crest of the postorbital. The sharp edge of this crest is inferred to be the attachment site for **the m. tensor periorbitae** (i.e., **m. levator bulbi**) (Holliday, 2009). The posterior face of this crest may have formed the ventral **bound of the m. pseudotemporalis superficialis** and the medial wall bounding the adductor chamber.

The lateral surface of the laterosphenoid is dorsoventrally concave, **and** the medial surface is flat and pierced by a small opening, possibly the foramen for the rostral middle cerebral vein (Fig. 7G–H). The dorsal edge of the laminar portion of the laterosphenoid is thin, possibly meeting the **crista cranii** of the frontal in a butt joint that reached the parietal (Fig. 7I). The posteroventral portion of the laterosphenoid is broken and the contact with the prootic is missing. A posterior-facing commissure is identified as the anterodorsal margin of the foramen for the **n. trigeminus** (CN. V). The overall anatomy of the laterosphenoid is more similar to that of *Hypsilophodon*, *Zephyrosaurus*, and *Orodromeus* (Galton, 1974; Sues, 1980; **Scheetz**, 1999) than to *Heterodontosaurus* (Norman et al., 2011, fig. 10).

Supraoccipital—This single bone contacts the prootic anteroventrally, the exoccipital-opisthotic complex lateroventrally, and the parietals anterodorsally (although these are disarticulated). The supraoccipital forms the dorsal margin of the foramen magnum, and roofs

the endocranial cavity posterodorsally. The participation of the supraoccipital in the dorsal margin of the foramen magnum is a plesiomorphic feature that *Manidens* shares with *Lesothosaurus* (Serenó, 1991; Porro et al., 2015), *Heterodontosaurus* (Norman et al., 2011), basally branching ornithomorphs (Galton, 1989; Norman et al., 2004b), stegosaurids (Gilmore, 1914), and protoceratopsids (Brown and Schlaikjer, 1940). In iguanodontians (Norman, 2004), hadrosaurids (Horner et al., 2004), and ceratopsids (Dodson et al., 2004), the exoccipitals contact each other dorsomedially, excluding the supraoccipital from the dorsal margin of the foramen magnum.

The supraoccipital thickens over the foramen magnum forming a lip-like dorsal margin that flares posteroventrally over the exoccipitals, a common feature among ornithischians (Fig. 12F). In occipital view, the supraoccipital is butterfly-shaped, with four wings: two directed dorsally and two ventrally. The median nuchal crest (supraoccipital knob) forms a dorsoventrally projecting crest with a small posteroventral prominence that marks the origin of the *m. transversospinalis capitis* (e.g., Snively and Russell, 2007). In posterior view, the right dorsal wing is preserved in its original position while the left one is fractured at its base and rotated over the supraoccipital knob. The dorsal wings of the supraoccipital underlie the posterolateral processes of the parietals in an overlapped articulation and are separated from each other by the nuchal crest, as in *Heterodontosaurus* (Norman et al., 2011), *Lesothosaurus* (Serenó, 1991), *Hypsilophodon* (Galton, 1974), and *Orodromeus* (Scheetz, 1999). The supraoccipital contacts the exoccipitals ventrally, and both wings of the opisthotic lateroventrally.

The ventral wings bear a slight ridge that courses lateroventrally from the supraoccipital knob; although its function is unclear, it might indicate the end of the overlapped articulation with the parietals. This slight ridge, which is obliquely oriented does not reach the lateralmost portion of the lateral wing, leaving a space between the supraoccipital and the dorsalmost

portion of the opisthotic. Based on new interpretations proposed by Norman et al. (2011) in *Heterodontosaurus*, the position of the post-temporal foramen is reinterpreted from being within the paroccipital process (Pol et al., 2011), to between the lateral end of the oblique ridge and the dorsalmost portion of the opisthotic, within the junction between the parietal-supraoccipital-opisthotic. The supraoccipital does not contact the laterosphenoids anteriorly as in *Orodromeus* (Scheetz, 1999), whereas its ventral wings do not project anteriorly above the prootic. Assuming that the occipital component of the parietal contacts the supraoccipital medially and the opisthotic wing ventrally, it can be conditionally stated that there is no contact between the squamosal and the supraoccipital.

Prootic—Both prootics are almost complete (they lack their dorsal edges, which seem to be eroded), although the dorsal portion of the right prootic is fractured and twisted. The prootic forms the lateral wall of the braincase and the anterior region of the otic capsule, contacting the laterosphenoid anteriorly, the parietal dorsally, the supraoccipital posterodorsally, the opisthotic posterolaterally and the basisphenoid ventromedially. Anterodorsally, the prootic forms the posteroventral margin of the CN. V foramen (which appears larger than it would have been in life due to fractures). The foramen for the facial nerve (CN. VII) is posteroventral to the trigeminal foramen on the right side of the skull, but is not preserved on the left side (Fig. 12C–D The foramina for CNs V and VII are separated by a smooth surface, similar to *Lesothosaurus*, but differing from *Thescelosaurus*, *Zephyrosaurus*, *Hypsilophodon*, and *Tenontosaurus*, which have foramina separated by a ridge (Galton, 1974; Sues, 1980; Boyd, 2015; Porro et al., 2015, Thomas, 2015)). Posteroventrally, the prootic contacts the opisthotic and together they form the otosphenoidal crest, which bounds medially a recess that houses the fenestra pseudorotunda and the jugular foramen (see **Opisthotic**).

In anterolateral view, the union between the external wall of the prootic with the anterior part of the otoccipital forms two broad and smooth ridges with two deep and concave fossae; one is above the most dorsal ridge, and the other between ridges, features that could possibly act as a reinforcement of the paroccipital processes against the strain of the nuchal musculature (Fig. 12 C–D). The dorsal concave fossa corresponds in position to the dorsal tympanic recess present in theropods (e.g., Witmer, 1997a). In medial view, an anteroposteriorly narrow and lateroventally oriented fossa is present in the prootic, which housed the floccular lobe. This feature is common in pterosaurs, theropods, and basally branching sauropodomorphs (Witmer et al., 2003; Bronzati et al., 2017; Paulina-Carabajal, 2015; Codorniu et al., 2016; Paulina-Carabajal and Filippi, 2018), and is also present and well developed in *Orodromeus* (Scheetz, 1999), *Zephyrosaurus* (Sues, 1980), *Hypsilophodon* (Galton, 1974), and reduced in *Tenontosaurus* (Thomas, 2015) and *Thescelosaurus* (Boyd, 2015).

Exoccipital–Opisthotic Complex / Otoccipital—The opisthotic is medially fused to the exoccipital. The opisthotic contacts the prootic and the squamosal anteriorly, the supraoccipital medially, and forms the posterior part of the otic capsule (Norman et al., 2011; Paulina-Carabajal, 2015). The paroccipital process is dorsoventrally high, relatively short laterally, and has rounded and thickened lateral margins (Pol et al., 2011). The paroccipital process is more prominent laterally, dorsoventrally higher, and less deflected ventrally than in *Heterodontosaurus* (Norman et al., 2011).

As previously mentioned, the overlapping opisthotic-squamosal articulation is preserved at the postquadratic process of the squamosal as the depressed surface with a step-like dorsal boundary (Fig. 8R, T, V). The squamosal-opisthotic articulation occupies the distal half of the paroccipital process anteriorly, with the contact extending obliquely from the distalmost to the dorsalmost portion of the process. In posterior view, the squamosal-opisthotic line starts at the

dorsal end of the thickened lateral margin of the paroccipital process and extends medially and dorsally, ending at the dorsalmost portion of the paroccipital process (following Norman et al., 2011). A wide foramen opens posteriorly within each paroccipital process and its path can be traced anteroventrally to open within the temporal space into the dorsal tympanic recess (see **Prootic**). The posterior exit for the left foramen is subcircular in shape, whereas the right opening is fusiform; such asymmetry is assumed to be a natural (possibly pathologic) deformation of the individual and not due to post-burial deformation (Fig. 12F). These openings were previously related to the post-temporal foramen for *Manidens*, *Heterodontosaurus*, and other **early** forms (Scheetz, 1999; Norman et al., 2004b; Barrett and Han, 2009; Pol et al., 2011; Norman, 2020). However, a similarly positioned passage, the cranioquadrate passage, has been identified as a communication between the occipital region and the middle ear in crocodyliforms and extant crocodiles (Montefeltro et al., 2016; Kuzmin et al., 2021, and references therein). In extant crocodiles, this canal acts as a passage for the hyomandibular branch of the facial nerve (CN VII_{hy}) and the stapedia artery and vein (e.g., Porter et al., 2016; Kuzmin et al., 2021), or the lateral head vein in squamates (e.g., Porter and Witmer, 2016). Similarly, Norman et al. (2011) reinterpreted the post-temporal foramen as a remnant of the cranioquadrate passage in *Heterodontosaurus*, a bony canal for the main trunk of the facial nerve, the orbitotemporal artery, and the lateral head vein. Although in some cases the foramen is reduced, the post-temporal foramen in archosauriforms, archosaurs, and dinosaurs is usually enclosed by the supraorbital, parietal and the opisthotic, in some cases involving the squamosal and/or the exoccipitals (Chapelle and Choiniere, 2018; Sookias et al., 2020; Kuzmin et al., 2021). The post-temporal fenestra in *Manidens* identified by Pol et al. (2011) is here reinterpreted as the cranioquadrate passage given its opening to the dorsal tympanic recess and its exit through the paroccipital process at the occiput (Norman et al., 2011). The post-temporal fenestra in *Manidens* is hypothetically located in the parietal-

supraoccipital-opisthotic contact, as in *Heterodontosaurus* (Norman et al., 2011). Given that remnants of the post-temporal fenestra are identified in other ornithischians as a subcircular opening near the dorsal margin of the paroccipital process (e.g., Galton, 1974; Boyd, 2014; Thomas, 2015; Norman, 2020), whose posterior exit is similar in location to the cranioquadrate passage for *Manidens* we identify here, other comparisons are hard to address and more investigations are needed.

Other small openings for vascular canals can be visualized on the posterior aspect of the paroccipital processes, although these open into the bone instead of crossing through it. In posterior view, the ventrolateral edge of the paroccipital process bears a small, pit-like cavity, possibly a relict pneumatic recess of the occipital region in *Manidens* shared with *Heterodontosaurus* (e.g., Witmer, 1997a; Norman et al., 2011). The lateral margin of the paroccipital process is thickened at its articulation with the squamosal and thins ventromedially into a lateroventrally oriented blade-like distal end. Medially, at the base of the paroccipital process, the ventral edge thickens anteromedially to form the **crista tuberalis** (Fig. 12B), which reaches the basal tubera of the basioccipital. The anterior aspect of the **crista tuberalis** bounds anteriorly a deep recess that excavates the opisthotic and forms a long fossa that extends mediolaterally and faces ventrally, here interpreted as the caudal tympanic recess (Fig. 12B). It is uncommon to identify a caudal tympanic recess in an ornithischian, however, this feature is similar in position to that in *Tyrannosaurus* and other **coelurosaurs** (Witmer, 1997a; Witmer and Ridgely, 2009), but rather less developed than in *Sinraptor* and *Llukalkan* among non-coelurosaurian theropods (Paulina-Carabajal and Currie, 2012; Gianechini et al., 2021). **Anterolateral** to the caudal tympanic recess and at the lateralmost portion of the **crista tuberalis**, a deep, rounded pit with sharp edges opens lateroventrally, possibly corresponding to an additional shallow pneumatic recess (Fig. 12B, ?pn). The opisthotic contacts the posterior wing of the prootic lateroventrally and forms the

otosphenoidal crest, although the suture between the two is unclear. The otosphenoidal crest laterally bounds an ellipsoidal fossa, which is excavated in the lateroventral side of the basisphenoid that might be related to the paratympanic system (**Basisphenoid**; Fig. 12B; Witmer, 1997a; Duffeau, 2011; Witmer and Ridgely, 2009; Paulina-Carabajal, 2015).

Both exoccipitals are preserved (fused with the opisthotics anterolaterally). They contact the supraoccipital dorsally and the basioccipital ventromedially, and form the lateral margins of the foramen magnum. Although most of its sutures are difficult to recognize, these are tentatively identified in this description based on the external morphology of the occiput and interpretations of this region in *Heterodontosaurus* (Norman et al., 2011, fig. 14). The thickening of the supraoccipital along the dorsal margin of the foramen magnum forms a prominence over the exoccipital-supraoccipital contact. From their contact with the supraoccipital, the exoccipitals extend ventrally, surrounding laterally the basioccipital and almost reaching the basal tubera and the **crista tuberalis**. Both exoccipitals are excluded from the occipital condyle, as in *Heterodontosaurus* (Norman et al., 2011), which differs from the primitive condition present in *Lesothosaurus* (Serenó, 1991; Porro et al., 2015), *Gasparinisaura* (Coria and Salgado, 1996; MUCPv-208, MGB **pers obs**), *Zephyrosaurus* (Sues, 1980), *Hypsilophodon* (Galton, 1974), *Jeholosaurus* (Barrett and Han, 2009), and other derived taxa, in which the exoccipital forms part of the occipital condyle. The exoccipital in *Manidens* presents a broad, robust kidney-shaped crest with a rounded edge parallel to the lateroventral side of the occipital condyle, with smooth periosteal bone between the occipital condyle and the exoccipital crest. The smooth periosteal bone is similar to that on articular surfaces, indicating that these crests of the exoccipitals might function as lateral limits of the joint with the atlas, or as accessory joints with the first cervical vertebra.

There are three foramina within a shallow fossa lateral to the occipital condyle, corresponding to the passages for the accessory (XI) and hypoglossal (XII) nerves (Fig. 12F),

as in *Heterodontosaurus* (Norman et al., 2011). The fossa enclosing the exit foramina has two well-marked notches on its margin, a ventral notch at the junction between the **crista tuberalis** and the basal tubera, and another notch between the basal tubera and the robust crest of the exoccipital. The position and posterior orientation of the external foramina below the occipital condyle is assumed to be related to postburial deformation.

Basioccipital—The basioccipital is complete, and preserved in articulation with the exoccipitals dorsally and the basisphenoid anteriorly. The basioccipital forms the occipital condyle, and the dorsal surface of the basioccipital contributes to the floor of the endocranial cavity. The lateromedial width of the occipital condyle (4.5 mm) is more than a half the width of the foramen magnum (7.98 mm). The occipital condyle is dorsally concave having a U-shaped appearance in occipital view, although its shape is more elongated laterally than dorsoventrally, contrary to the strongly dorsoventrally tall and lateromedially narrow condyle in *Heterodontosaurus* (Norman et al., 2011). In lateral view, the occipital condyle is low and projects from the basicranium, having a poorly developed neck with no constriction. Its articular facet is poorly differentiated from the base of the condyle. The low prominence of the condyle **has** not resulted from the deformation of the occipital region, as indicated by the excellent preservation of the inner spongy bone.

In posterior view, the exoccipital-basioccipital suture runs between the condyle and the superficial crest of the exoccipitals, turns ventrally laterally between these crests and the basal tubera, ending at the basal tubera-**crista tuberalis** contact. The basal tubera are ventrally directed below the occipital condyle; they are squared-shaped and short in length, lateromedially wide, and well separated from each other (Pol et al., 2011). There is a roughened surface at the distalmost portion of the tubera for the insertion of cervical muscles (Baumel and Witmer, 1993; Snively and Russell, 2007). The basituberal lamina –joining transversely the basal tubera– is robust and short, and bounds posteriorly the basisphenoid

recess (see **Basisphenoid**). The **position of the** basisphenoid-basioccipital contact indicates that the basal tubera are completely formed by the basioccipital.

Basisphenoid–Parasphenoid Complex—The basisphenoid is fractured in two halves (with the anterior portion displaced to the right), articulates with the laterosphenoid and the prootic dorsally, the pterygoid anteroventrally, the basioccipital posteriorly, and the parasphenoid anteriorly. The parasphenoid-basisphenoid are indistinguishably fused and they contact each other **to bind** the pituitary fossa, which is wide and dorsoventrally deep. The robust rims forming blunt, low pillars at the posterior edge of the pituitary fossa may indicate a butt-like contact between the orbitosphenoids and the basisphenoid-parasphenoid complex. The basisphenoid was previously described as an anteroposteriorly short and lateromedially wide element (Pol et al., 2011), although its anatomy - evidenced by the reconstructed basicranium - is more complex and more similar to *Heterodontosaurus* than previously thought (Fig. 12). The basisphenoid is ventrally excavated by a well-developed and deep basisphenoidal recess that contrasts with the shallow groove present in *Heterodontosaurus* (Norman et al., 2011), *Lesothosaurus* (Porro et al., 2015), *Hypsilophodon* (Galton, 1974), and other ornithischians (e.g., Witmer, 1997a). The basisphenoidal recess deepens dorsally in the main body of the basisphenoid. It is **delimited** by a transverse crest communicating **with** the posterior portion of both preotic pendants anteriorly, by the basituberal lamina posteriorly, and at the sides by two longitudinal laminae from the transversal crest to the base of the basal tubera. The lateral limits of the basisphenoidal recess also bound the medial wall of a lateroventrally oriented region that encloses an elliptical, shallow, and anteriorly deepening fossa in its anterior half and several openings in its posterior half, enclosed laterodorsally by the otosphenoidal crest. Given its position at the side of the basisphenoid, the former recess might be related to the paratympanic system, possibly a posterior diverticulum from the rostral tympanic recess; however, it is more anteriorly located than expected for a subotic

recess as recognized in theropod dinosaurs (Witmer, 1997a). The posterior half of this region encloses at least three openings. **The posteriorly placed opening is interpreted as a passage for the jugular vein, or jugular opening** (forming a commissure in the posterolateral edge of the recess) and the two anterior openings open to a wide space considered as the fenestra pseudorotunda, formed by the fenestra ovalis anteriorly and the foramen metoticum posteriorly, separated by the **crista interfenestralis** (Fig. 12B). The paths leading from these foramina are hard to trace due to damage to the overall region, but almost certainly include communication with the cochlea, and courses of CNs IX-XI, and the internal jugular vein.

In lateral view, the lateroventral margin of the basicranium forms an alar crest as a continuation of the otosphenoidal crest (that bounds the rostral tympanic recess laterally). There is a prominent and lateroventrally oriented flange at the posterior aspect of this alar crest posteriorly (noticeable in lateral view), and projects anteriorly to reach the base of the basipterygoid processes, delimiting a deep recess ventral to the pituitary fossa. Due to its location in the basisphenoid and its relation to the pituitary fossa, this crest is identified here as the "basisphenoidal flange" present in *Heterodontosaurus* (Norman et al., 2011) and part of the preotic pendant of saurischians (**ala basisphenoidalis**: Chure and Madsen, 1998; Rauhut, 2007; **crista prootica**: Chure and Madsen 1998; Madsen and Welles, 2000; Brochu, 2003). The prominent flanges at the sides of the basisphenoid in lateral view were previously misinterpreted as the basipterygoid process (Pol et al., 2011), and are now considered the posterior portion of the preotic pendant, which becomes ventrolaterally prominent forming a triangular-shaped alar crest. Thus, the basisphenoidal flanges are an alar projection of the preotic pendant that posteriorly contacts the otosphenoidal crest (Fig. 12B). The preotic pendant (and its ventrolaterally prominent crest) is wide and offers an insertion for the **m. levator pterygoideus** (Holliday, 2009) and laterally bounds an elongated recess facing ventrally, interpreted here as the rostral (lateral) tympanic recess, located below the foramen

of the internal carotid artery that enters ventral to the pituitary fossa (Witmer, 1997a; Paulina-Carabajal, 2015). The prominent posterior flanges of the preotic pendant are supported medially by a transversely oriented robust crest, forming the anterior limit of the possible posterior diverticulum of the rostral tympanic recesses and the basisphenoidal recess, as well as the posterior end of the main rostral tympanic recess (which deepens posteriorly within the anterior portion of the basisphenoid and dorsally to this crest, forming a multi-lobed space). A narrow basisphenoidal septum crosses from the transverse crest to the base of the basiptyergoid processes, dividing the rostral tympanic recesses and the ventral openings of the internal carotid arteries. This ventral basisphenoidal septum is likely a laminar extension of the anterior projection of the basisphenoid that houses the pituitary fossa and contacts the parasphenoid.

In ventral view, the basiptyergoid processes are positioned posteroventral to the cultriform process and anterior to the pituitary fossa, and are reached posteriorly by the preotic pendant (Fig. 12). They project anterolaterally, and are formed by dorsoventrally narrow and anteroposteriorly wide pedicels with the articular face for the pterygoid facing anteriorly. These basiptyergoid processes contact posteriorly the medial basisphenoid septum to form a triradiate structure, and bound the posterior limit of a small and blind pit, here identified as a remnant of the subsellar recess, topologically resembling the same structure in other archosaurs (e.g., Witmer 1997a). The cultriform process is 16.6 mm long from the pituitary fossa to its anterior end (proportionally similar to that of *Heterodontosaurus*; Norman et al., 2011), which is completely preserved but slightly rotated and displaced from its base. The cultriform process is dorsoventrally deep and mediolaterally compressed, and bears a narrow, sagittal groove dorsally, resembling *Heterodontosaurus*, *Lesothosaurus*, and ornithomimids (Norman et al., 2011; Boyd, 2014; Porro et al., 2015). In life, this groove may have supported the cartilaginous interorbital septum (Norman et al., 2004). The presence of expanded deep

flanges or “basisphenoid flanges” were described as an autapomorphic feature of *Heterodontosaurus* (Norman et al., 2011, page 26, fig. 10, bsf), which curve medially beneath the trigeminal area on the sidewall of the braincase, project anteriorly to the cultriform process, merge into the base of the basiptyergoid processes, and limit the basisphenoidal recess. However, new evidence from *Manidens*, homologies with *Heterodontosaurus*, and shared with basally branching theropods and other archosaurs (Raath, 1977; Wilmer, 1990, 1997a; Tykoski, 1998; Dufeu, 2011; Paulina-Carabajal et al., 2015), indicate that in *Heterodontosaurus* (*sensu* Norman et al., 2011): 1, the shallow sulcus in the ventral aspect of the basisphenoid corresponds to a reduced basisphenoid recess (strikingly large in *Manidens*); 2, the recess surrounded by the “basisphenoidal flanges” below the region of the pituitary fossa corresponds to the rostral tympanic recess instead of the basisphenoidal recess (as in *Manidens*); and 3, the “basisphenoidal flanges” that contact the pedicels of the basiptyergoid processes anteriorly and the trigeminal region posteriorly correspond to the preotic pendant identified in saurischians and are not autapomorphic of *Heterodontosaurus*, due to its presence in *Manidens* as well (Witmer, 1997a; Paulina-Carabajal, 2015). Although these basisphenoidal flanges or preotic pendants are shared between *Manidens* and *Heterodontosaurus*, they do not deviate posterodorsally to reach the trigeminal area in *Manidens* (instead these contact the otosphenoidal crest), whereas these reach across the trigeminal area in *Heterodontosaurus* (Norman et al., 2011). The presence and development of the basisphenoidal recess and the presence of a remnant of the subsellar recess might indicate that *Manidens* had a well-developed pharyngeal pneumatic system (Witmer, 1997a), which is observed in theropods (e.g., Sampson and Witmer, 2007; Witmer and Ridgely, 2009) and other archosaurs (Witmer, 1997a; Witmer and Ridgely, 2008; Dufeu, 2011; *Caiman latirostris*, MACN-V-1420, MGB *pers obs*). In addition, the identification and development of dorsal, rostral, and caudal tympanic recesses in *Manidens* is particularly interesting in a

phylogenetic context and in relation to the development of the middle ear, due to its uncommon presence within Heterodontosauridae (although a middle ear recess is mentioned for *Heterodontosaurus*: Norman et al., 2011) and Ornithischia, in which there is an evolutionary trend to reduce and lose pneumaticity in the skull (Witmer 1997a).

Lower Jaw

General Comments—The overall description of the lower jaw does not differ substantially from that in Pol et al. (2011). The lower jaw is dorsoventrally tall and lateromedially expanded when compared to other heterodontosaurids (Fig. 13). The dorsal end of the coronoid eminence is located slightly above the tooth row, being an intermediate state between that observed in *Tianyulong* and *Heterodontosaurus* (Zheng et al., 2009; Norman et al., 2011; Sereno, 2012). Similarly, the jaw joint is ventrally offset relative to the tooth row, more so than in *Tianyulong* and *Lesothosaurus*, but not as displaced as in *Heterodontosaurus* (Zheng et al., 2009; Norman et al., 2011; Sereno, 2012; Porro et al., 2015). The tooth row is marginal instead of medially inset, and the apex of the caniniform tooth orients dorsolaterally to the sagittal plane of the jaw, contrasting with the vertically directed caniniform tooth of *Heterodontosaurus* (Norman et al., 2011). The mandibular fenestra is absent in *Manidens*, although a small foramen pierced the lateral wall of the surangular near the dentary-surangular-angular contact. The dentary is laterally concave in dorsal view, with the curvature of the dorsal margin more pronounced than the ventral margin. In lateral view, the dorsal margin of the jaw posterior to the coronoid eminence does not drop ventrally to the jaw joint in a conspicuous way as in *Heterodontosaurus* (forming a dorsally convex outline). Instead, the coronoid eminence and the jaw joint are joined by a nearly straight dorsal margin of the surangular forming the dorsal margin of the posterior jaw

(see [Surangular](#)). The lateral fossa of the lower jaw is rather shallow with less prominent boundaries compared to *Heterodontosaurus*.

Dentary—Both dentaries are preserved. The anterior third of both elements is transversely fractured and displaced dorsally relative to the rest of the jaw. The most anterior point of the right dentary corresponds to the base of the caniniform and part of the mandibular symphysis (although fractured), while the left dentary is preserved from the first postcaniniform tooth and only preserves a portion of the caniniform root within the dentary (Becerra et al., 2020). Consequently, most of the mandibular symphysis and the pre-dentary contact are unknown (Pol et al., 2011; Becerra et al., 2020). Both dentaries, despite being partially covered by the right maxilla and jugal, are almost complete (Fig. 14). As Pol et al. (2011) and Sereno (2012) detail, the dentary of *Manidens* is a dorsoventrally expanded element, which is similar to that of *Pegomastax* among heterodontosaurids (Sereno, 2012). The dorsoventral height of the right dentary of *Manidens* in its middle portion corresponds to 11.55 mm (at the D8 tooth position: Becerra et al., 2020), being 33.5% of its length (34.47 mm, from the anterior base of the caniniform to the most posterior portion of the coronoid process of the dentary: not the same measurement taken by Becerra et al., 2020). This condition contrasts with the slender dentaries of other heterodontosaurids (Thulborn, 1974; Norman and Barrett, 2002; Norman et al., 2004b; Zheng et al., 2009; Butler et al., 2010; Pol et al., 2011; Sereno, 2012), being greater than the 30% measured in *Pegomastax* (Sereno, 2012), 25% in *Echinodon* (NHMUK OR 48215b, measured from Sereno, 2012, fig. 15), 19% in *Tianyulong* (IVPP V17090; photographic material), 24% in *Heterodontosaurus* (SAM-PK-K1332; Norman et al., 2011, Appendix 6), and 24% in *Lycorhinus* (NHMUK A100; Sereno, 2012).

The right dentary bears 11 teeth, whereas the left has 10 tooth positions including the caniniform tooth (Becerra et al., 2020). A low tooth count is common in Heterodontosauridae:

11 teeth occur in the lower jaws of *Pegomastax* (Sereno, 2012) and *Echinodon* (NHMUK OR 48214, 48215a, 48215b; Norman and Barrett, 2002; Sereno, 2012); 10 in *Fruitadens* (Butler et al., 2012) and *Tianyulong* (Sereno, 2012); 11-12 in *Heterodontosaurus* (Norman et al., 2011; Porro et al., 2011); 12 in *Lycorhinus* (Hopson, 1975, 1980); and 14 in *Abrictosaurus* (Thulborn, 1974). The alveolar margin in the dentary is dorsoventrally level in MPEF-PV 3211, more similar to *Fruitadens* (Butler et al., 2012) and *Tianyulong* (Zheng et al., 2009), than to the posteriorly bowed dorsally alveolar rows of *Heterodontosaurus* (Norman et al., 2011) and *Abrictosaurus* (Sereno, 2012). However, although the alveolar row is mostly straight in the largest specimen of *Manidens* (MPEF-PV 3808), the last two or three alveoli are positioned on the base of the coronoid eminence of the dentary and result in a dorsally curved the alveolar margin posteriorly (Becerra et al., 2020). The dentary is slightly laterally concave in dorsal view, with the alveolar row being straight and slightly laterally deflected posteriorly in larger individuals (Fig. 14A–B, G–H; Becerra et al., 2020). The tooth row lacks a ventral ridge parallel to the alveolar margin to mark the cheek emargination (Fig. 14C, E), being more similar in this respect to *Fruitadens* and *Echinodon* than to other heterodontosaurids (Norman and Barrett, 2002; Sereno, 2012), and similar to *Lesothosaurus* and *Scutellosaurus* among early ornithischians (Colbert, 1981; Sereno, 1991; Zheng et al., 2009; Butler et al., 2012; Sereno, 2012; Porro et al., 2015). Due to the difference in medial curvature between the dorsal and ventral margins of the dentary, the tooth row is slightly inset medially relative to the lateral aspect of the bone, however a true medial inset of the dentary tooth row is absent. The Meckelian canal has a wide opening posteriorly to the well-developed adductor fossa of the mandible; anteriorly, it tapers and begins to branch, being composed of various branches directed anteriorly (following the axis of the dentary) from tooth position D6 onwards, similar to *Heterodontosaurus* (Norman et al., 2011).

There is a large anterior dentary foramen on the lateral aspect of the dorsal half of the dentary, below D4. The anterior dentary foramen leads posteroventrally to reach the Meckelian canal, as is common in Ornithischia and shared with *Heterodontosaurus*, although the opening in the latter is positioned in the ventral half of the dentary (Norman et al., 2011). Anterior to this foramen, additional neurovascular foramina are aligned parallel to the tooth row and below a slight rim or ridge (as seen in the right dentary), which are fewer in number and smaller in size than those preserved in the maxillae of *Manidens* (see [Maxilla](#)). The presence of neurovascular foramina is associated with the presence of at least a soft-tissue cheek, which thought to have been common in Ornithischia ([Galton, 1973a](#); Morhardt, 2009; Sereno, 2012). However, the lack of a well-developed medial insertion of the tooth row indicates that an oral recess lateral to the dentition was [comparatively](#) underdeveloped, potentially indicating reduced intraoral food processing in *Manidens*. Similar conclusions were made based on the absence of extensively developed wear facets along the tooth row and the presence of polished enamel on the non-functional face of the [tooth crowns](#) (Becerra et al., 2018, 2020). The presence of alveolar foramina was confirmed for the maxillary replacement teeth of MPEF-PV 3809 and MPEF-PV 3211; in contrast, although [11](#) replacement teeth in different stages of development were identified in both dentaries (Becerra et al., 2020), no alveolar foramina were identified opening [into](#) the buccal cavity, as in *Fruitadens* (Butler et al., 2012).

Posterior to the last preserved tooth, the dentary rises posterodorsally to form, along with the coronoid medially, the anterior half of the coronoid eminence; the surangular forms the posterior half, as is common in Ornithischia (e.g., Norman et al., 2004a). The anterior contribution to the coronoid eminence by the dentary forms a finger-like process and is not basally constricted (contrary to *Echinodon*; Sereno, 2012), is complete but basally fractured and rotated slightly in the right dentary, and dorsally incomplete but preserved in a natural

position in the left dentary. The maximum height of the dentary at the coronoid region is 15.72 mm in the right dentary and 14.78 mm in the left. In both cases, these measurements are slightly higher than the dorsoventral height of the dentary at the middle region (11.75 mm), being 25% higher than the jaw at its middle point (instead of 160%; Pol et al., 2011) and is only slightly higher than the tallest crowns of the tooth row. In lateral view, the axis of the coronoid process of dentary orients at 44° with respect to the axis of the left dentary, while around 67° in the right one, the latter value being higher due to its basal fracture and displacement (Fig. 14B, G). An angle of 45° is also measured on the larger specimen of *Manidens* MPEF-PV 3808. This angle of the coronoid process is close to 45° in *Echinodon*, *Heterodontosaurus*, and *Pegomastax* (Serenio, 2012), an angle that is greater than the 30° of *Lesothosaurus* (Serenio, 1991). The coronoid process of the dentary does not extend as far dorsally and posteriorly as the coronoid, leaving a space between the dentary and the surangular, and exposing the coronoid-surangular articulation in lateral view. This feature contrasts with *Heterodontosaurus*, in which a posterior projection of the coronoid process of the dentary reaches the surangular dorsally and covers the coronoid-surangular contact in lateral view (Norman et al., 2011). On its lateral face and towards its posterodorsal margin, the periosteal surface of the coronoid process of the dentary in MPEF-PV 3211 and MPEF-PV 3808 (Fig. 14I) is covered by rugosities and oblique striations, resembling the condition of *Heterodontosaurus* (Norman et al., 2011), *Dysalotosaurus* (MGB, pers obs), and other ornithischians. This region is assumed to be the insertion for the m. adductor mandibulae externus medialis on its dorsal and lateral face, and for the m. pseudotemporalis superficialis on its medial aspect along the anterior boundary of the medial mandibular fossa, which continues along the splenial.

The posteroventral region of the dentary features a ventral process and a wide notch that articulates with the remaining postdentary bones. In lateral view, the medial portion of the

posterior margin of the dentary overlaps the anterior margin of the surangular to the base of the coronoid process; anteriorly, the dentary envelopes both sides of the surangular, which then deviates posteriorly and loses contact with the dentary. The anterior half of the angular is incomplete in both mandibles, but it is assumed that the anterior angular is laterally overlapped by the dentary. The medial face of the posteroventral process of the dentary contacts the splenial, a contact that extends anteriorly to the posterior opening of the Meckelian canal medially. The articulated dentary-splenial complex forms a deep groove that cups the ventral portion of the prearticular. The dentary articulates medially with the coronoid in an overlapping contact from the D6 tooth position; the coronoid medially overlaps the coronoid process of the dentary (Fig. 14B, H). **The laterally depressed postdentary region forms a shallow external mandibular fossa, with its anterior and ventral boundaries delimited by the posterior portion of the dentary and its posteroventral process respectively.**

Manidens is unique among heterodontosaurids (with complete lower jaw preserved) in lacking a mandibular fenestra in the vertex formed between the coronoid eminence and the posterior dentary process (Pol et al., 2011). The absence of a mandibular fenestra contrasts with *Heterodontosaurus* and *Tianyulong* (Zheng et al., 2009; Norman et al., 2011), and has been defined as an autapomorphic character of the species. The use of computed microtomography **confirms** the absence of this feature: the surangular articulates with the dentary along its entire posterior margin, and although the articulation of the angular with the dentary is not preserved, several fragments were identified and associated with the angular near its articulation region with the dentary. Thus, the dentary-surangular-angular suture line is completely closed (Fig. 13).

Coronoid—Both coronoids are preserved and seemingly complete, although due to their fusion with the dentaries these can only be partially rendered from CT data. The coronoid in *Manidens* is composed of three portions: a thin anterior process, a ventral projection that is

short and lobe-like, and a posterodorsal portion forming part of the coronoid eminence (Fig. 15A, C) that is intermediate in morphology between the ornithopod *Thescelosaurus* and the early ornithischians *Heterodontosaurus*, *Lycorhinus*, and *Lesothosaurus* (Sereno, 1991; Norman et al., 2011; Boyd, 2015; Porro et al., 2015). Most of the coronoid articulates with the medial aspect of the dentary and forms the medial limit of the alveoli for the lower dentition, reaching at least to the D6 tooth position and possibly further anteriorly (Fig. 15A, C). At the coronoid eminence, the coronoid divides into the ventral lobe and the posterodorsal portion that contacts the coronoid process medially. The coronoid does not contact the splenial ventrally, whereas exists a coronoid-splenial contact in *Heterodontosaurus*, *Lesothosaurus* and other ornithischians (e.g., Norman et al., 2011, Porro et al., 2015; Boyd, 2015). The posterodorsal projection of the coronoid extends more dorsally than the coronoid process of the dentary, and forms a posteriorly oriented alar process that extends further posteriorly than the dentary-surangular contact, and over the dorsal margin of the surangular. Instead of being obscured by the dentary in lateral view, the coronoid is visible both dorsally and posteriorly to the coronoid process of the dentary (Fig. 15B, D). This posterior alar projection of the coronoid is absent in *Heterodontosaurus* and *Lycorhinus* (Norman et al., 2011; Sereno, 2012), *Lesothosaurus* (Porro et al., 2015) and other early ornithischians, and is considered a unique feature of *Manidens*. The distal end of the posterodorsal portion of the coronoid and its posterior alar process limit dorsomedially a concave and anteroposteriorly oriented depression, which is confluent with a longitudinal depression along the dorsal margin of the surangular, forming a common depression that turns from dorsomedially to dorsally oriented in anteroposterior direction. In addition, the alar process of the coronoid forms laterally a sharp division between the former depression and the sulcus formed laterally by the coronoid-surangular-dentary. The dorsal aspect of the coronoid at the eminence bears a porous and striated periosteum. The development the sulcus along the coronoid-surangular-dentary

articulation and the rugose periosteum indicate that this area was an important insertion region for the jaw musculature, and that the posterior alar process of the coronoid might function as a structural boundary between two muscular groups: the m. *adductor mandibulae externus medialis* laterally, and the m. *adductor mandibulae externus profundus* medially. The posterior margin of the coronoid and part of its ventral process forms part of the anterodorsal limit of the medial adductor mandibular fossa.

Surangular—Both surangulars are preserved and damaged: however, the complete anatomy of the bone can be described. The right surangular is complete from its contact with the dentary to the constriction before reaching the articular and is posteriorly incomplete, while the left surangular is complete posteriorly but its mid-dorsal section is fragmented and incomplete (Fig. 15). The surangular is formed by a main body at the glenoid region, from which radiates a finger-like and robust anterodorsal portion (instead of “anterodorsal process” as termed for *Heterodontosaurus*; Norman et al., 2011) and a sheet-like anteroventral lamina, forming a dorsally thickened laminar bone that resembles, overall the anatomy of the surangular in *Heterodontosaurus* (Norman et al., 2011; Sereno, 2012). The anterior margin of the surangular medially overlaps the posterior margin of the dentary to the base of the coronoid process, at which point these bones separate to form the aforementioned sulcus at the dentary-coronoid-surangular articulation (Fig. 15). The overlapped dentary-surangular contact is continuous instead of interrupted by the presence of the anterior surangular foramen, a feature shared with *Heterodontosaurus* (contra Norman et al., 2011; following Sereno, 2012). Although the surangular forms part of the dorsal margin of the posterior lower jaw, the dentary and the coronoid project further dorsally than the surangular. Anterodorsally, the surangular contacts the posterodorsal projection and alar process of the coronoid. Anteriorly, the ventral margin of the surangular contacts the dorsal margin of the angular in a butt joint; posteriorly, the angular overlaps the surangular at the region where it expands

dorsoventrally to reach the articular. The surangular-angular suture forms a convex line upwards in lateral view. The surangular contacts the prearticular medially and laterally to form a cup-like structure that receives the narrowed anterior process of the articular and the posteriormost portion of the angular into a complex contact. At this point, the surangular forms a butt joint laterally with the dorsal edge of the prearticular and an overlapped articulation with the medial aspect of the prearticular. Posteriorly, the surangular embraces anterodorsally the anterior process of the articular. Unlike *Heterodontosaurus*, the posteromedial extension of the surangular only ventrally supports the articular near the glenoid and does not extend posteriorly to the retroarticular region (Norman et al., 2011).

The finger-like dorsal bar of the surangular is wider lateromedially than dorsoventrally, and bears a dorsomedially oriented concave face as a continuation of a similar structure formed by the alar process of the coronoid. This region is the insertion for the m. **adductor mandibulae externus medialis**. Below this dorsal bar, the surangular is pierced by an elliptical foramen that opens **into** the adductor fossa medially and is limited ventrally by a laterally thickened crest that runs parallel to the dorsal margin, forming a fusiform and posteriorly narrowing fossa that surrounds this foramen. This region is assumed to comprise the insertion for the m. **adductor mandibulae externus superficialis** (see **Discussion**). A surangular foramen (or anterior surangular foramen) is shared with *Lesothosaurus* and *Heterodontosaurus* among **early** ornithischians, and is present among **neornithischians** as *Changechunsaurus*, *Gasparinisaura*, *Thescelosaurus*, *Hypsilophodon*, *Jeholosaurus*, *Orodromeus*, the **basally branching** ceratopsian *Yinlong*, and most **basally branching** iguanodontians (Galton, 1974; Coria and Salgado, 1996; Scheetz, 1999; Norman, 2004; Xu et al., 2006; Barrett and Han, 2009; Jin et al., 2010; Norman et al., 2011; Boyd, 2015; Porro et al., 2015; Han et al., 2016). The features described in *Heterodontosaurus* as “dorsal and ventral surangular rami” (Norman et al., 2011) are recognized in *Manidens* as thickened dorsal and laminar ventral

portions of the surangular (following Sereno, 2012), while in *Tianyulong* the surangular is a laminar bone without a distinctive dorsal thickening, and also lacks a surangular foramen (Zheng et al., 2009; Norman et al., 2011: fig. 19, sfor). *Heterodontosaurus* and *Manidens* differ in the shape of the surangular foramen (slightly rounded instead of elongated) and that the ventral region of the surangular becomes shallow anteriorly and does not reach the dentary-surangular suture in the latter.

Near the dentary-surangular-angular suture there is a small foramen that is entirely delimited by the surangular (Fig. 13, 15). This opening is located near the region where the external mandibular fenestra is expected to be in archosaurs. As originally stated by Pol et al. (2011), the external mandibular fenestra is evidently closed in *Manidens* (see Dentary), however the homologies between this anteriorly placed surangular foramen and the former are not clear, and new fossil remains may help to shed light on this matter. The lateral aspects of the surangular and angular form a shallow external mandibular fossa, limited posterodorsally by the ventral portion of the surangular, and ventrally by the laterally rounded prearticular. The dorsal margin of the surangular gradually extends ventrally to the glenoid instead forming the dorsally convex margin seen in *Lesothosaurus* and *Hypsilophodon* or dropping sharply downwards posteriorly as in *Heterodontosaurus* (Norman et al., 2011). The surangular features a posterior foramen near its contact with the articular and anterior to the glenoid, but its path cannot be traced due to poor preservation (Fig. 15B, D). This feature is shared with *Heterodontosaurus* and is common in small-sized ornithischians such as *Gasparinisaura* (MUCPv-208, MGB pers obs.), *Hypsilophodon* (Galton, 1974), and *Thescelosaurus* (Boyd, 2015), among others (e.g., Norman et al., 2004b). A second opening nearby and confluent with the posterior surangular foramen is present in *Manidens*, and although its identification as a true foramen is doubtful, a similar feature is present in *Thescelosaurus* and corresponds to a variation of the posterior surangular foramen (Boyd,

2015). The posterior surangular foramen is excluded from the fossa of the anterior foramen in *Manidens* while in *Heterodontosaurus* it is included at the posterior end of this fossa (Norman et al., 2011). The medial or adductor mandibular fossa is limited dorsally by a medial thickening of the dorsal portion of the surangular that forms a prominent crest from its contact with the coronoid and the main body of the surangular, while the ventral portion below the anterior surangular foramen is not expressed medially. The adductor mandibular fossa is delimited posteriorly by the main body of the surangular, ventrally by the prearticular and the splenial, and anteriorly by the splenial and the dentary. The surangular-angular suture lies within the mandibular adductor fossa.

Angular—The angular is preserved in both jaws, with the right element being broken anteriorly, and only the ventral and posterior portions preserved in the left element. Nevertheless, the available material allows description of its anatomy. The narrowed anterior portion of the angular contacts the dentary via a laterally overlapping suture, and the surangular dorsally via a butt joint that partially overlaps posteriorly. Its entire ventral margin laterally overlaps the medial face of the lateral crest of the deep sulcus formed dorsally in the prearticular. Unlike *Heterodontosaurus* (Norman et al., 2011), the angular does not contact the splenial ventrally. The angular is laterally concave, thickens mediolaterally posteriorly, and is completely included within the lateral mandibular fossa and forms the medial wall of the adductor fossa; however, it is excluded from the thickened boundaries of both the mandibular fossa and the adductor fossa (Fig. 15A, C), which are delimited by the dentary, surangular, prearticular, and splenial. Thus, unlike in *Heterodontosaurus* (Norman et al., 2011), the angular does not form part of the thickened ventral edge of the jaw that functions as a pulley-like region for part of the *m. pterygoideus* musculature, which is instead formed by the posterior process of the dentary and the ventral edge of the prearticular. The ventral boundary of the external mandibular fossa is less prominent laterally in *Manidens* than in

Heterodontosaurus (Norman et al., 2011), the former having a shallower fossa with lower boundaries than the latter.

The surangular-angular suture in lateral view is dorsally convex, and its greatest dorsoventral height is smaller than that of the surangular. The angular was described by Pol et al. (2011) as occupying more than half of the height of the lower jaw at the coronoid process, a derived feature shared between *Manidens* and *Heterodontosaurus* (Norman et al., 2011; Pol et al., 2011). Subsequently, Sereno (2012:148) noted that the higher proportions of the angular compared to the surangular are erroneous for *Heterodontosaurus*, but valid for *Manidens*. This new study reveals that the angular is not only less than half the height of the jaw at the coronoid region (contra Pol et al., 2011) but also is less deep than the surangular (contra Pol et al., 2011 and Sereno, 2012), being similar to *Heterodontosaurus* and both exhibiting the plesiomorphic condition of the character. The angular does not participate in the ventral margin of the anteroventral foramen of the surangular, which is completely enclosed by the surangular.

Splénial—Both splénials are preserved in *Manidens* and are complete but fractured. The splénials are laminar plates with an anteriorly tapering short process that does not extend further than the D9 tooth position (contrary to *Heterodontosaurus*). The splénial has a dorsal process that forms the anteroventral corner of the adductor fossa, and a dorsoventrally wide middle region that narrows posteriorly while twisting from its dorsoventral to lateromedial configuration before reaching the dentary-prearticular-splénial contact. This bone medially covers the posterior exit of the Meckelian canal, and medially overlaps the posterior process of the dentary to its contact with the prearticular, at which point it overlaps the prearticular until near the articular (Fig. 13, 15). The anterodorsal process of the splénial overlaps the posterior edge of the coronoid eminence of the dentary but does not reach the coronoid in either jaw. The splénial does not contact the angular in *Manidens*. In medial view, the splénial

and prearticular form a crest-like edge at the ventral boundary of the adductor mandibular fossa, with the contribution of the splenial at this crest not overpassing dorsally the medial edge of the prearticular. In addition, and unlike *Heterodontosaurus* (Norman et al., 2011), the splenial does not form the dorsal margin of the internal mandibular fenestra. The m. **adductor mandibulae posterior** inserts along the ventral boundary of the adductor mandibular fossa, which is comprised of part of the dorsal aspect and lateral wall of the splenial, as well as parts of the angular and the surangular, as in *Heterodontosaurus* (Norman et al., 2011). **The m. pseudotemporalis superficialis is assumed to insert anteriorly along the dorsal edge of the splenial, which also bounds medially the adductor mandibular fossa.**

Preaticular—Both prearticulars are preserved. The prearticular is an anteroposteriorly long bone with its anterior region fitting into a dorsally oriented groove **delimited** laterally and ventrally by the dentary, and medially by the splenial; this overlapping articulation extends posteriorly along the posteroventral process of the dentary and the lateral face of the splenial. The dorsal aspect of the anterior process of the prearticular features a longitudinally oriented, deep groove that accommodates the ventral margin of the angular along its entire length, and posteriorly forms a butt to overlapped joint with the lateromedially thickened main body of the surangular; together, these form a cup-like structure that embraces the anterior region of the articular (Fig. 13) The cross-section of most of the prearticular is triangular, with a wide ventral region and the longitudinal groove dorsally. In the ventral region of its posterior half, there is a shallow groove in the prearticular for the posterior portion of the splenial. The superficially bulging splenial-prearticular suture forms a thickened crest corresponding to the ventral and medial limit of the adductor fossa; dorsal to this crest, the prearticular forms the floor of the fossa, and the splenial forms the ventral margin of the jaw (Fig. 13D, F). **In medial view, the medially concave posterior portion of the prearticular widens to house the m. adductor mandibulae posterior, which surrounds the**

ventral margin of the jaw to insert into the adductor fossa, delimited anteriorly by the crest-like splenial-prearticular articulation, and posteriorly by the surangular. Within this canal for the mandibular musculature, and near the medial prearticular-surangular suture, a wide foramen opens medially in the prearticular, a feature observed in the left jaw but absent (or not preserved) in the right jaw. The surangular overlaps the medial face of the prearticular, the latter extending posteriorly below the surangular to reach the anteromedial aspect of the articular, similar to the posterior extension on the lateral face of the jaw (Fig. 13D, F).

The insertion region for the m. *pterygoideus ventralis* is assumed to include the thickened lateral margin of the articular and its ventral concave face, with the wide canal formed by the prearticular and surangular containing the muscle on its way from the pterygoid to the retroarticular process. As with the surangular, the prearticular does not extend posterior to the jaw articulation or form any of its boundaries (Fig. 15). The boundaries between these bones and the articular can be seen ventral to the thickened medial border of the articular, where an excavated fossa subdivided by a posterodorsal oriented ridge marks the insertion for the m. *pterygoideus dorsalis*. Anteriorly, the prearticular does not bifurcate, and it does not form the posterior margin of the internal mandibular fenestra unlike the condition in *Heterodontosaurus* (Norman et al., 2011).

Articular—Both articulars are preserved in the holotype of *Manidens condorensis*; the right articular is disarticulated and posteriorly displaced, giving the impression that the right jaw is longer than the left (Fig. 13). The articular is formed from posterodorsally and anteroventrally facing halves. The anteroventrally facing half is formed by the narrow anterior process, a ventrolaterally facing smooth and dorsoventrally convex face, and an anteroposteriorly concave medial face. Both of these faces form a thick rim ventrally from the anterior process to the posteriormost portion of the retroarticular process, as a continuation of the ventral edge of the jaw (Fig. 15). The narrow anterior region of the articular fits into a

cup-like structure formed by the surangular dorsally and the prearticular ventrally, and does not contact the angular or the splenial. The posterodorsally facing half includes the glenoid facet and the dorsal aspect of the retroarticular process (Fig. 13C, E).

The left articular is in natural articulation with the condyles of the corresponding quadrate (Fig. 10A–B). The glenoid facet is ellipsoidal in shape, and wider lateromedially than anteroposteriorly. Its anterolateral corner is anteriorly elongated near the base of the dorsal eminence of the articular, and its posteromedial corner is posteriorly elongated, both of these giving the glenoid a fusiform shape in dorsal view (Fig. 13C, E). The glenoid facet is biconcave with a low intercotylar crest, and posterolaterally bounded by a robust V-shaped crest (with its apex directed posteriorly). If compared with the level of the glenoid facet, the V-shaped crest forms a robust and dorsally offsetted edge in its lateral portion and only a slight unevenness in its medial half (Fig. 13C, E). These posterior boundaries characterize a dorsally concave lateral cotylus that is markedly deep, while the medial cotylus shows a low posteromedial boundary and slopes ventromedially to reach the medial fossa of the retroarticular process (Fig. 13C, E). The lateral cotylus of the glenoid is dorsally positioned, and the medial cotylus is deflected ventrally and oriented slightly posteriorly. The longest axis of the glenoid facet is oriented 15° anteromedially to the transverse plane of the skull in dorsal view, and in posterior view is deflected ventrally and medially about 20° with respect to the horizontal plane. If considering the articulated quadrate and articular on the left side of the skull, the lateral condyle fits tightly within the lateral cotylus of the glenoid, but there is a dorsoventrally wide gap between the medial condyle and the margins of the medial cotylus of the glenoid (Fig. 8A–B). This space supports the inference of a fibrous/cartilaginous covering of this articular region.

The retroarticular region is formed by the medial and lateral fossae of the articular, which are separated by a posteroventral extension of the V-shaped posterior boundary of the glenoid,

which also forms the median crest of the retroarticular process (Fig. 13C, E). The lateral fossa faces posterolaterally, and is smaller than and positioned dorsal to the medial fossa. The medial fossa faces posteromedially, is longer than the lateral fossa, and its anterior region forms a deep subcircular pit that penetrates below the glenoid (Fig. 13C, E). The dorsal eminence in front of the jaw joint is entirely formed by the articular, with the surangular forming the anterior part of the base of this eminence (*contra* Pol et al., 2011). The jaw joint is separated from the anteroventral aspect of the articular by prominent crests on both sides of the joint that develops prominently medially (forming a protruding lip that overhangs the surangular-articular suture), and is less prominent laterally (Fig. 15). Both crests originate at the base of the dorsal eminence of the articular and *extend* posteroventrally: the lateral crest reaches the posteroventral end of the median crest of the retroarticular process (interfossae crest), while the medial crest reaches the dorsal end of the median crest. The median crest of the retroarticular process is oriented parallel to the long axis of the jaw, features a sharp edge but low prominence, and extends to the posterior end of the retroarticular process. The overall anatomy of the articular in *Manidens* differs from *that of Heterodontosaurus* (SAM-PK-K1332, Norman et al., 2011) in several aspects. In *Heterodontosaurus*, the biconcave glenoid facet is located "on a pedestal" dorsal to the retroarticular region, and separated from this region by a prominent transverse ridge that forms a lip-like prominence above the retroarticular region, instead of the lower and less prominent V-shaped crest in *Manidens*. The intercondylar crest is more prominent in *Heterodontosaurus* than in *Manidens*. The lateral fossa is larger than the medial fossa in *Heterodontosaurus*, with the opposite occurring in *Manidens*. The middle crest of the retroarticular is more prominent and well defined in *Heterodontosaurus*, and is between both fossae, whereas it is posterior to the lateral fossa and forms the lateral boundary of the medial fossa in *Manidens*. In addition, in *Heterodontosaurus* (SAM-PK-K1332, Norman et al., 2011), the middle crest of the retroarticular process reaches

the posteroventral edge of the articular, while in *Manidens* the crest extends posterior and ventral to the articular. In *Manidens*, the anteroposterior length of the retroarticular region is shorter than the length of the mandibular joint (as in other ornithischians), while the opposite occurs in *Heterodontosaurus* (Norman et al., 2011; Pol et al., 2011; Porro et al., 2015). The lateral fossa of the retroarticular is significantly smaller than the same in *Heterodontosaurus*. This lateral fossa extends from the posterior point of the glenoid facet to the posterior end of the retroarticular in *Heterodontosaurus*, while in *Manidens* the medial fossa is similarly elongated and the lateral fossa does not reach the end of the jaw. In *Manidens*, the ventral limit of the lateral fossa of the retroarticular forms a laterally prominent rim that results in a concave and anteroventrally oriented lateral face. This feature is absent in *Heterodontosaurus*; instead, the ventral limit of the lateral fossa of the retroarticular almost reaches the ventral margin of the mandible, and turns to face ventrally the region below it. Based on the reconstructions proposed for *Heterodontosaurus* (Norman et al., 2011), this face forms the insertion region for the *m. pterygoideus ventralis*. In their *short* description, Pol et al. (2011) interpreted the mandibular joint as an anteroposteriorly elongated facet, which exceeded the distal head of the quadrate in length. Based on the conclusions of Pol et al. (2011), Sereno (2012) reinterpreted this statement in a functional way, concluding that *Manidens* was capable of propalinal (forward and backward) movement of the mandible. However, new evidence indicates that Pol et al. (2011) might have interpreted part of what is now considered the medial retroarticular fossa as part of the glenoid facet, resulting in an *erroneously* larger jaw joint. As described here, a definite boundary *exists* between the medial retroarticular fossa and the glenoid facet *that is low* compared to *Heterodontosaurus*, but *it* delimits a glenoid *that is* only slightly longer anteroposteriorly than the condylar end of the quadrate. Thus, a propalinal component is not possible *in Manidens* due to the tight quadrate-articular articulation. This interpretation *is also* supported by the morphology and vertical orientation

of the wear facets on isolated crowns referred to *Manidens* (Becerra et al., 2014, 2018, 2020), which indicate that only orthal movement was possible.

Dentition

General Comments—The dentition of *Manidens condorensis* was described by Pol et al. (2011), and aspects of heterodonty, function, dental replacement, and enamel micromorphology were addressed by Becerra et al. (2014, 2018, 2020) and Becerra and Pol (2020). General aspects of the maxillary and dentary dentitions are summarized in Supplemental Data 2 to avoid repetition, and more detailed descriptions can be found in the aforementioned research. We refer a possible premaxillary tooth to the species *Manidens condorensis*, and aspects of its morphology are described.

Premaxillary Dentition—The premaxillary dentition is unknown for *Manidens* so the presence of the enlarged caniniform premaxillary tooth crowns known in *Tianyulong* and *Heterodontosaurus* cannot be confirmed (Zheng et al., 2009; Norman et al., 2011). One isolated tooth (MPEF-PV 3819, Fig. 16) is consistent in size and shape with the identification as a premaxillary/anterior maxillary tooth of an ornithischian dinosaur, possibly *Manidens*. The basal part of the crown in MPEF-PV 3819 bulges above a basal constriction between the crown and the root, and the root is more than twice as tall as the crown. The apex is aligned to the long axis of the crown, but the convex mesial carina and the concave distal carina in labial or lingual view indicates posterior curvature of the apex. The marginal denticles differ in size and number between carinae, with more numerous and smaller denticles mesially and larger but fewer denticles distally, the latter also exhibiting subsidiary small serrations, as occurs in the dentary dentition of *Manidens* (i.e., enamel crenulations; Becerra et al., 2014). The mesial serrations increase in size towards the apex. The basalmost part of the mesial carina is positioned more apically than the base the distal carina in labial or lingual views, with the

basal portion of the distal carina featuring an abrupt change in orientation and an extremely low, denticle-like structure pointing apically. The lingual face of the crown is apically concave and basally convex in mesial or distal view, while the labial face is convex. Both faces are enameled, but these differ from each other in that the labial face of the crown is smoothly enameled, while thickened enamel structures forming a wave-like pattern pointing through the apex are present on the lingual face, covering the swollen region of this crown surface from the basal constriction to the distal end of the distal carina. The overall shape and distal curvature of the crown resembles the premaxillary teeth of other ornithischians (e.g., Norman et al., 2004a), and the root being more than twice the length of the crown is similar to the cheek dentition of Heterodontosauridae. The thickened enamel in a wave-like arrangement resembles a rudimentary and poorly developed basal cingulum, as in the cheek crowns of basally branching thyreophorans and *Alocodon* (Becerra et al., 2018). Additionally, the presence of subsidiary denticles distally resembles the enamel crenulations on the edges of the denticles of the dentary teeth of *Manidens*, while the wave-like thickened enamel on the lingual face of the crown resembles the complex cingular edges in the maxillary dentition of *Manidens* (Becerra et al., 2014, 2018). In addition, the difference in size between the denticles of the mesial and distal carinae and their size variation through the apex also resembles the anterior maxillary and dentary teeth of *Manidens* (MPEF-PV 3815 and 3818: Becerra et al., 2018, 2020, this paper). Although there are no confirmed premaxillary teeth of *Manidens*, it is highly likely that MPEF-PV 3819 is a premaxillary tooth for the species.

DISCUSSION

Amended Diagnosis

General Comments—Continuing research has increased our knowledge of *Manidens condorensis* since the original description by Pol et al. (2011). Although some of the autapomorphic features mentioned by the authors and confirmed by Sereno (2012) and Becerra et al. (2014) remain valid in this diagnosis (*), others were re-defined (**) or not considered, and additional features were added (***) in light of new research. The description of novel features related to the dentition can be found in Becerra et al. (2014, 2018, 2020) and Becerra and Pol (2020), and are also addressed in the Supplemental Data 2. Given the fragmentary nature of most of the specimens from species in Heterodontosauridae and the available descriptions, not all of the following features present in *Manidens* can be assessed for presence/absence in other heterodontosaurids. In addition, given the lack of different well-preserved ontogenetic stages for the species *Manidens*, and the already known variation between different sized individuals (e.g., Becerra et al., 2020), is no clear how many of these features can be subject to ontogenetic or individual variation. The following list is provisional pending better information becoming available on other heterodontosaurids.

Autapomorphies—Lateral “boss” of the postorbital as a tubercle-like thickening positioned at the base of the jugal process of the postorbital, located between the orbit and the most ventral portion of the excavated fossa of the postorbital, and dorsoventrally oriented ***; jugal process of the postorbital reaches the main body of the jugal, with the jugal restricted to a small contribution in the posterior boundary of the orbit in lateral view ***; coronoid with a triangular-shaped posterior process (posterior alar process) that extends further posteriorly than the coronoid process of the dentary ***; anterior foramen of the surangular with an anteriorly developed wide fossa that becomes fusiform posterior to the foramen ***; mandibular fenestra completely closed, although there is a small foramen completely within the surangular in the location where the mandibular fenestra is expected (homologies between these are not addressed) **; posterior foramen of the surangular

excluded from the dorsally placed fusiform fossa ***; strong heterodonty between the maxillary and dentary cheek dentitions ***; symmetrical diamond-shaped maxillary dentition and asymmetrical diamond-shaped (hand-shaped) dentary dentition **; mesial and distal sharp-edged entolophs in the mid-posterior maxillary crowns, and a distal entoloph in the anterior maxillary dentition ***; lingual entolophs in the maxillary dentition obliquely oriented to each other, forming V- to Z-shaped cingular complexes ***; cingular entolophs in the maxillary dentition located near the half of the lingual crown face and apically directed ***; paracingular fossae between the cingular entolophs and the remainder of the crown in the maxillary dentition ***; mesial and distal cingular entolophs differently ornamented in the maxillary dentition, with the mesial entolophs bearing from two to six denticles and distal entolophs bearing a variable number of small serrations ***; obliquely disposed distal entolophs in most of the maxillary dentition forming a conspicuous crest (labial face) ***; small, shelf-like denticulated mesial ectoloph present in posterior maxillary crowns ***; sub-cingular crest apicobasally directed at the distal end of mesial entoloph of mid-posterior maxillary crowns ***; anterior dentary dentition includes an enlarged caniniform, a postcaniniform diastema, a small conical tooth, a possible dimorphic small caniniform with a sharp distal edge, and a fourth crown with transitional features between the cheek dentition and the small caniniform ***; mesial denticulate margin approximately 60% of the length of the distal margin in the mid-posterior dentary dentition **; the posterior dentary dentition is 'hand shaped' in lateral view, with only one or two mesial denticles, the most anterior of which diverges mesially from the margin of the crown (being the 'thumb' in the 'hand-shaped' crown) and four to five distal denticles apically to distally oriented (being the remaining 'fingers' in the crown) *; vertically oriented wear facets comprising apical and basal facets in the dentary dentition corresponding to the apical and cingular interaction with the opposing maxillary dentition **; cutting edges of denticles are thickened and sharp in the

maxillary dentition, and thickened and crenulated in the dentary dentition, in both cases this thickening is exclusively formed by the enamel (the underlying dentine is unaltered) **; mesial concavity in the mid-posterior dentary and maxillary teeth that allows a tight packing of the dentition by accommodating the distal margin of the preceding tooth **.

Additional features, which are absent or unknown in other heterodontosaurids, distinguish *Manidens* from *Heterodontosaurus*, which can be casted in a differential diagnosis: postorbital fossa excavated and deep only in the junction between the main body and the squamosal process of the postorbital, without forming a pocket-like recess ***; crest-like limit of the postorbital fossa absent on the lateral face of the squamosal process of the postorbital ***; posterior exit of the foramen of the quadrate (paraquadratic foramen or quadratic foramen) wide and facing posterolaterally, limited by the lateral laminar process of the quadrate and the quadratojugal ***; lateral process of the jugal (“jugal boss”) as a robust crest posterodorsally inclined, with the most prominent portion of the crest located posteriorly and directed posterolaterally **.

Comments on the Amended Diagnosis—Serenó (2012) indicates that some of the features originally defined as autapomorphies to *Manidens* are widely present in Ornithischia, whereas others were misinterpreted or too broadly defined. Pol et al. (2011) includes the strongly prominent lateral process of the jugal as an autapomorphic feature of *Manidens* shared with *Heterodontosaurus* in Heterodontosauridae (Pol et al., 2011; Sereno, 2012), which is absent in *Tianyulong* (Zheng et al., 2009) and unknown for other heterodontosaurids (Serenó, 2012). Although the disposition of this process might vary between specimens of *Heterodontosaurus* (Norman et al., 2011), the shape of this process in *Manidens* strongly differs from those present in *Heterodontosaurus* specimens. Considering this variation, the presence of a strong “jugal boss” should not be considered as an autapomorphy for *Manidens*, but its shape and orientation might be. Thus, the presence of a “jugal boss” is currently

considered as an autapomorphic feature only in its orientation (see above for a differential diagnosis between *Manidens* and *Heterodontosaurus*, disregarding the position of this process within the jugal as an autapomorphy).

Pol et al. (2011) considered the abruptly flexed postorbital process of the jugal as an autapomorphy of the species. Becerra et al. (2014) also mentioned this feature as unique for *Manidens* but previously Sereno (2012) noted this feature was widely distributed in Ornithischia. Our CT scanning and 3D reconstruction allows refinement of this interpretation. This portion of the postorbital process (of the left jugal) has two fractures, with a clear mismatch between fragments, resulting in posterior flexion due to taphonomic processes. This mismatch is clearly demonstrated by: the offset of the articular surface for the postorbital in the jugal process; a subtle mismatch between fragments; the articular surface for the jugal in both postorbitals is significantly less curved posteriorly; and the preservation of the right jugal, which has a complete and straight postorbital process. Thus, the posteriorly oriented postorbital process of the jugal has the condition more commonly observed among ornithischians (Sereno 2012), and is excluded from our amended diagnosis.

As stated by Pol et al. (2011) and Sereno (2012), the absence of a mandibular fenestra at the surangular-angular-dentary contact is considered an autapomorphic feature of *Manidens*. However, CT scanning revealed a small external opening that is completely delimited by the surangular and located in its anteroventral region, which is considered an autapomorphy in this diagnosis combined with the absence of a mandibular fenestra enclosed by the dentary, angular, and surangular. The presence of a mandibular fenestra is verified for *Heterodontosaurus* (e.g., Norman et al., 2011) and *Tianyulong* (Zheng et al., 2009), whereas its presence is considered likely for *Abriktosaurus* (Sereno, 2012) but cannot be confirmed for any other heterodontosaurid (Norman et al., 2011; Butler et al., 2012; Sereno, 2012).

In their amended diagnosis, Becerra et al. (2014) presented additional features as cranial autapomorphies based on a preliminary revision of the holotype material, but these were never fully addressed until now. One of these features is the shallow continuation of the antorbital fossa over the anterior process of the jugal that continues ventrally to the “jugal boss” and extends beyond its posterior end. The results presented here, however, indicate that the antorbital fossa does not extend posteriorly along the main body of the jugal, and that the jugal does not participate in the boundaries of the antorbital fenestra and the antorbital fossa, being excluded by the maxilla-lacrima articulation. Instead, the lateral depression of the maxillary wall, which is pierced by neurovascular foramina of variable sizes, extends further posteriorly along the main body of the jugal and below the “jugal boss”, indicating that the anchoring of a soft-tissue cheek may have extended further posteriorly along the jugal.

Pol et al. (2011) considered the enlarged forebrain facet on the ventral surface of the frontal, with its significantly raised margins, as autapomorphic for *Manidens*, a feature unknown for other heterodontosaurids. Our new CT data indicates that a transverse fracture of the frontals has taphonomically increased the depth of the inner cast of the frontals and that the forebrain facet is less prominent than previously considered. Therefore, in the absence of evidence on the endocranial anatomy of other heterodontosaurids and the less prominent nature of the forebrain endocast, further comparative information of other early ornithischians and heterodontosaurids are needed to regard this feature as unique in *Manidens*.

Skull Reconstruction

The description and 3D rendering of the cranial bones of *Manidens* allows us to present a hypothetical reconstruction of the skull (Fig. 17; Tab. 1), and it is the only heterodontosaurid besides *Heterodontosaurus* that has a near complete skull. The skull length, measured in dorsal view from the anterior tip of the nasal to the most posterior portion the left squamosal,

is closer to that estimated by Pol et al. (2011) based on lower jaw length. However, the former authors based this estimation on the length of the right lower jaw without considering the disarticulation and posterior displacement of the right articular, which was not evident until this study. When all of the jaw bones are placed in a more natural position, the right lower jaw is shorter than that presented by Pol et al. (2011) (Tab. 1). The antorbital region is shorter than the postorbital region, indicating that *Manidens* was a short-snouted species with an external antorbital fenestra smaller in size than the orbit, as in *Heterodontosaurus*, *Abrictosaurus* and some basally branching ornithopods as *Hypsilophodon* and *Orodromeus* (Galton, 1974; Norman et al., 2004b; Sereno, 2012). The outline of the orbit is sub-squared in lateral view, being more similar to other heterodontosaurids than to early ornithopods (Galton, 1974; Scheetz, 1999; Norman et al., 2004b; Sereno, 2012; Boyd, 2014). In addition, the shape of the orbit differs with *Heterodontosaurus* and *Tianyulong* in being less posterodorsally elongated (Zheng et al., 2009; Norman et al., 2011; Sereno, 2012). This difference is mainly due to the ventrally straight disposition of the jugal process of the postorbital and the null participation of the jugal in the posterior margin of the orbit, while in other heterodontosaurids the jugal process of the postorbital is anteriorly directed distally and continues its orientation along the postorbital process of the jugal. The orbit is anteroposteriorly shorter than the supratemporal fenestra in dorsal view and both the orbit and the supratemporal fenestra are smaller in size than the infratemporal fenestra (which is sub-rhomboidal in shape) in lateral view, differing from *Heterodontosaurus* in which the orbit is larger than the former (Norman et al., 2011). In *Manidens*, as in other heterodontosaurids and short-snouted ornithopods, these openings are larger than the external antorbital fenestra (Fig. 17A). The outline of the orbit can be traced in the dorsal view of the skull, and in both dorsal and lateral views it is only interrupted by the supraorbital, which is aligned with the thickened laterodorsal edges of the skull in lateral view and is laterally deflected in dorsal view. The thickened lateral margins of the skull are a

conspicuous feature of the heterodontosaurid skull, **not only** shared with *Heterodontosaurus* but also with *Homalocephale*, *Goyocephale*, and *Dracorex* among pachycephalosaurids (Perle et al., 1982; Bakker et al., 2006; Evans et al., 2011; Norman et al., 2011; Sereno, 2012).

In dorsal view, the widest portion of the skull **extends between the** jugal **bosses**, as in *Heterodontosaurus* (e.g., Norman et al., 2011) and likely other **early** ornithopods with a “**jugal boss**” (e.g., *Orodromeus*, *Zephyrosaurus*; Scheetz, 1999; Sues, 1980), the **basally branching** neoceratopsian *Aquilops americanus* (Farke et al., 2014), and psittacosaurids (e.g., Sereno, 2010). This feature contrasts with neornithischians and **early** ornithopods where the jugal-quadratojugal bar **is oriented** laterally and posteriorly to reach the quadrate shaft (e.g., *Gasparinisaura*, *Hypsilophodon*, *Thescelosaurus*, *Tenontosaurus*; Coria and Salgado, 1996; Galton, 1974; Boyd, 2015; Thomas, 2015). Similarly, the lateral prominence of the skull at the postorbitals is subequal to the lateral width of the occipital region (from the lateral end of one paroccipital wing to the other), similar to *Heterodontosaurus* and psittacosaurids where the width of the postorbitals is similar to or wider than the width at the paroccipital processes (Norman et al., 2011; Sereno, 2010). The overall proportions and other skull traits of *Manidens* are clearly similar to those in *Heterodontosaurus*, but also share **some similarities with psittacosaurids and pachycephalosaurids, as well as with early ornithopods.**

Cranial Musculature

General Comments—Holliday and Witmer (2007) and Holliday (2009) recognized homologies across extant diapsids (e.g., crocodylians, lepidosaurs, sphenodontians, birds), and Norman et al. (2011) used these homologies to infer the **arrangement** of the principal jaw muscles in *Heterodontosaurus*. Norman et al. (2011) also **addressed the anatomy** of the m. **constrictor internus dorsalis** group in *Heterodontosaurus* (m. **levator pterygoideus**, m. **protractor pterygoideus**, and m. **levator bulbi**). Sereno (2012) reinterpreted the attachment

regions of some of the muscle groups reconstructed by Norman et al. (2011) based on comparative evidence with extant diapsids and also inferred the presence of a new hypothetical jaw muscle: the m. adductor mandibulae externus ventralis. Although skull remains of *Manidens* are damaged, the available remains permit detailed reconstruction of the jaw musculature. The osteological correlates (Bryant and Seymour, 1990) on the preserved skull bones of *Manidens* allow us to formulate hypotheses for the origin and insertion sites of the cranial musculature, and these are discussed and compared with *Heterodontosaurus* (Fig. 18–20).

M. Tensor Periorbitae (M. Levator Bulbi)—The preservation of the laterosphenoid buttress (antotic crest) with its sharp laterally oriented crest allows identification of the origin site for this muscle, although there are no correlates to confirm an anterior extension of this origin onto the posterior wall of the orbit delimited by this crest (Fig. 18C).

M. Levator Pterygoideus—The laterodorsal face of the basisphenoid is the site of origin for this muscle, comprising the region included between the level of the posterior half of the pituitary fossa and the trigeminal opening (Fig. 18B), but likely not extending further ventrally to the lateral side of the laminar preotic pendant (Holliday, 2009). However, due to the presence of disruption and fractures, the symmetrical presence of concave surfaces or low, striated crests for the attachment region (as in more derived ornithopods) are hard to determine (Holliday, 2009). *Manidens* lacks of any laterodorsally oriented striated flange along the dorsal edge of the main body of the pterygoid for the insertion of the m. levator pterygoideus, which are present and well developed in *Triceratops* and *Brachylophosaurus* (Holliday, 2009). A small concave surface at the base of the anterior process of the pterygoid and above the pterygoid flange is oriented mostly dorsally and slightly medially, and may include the insertion for the m. levator pterygoideus (Fig. 18A).

M. Protractor Pterygoideus—The origin for this muscle is located along the dorsolateral face of the preotic pendant (ala basisphenoid), anteroventral to the trigeminal opening, posterior to the basipterygoid process, and ventral to the origin for the m. **levator pterygoideus** (Fig. 18B) (Holliday, 2009). It is likely that the origin of this muscle extended further lateroventrally reaching the edge of the ala basisphenoid and/or possibly **extending onto** the ventral face posteriorly, to reach the anterolateral portion of the thickened transversal crest limiting the rostral tympanic recess **posteriorly**. The m. **protractor pterygoideus** inserted along the lateral face of the pterygoid wing near to the pterygoid-quadrato articulation (Holliday, 2009); however, details of this insertion are uncertain because this region is damaged.

M. Pterygoideus Dorsalis—The attachment regions of **the m. pterygoideus dorsalis** and **ventralis** can be inferred based on the available material, although the extent of their origins might be affected by the incompleteness of the pterygoid flange. The origin of **the m. pterygoideus dorsalis** (= m. **pterygoideus anterior**; Norman et al., 2011) is assumed to be **in** a slightly concave depression on the dorsal aspect of the posterior pterygoid flange, although an anterior extension of this muscle on the dorsal aspect of the anterior process of the pterygoid and over the ectopterygoid/palatine cannot be determined for *Manidens* (Fig. 19A, 21C). This muscle inserts onto the medial rim of the articular and near the articular-prearticular posterior contact, reaching the posteromedial aspect of the retroarticular process, which, as in *Heterodontosaurus*, features a well-excavated surface (Fig. 20D–E, 21C).

M. Pterygoideus Ventralis—This muscle originates on the posteromedial edge of the pterygoid flange, with its origin extending dorsomedially up to a prominent crest that forms a deep groove at the base of the pterygoid wing (Fig. 19A, 21C). The ventral end of the muscle normally wraps around the ventral edge of the lower jaw, inserting on the lateral aspect of the prearticular. **In** this area *Manidens* **bears** a ventrolaterally facing planar surface surrounding

the jaw joint (Fig. 20H–I, 21C), as in *Heterodontosaurus* and other archosaurs (Holliday, 2009; Norman et al., 2011; Sereno, 2012; Nabavizadeh, 2020).

M. Pseudotemporalis Profundus—As in *Heterodontosaurus*, the absence of the epipterygoid prevents us from determining the origin and insertion sites for this muscle (Holliday and Witmer, 2007; Holliday, 2009; Norman et al., 2011; Sereno, 2012).

M. Pseudotemporalis Superficialis—Although we can hypothesize an origin for this muscle based on the topology seen in other extant diapsids, there are no osteological correlates to verify this origin (Holliday and Witmer, 2007; Holliday 2009; Norman et al., 2011, and references therein). Holliday et al. (2020) regarded the smooth fossa on the posterior portion of the frontals that does not reach the sagittal crest as the frontoparietal fossa, a structure previously recognized as the anterior region of the supratemporal fossa. This distinctive region outside the supratemporal fenestra but enclosed within the supratemporal fossa likely housed large vessels as seen in extant archosaurs, and was not related to the origin of the m. *pseudotemporalis superficialis* as previously thought (Holliday, 2009). Instead, it is likely that the m. *pseudotemporalis superficialis* originated on the anterior third of the dorsotemporal fossa formed by the parietals and may have reached the anterior end of the sagittal crest on the posterior portion of the frontals (extending medial and anterior to the frontoparietal fossa), as interpreted also for *Heterodontosaurus* (Norman et al., 2011). This origin likely excluded the laterosphenoids, which may have formed part of the funnel-shaped passage for the mandibular musculature (Fig. 19C–D, 21D). In medial view, the posterior edge of the dentary, together with the coronoid at the coronoid eminence and the splenial ventrally, form a conspicuous edge and a deep Meckelian canal for insertion of the m. *pseudotemporalis superficialis* (Fig. 20C, F, 21D). A similar insertion has been proposed for *Heterodontosaurus*, *Scelidosaurus*, and other ornithischians, and would represent the plesiomorphic condition for Ornithischia, whereas the derived condition (insertion comprising

the coronoid eminence only) is more likely for hadrosaurids and ceratopsids (Norman et al., 2011; Norman, 2020; Holliday and Witmer, 2007; Holliday, 2009). Regardless of its extensive insertion along the anterior boundary and lateral wall of the medial mandibular fossa along the dorsal process of the splenial, the assumed origin of this muscle is proportionally smaller in *Manidens* than in *Heterodontosaurus* (Norman et al., 2011).

M. Adductor Mandibulae Posterior—There is a fossa along the anterior face of the quadrate shaft, extending from dorsal to the condyles to the level of the dorsal end of the paraquadratic foramen delimited by the quadrate. This shallow fossa is wide ventrally and narrows dorsally, extending anteriorly along the lateral aspect of the pterygoid wing of the quadrate, and with low boundaries. As in extant archosaurs and other dinosaurs, and as assumed for *Heterodontosaurus* (Holliday and Witmer, 2007; Norman et al., 2011; Button et al., 2016; Nabavizadeh, 2020), the origin of the m. adductor mandibulae posterior is enclosed within this fossa, comprising (at least in part) the anterior face of the quadrate shaft and the lateral aspect of the pterygoid wing of the quadrate (Fig. 19B, 21C). The insertion of the m. adductor mandibulae posterior may be located on the medial wall of the mandibular adductor fossa, as assumed for *Heterodontosaurus* (Norman et al., 2011). This insertion region comprises part of the angular and the surangular, and the ventral boundary and part of the lateral wall of the splenial (Fig. 20A). However, in comparison to *Heterodontosaurus* (Norman et al., 2011), *Manidens* has a less developed medial crest of the splenial, and a lower prominence of the ventral and posterior boundaries of the medial adductor fossa, which are the most likely insertion regions for this muscle.

M. Adductor Mandibulae Externus Superficialis—This muscle originates along the lateral aspect of the upper temporal bar in diapsids (Holliday, 2009). The corresponding area of origin in *Manidens* (Fig. 19D–E, 21A) includes the lateral fossa of the postorbital bounded by the lateral “boss”, extending along a shallow fossa on the posterior process of the

postorbital and the anterior process of the squamosal, and before finally anchoring along the prominent lateral rim of the squamosal and ventral fossa. As in *Heterodontosaurus* (Norman et al., 2011), the m. **adductor mandibulae externus superficialis** was probably bounded anteriorly by the lateral “boss” of the postorbital and its prominent continuation along its ventral process; posterodorsally by the laterally prominent lateral rim of the squamosal; and posteroventrally by the laterally prominent oblique crest that originates at the quadratojugal-quadratoangular suture and **continuing** along the posterior portion of the prequadratoangular process of the squamosal, as proposed for *Heterodontosaurus* (Norman et al., 2011). This muscle extends ventrally (medial to the lower temporal bar) to insert along the lateral aspect of the dorsal edge of the surangular (Holliday, 2009; Nabavizadeh, 2020). In *Manidens*, the dorsal edge of the surangular for the insertion of this muscle is laterally prominent, but the insertion for this muscle likely extended ventrally to reach the anterodorsal fossa of the anterior surangular foramen, and as far posteriorly as the laterally prominent edge forming the ventral boundary of the fossa (Fig. 20B, 21A). Norman et al. (2011) presented two hypothetical insertion regions for the m. **adductor mandibulae externus superficialis** in *Heterodontosaurus*: the dorsolaterally prominent edges surrounding the surangular foramen; and the laterally concave face of the angular with its strongly pronounced ventral boundary, ultimately proposing the latter as more probable (and the former as an insertion site for m. **adductor mandibulae externus medialis**). A similar inference is made for the insertion of the m. **adductor mandibulae externus superficialis** along the lateral face of the posterior jaw for other ornithischians by Nabavizadeh (2019). However, the insertion of this muscle along the lateral face of the dorsal edge of the surangular is documented in lepidosaurs and crocodiles, and was inferred for other dinosaurs (Holliday and Witmer, 2007; Holliday, 2009) including *Heterodontosaurus* (Serenó, 2012), as proposed here for *Manidens*. Nevertheless, both *Manidens* and *Heterodontosaurus* share a deep lateral mandibular fossa located along the

lateral wall of the angular and limited ventrally by a prominent edge formed by the angular and the prearticular (Norman et al., 2011). Is evident when comparing with *Heterodontosaurus* that the lateral fossa of the postorbital relating to the origin of the m. adductor mandibulae externus superficialis is shallower in *Manidens*, and that the lateral rim and lateral fossa of the squamosal surrounding the infratemporal fenestra are proportionately smaller in the latter than the former.

M. Adductor Mandibulae Externus Medialis—As in other archosaurs (Holliday and Witmer, 2007; Holliday, 2009) and *Heterodontosaurus* (Norman et al., 2011) its main origin is located in the posterolateral corner and posterior portion of the supratemporal fossa. In *Manidens* this region is formed by the squamosal but likely included the medial aspect of the posterior process of the postorbital (Fig. 19F, 21B). The squamosal bears medially a longitudinal ridge along its anterior process that fades but continues anteriorly on the medial side of the posterior process of the postorbital, forming a shallow groove ventrally, a feature present more markedly in *Heterodontosaurus* (Norman et al., 2011). This shallow groove may enclose the origin for the m. adductor mandibulae externus medialis. Posteriorly, the origin likely extended medially to, but no further than, the parietal-squamosal contact (Fig. 19F, 21B). In lateral view, the anterodorsal aspect of the surangular forms a dorsomedially facing concave facet, a region for the insertion of the m. adductor mandibulae externus medialis in other archosaurs. Additionally, this concave face on the dorsal aspect of the surangular communicates anteriorly and laterally with an empty space formed between the surangular and the coronoid process of the dentary; this is limited medially and dorsally by the posterior alar process of the coronoid. Given the striations on the edge of the coronoid process of the dentary that continue along the posterior alar process of the coronoid and the empty “fossa-like” space ventral to this edge, we infer that the m. adductor mandibulae externus medialis extended further anteriorly and laterally to cover the lateral aspect of the coronoid eminence

(Fig. 20B, 21B), as occurs in several archosaurs (Holliday and Witmer, 2007; Holliday, 2009; Button et al., 2016).

M. Adductor Mandibulae Externus Profundus—This muscle originates in archosaurs on the medial surface of the supratemporal fenestra. This muscle likely reached the sagittal crest of the parietals of *Manidens*, occupying the posterior two thirds of the sagittal crest, whereas the anterior third (frontals and part of the parietals) forms the origin for the m. **pseudotemporalis superficialis** (Fig. 19C–D, 21C). As in *Heterodontosaurus*, the posterior extension of the origin of the m. **adductor mandibulae externus profundus** and its boundary with the m. **adductor mandibulae externus medialis** cannot be determined with certainty, and here we tentatively place it at the squamosal-parietal contact. The insertion of the m. **adductor mandibulae externus profundus** is commonly located on the medial aspect of the coronoid process (Holliday, 2009), and we interpret this as attaching to the medial face of the alar process of the coronoid and most of the medial face of the dorsal aspect of the coronoid, extending posteriorly along a longitudinal groove over the medial side of the dorsal edge of the surangular (Fig. 20A–C, F, 21C). Given the unique nature of the coronoid eminence of the coronoid in *Manidens* that entirely covers the medial aspect of the coronoid process of the dentary, it is likely that the m. **adductor mandibulae externus profundus** did not attach to the dentary, contrary to what was inferred for *Heterodontosaurus* (Norman et al., 2011).

M. Depressor Mandibulae—The origin of this muscle in extant crocodiles and birds, and in other extinct dinosaurs, locates along the ventrolateral margin of the paroccipital processes, at the caudolateral surface of the braincase (e.g., Ostrom, 1961; Nabavizadeh, 2020). Norman et al. (2011) **inferred** a similar origin for this muscle in *Heterodontosaurus* involving the ventrally flexing and **thickened** edges of the paroccipital processes, but also **considered** that this origin could likely reach to the posteroventral portion of the laterally prominent crest of the squamosal. As in *Heterodontosaurus*, there is a similar lateral rim of the squamosal in

Manidens, with a thickened edge that continues along the posteroventral edge of the paroccipital process. It is likely that this muscle originated along this edge, but this origin did not reach further anterior to the prequadratic process of the squamosal, where the origins of the m. adductor mandibulae externus superficialis are situated (Fig. 19E, 21A). As in other archosaurs (Holliday, 2009; Norman et al., 2011), the insertion of this muscle would have comprised the entire dorsal aspect of the retroarticular process (Fig. 19D–I, 20A). The reconstructed origin and insertion of this muscle are similar in *Manidens* to those in *Heterodontosaurus*. However, this species differ in that the paroccipital processes of *Manidens* are less ventrally pointing in the origin of this muscle, and a retroarticular process less prominent posteriorly with a lower longitudinal crest and shallower fossae in the insertion of this muscle (Norman et al., 2011).

Additional Musculature—Two additional hypotheses should be discussed for *Manidens*: the presence of an m. adductor mandibulae externus ventralis (Sereno, 2012) and cheek musculature. The presence of a laterally prominent horizontal rim on the maxilla, and a jugal flange with a thickened ventral edge in *Heterodontosaurus* were related by Sereno (2012) to an attachment region for a novel jaw muscle: the m. adductor mandibulae externus ventralis. This muscle, present only in extant psittaciform birds and inferred to be present in psittacosaurid ornithischians, was inferred for *Heterodontosaurus* to increase the bite force and enhance jaw adduction by facilitating long-axis rotation of the lower jaw (Sereno et al., 2010; Sereno, 2012). The maxilla of *Manidens* bears a laterally prominent posterior edge and the jugal presents a prominent “jugal boss” with a conspicuously developed ventral fossa, as well as a jugal flange with a thickened ventral edge, as in *Heterodontosaurus*. Furthermore, below the “jugal boss” there is a deep concavity facing posteroventrally, oriented similarly to the jugal flange. Despite these similarities, the wear facets in the dentition of *Manidens condorensis* lack evidences of long-axis rotation of the lower jaw. The presence of vertically

and randomly developed wear facets with polished edges present on most of the teeth of *Manidens* are compatible with orthal movements rather than indicative of a systematic and important lateral component (by long-axis rotation) of the jaw motion. Based on the information provided by tooth wear facets, the presence of an m. *adductor mandibulae externus ventralis* is considered unlikely. A more conservative explanation for some of the features used to infer this muscle, such as the jugal flange, is the development of a bony slot into which the surangular inserted during jaw closure, as indicated by Norman et al. (2011) for *Heterodontosaurus*. Additionally, the evidence of osteoregeneration over the dorsal aspect of the “jugal boss” in *Manidens*, possibly related to lateral head butting, may also indicate that the jugal flange had a protective function for the jaw musculature during intraspecific displays (see Jugal).

Regarding the presence of a muscular cheek or a buccal soft covering over the cheek teeth, the discussions on the existence of a muscular cheek in Ornithischia presented by Knoll (2008) and Nabavizadeh (2020) are justified using empirical data from extant diapsids. However, the neurovascular foramina dorsally and ventrally adjacent to the toothrow in the lateral aspect of the tooth-bearing bones (premaxilla, maxilla, and dentary), a feature present in saurischians and ornithischians, have been suggested to support the presence of least pliable and soft extraoral tissues, similar to cheeks, but not necessarily muscular (Morhardt, 2009). Given the construction of the skull of *Manidens* and other heterodontosaurids and their shallow external mandibular fossa, it is likely that there was no place for the insertion of the m. *adductor mandibulae externus superficialis* along the ventral edge of the external mandibular fossa to form a “muscular cheek” (contra Norman et al., 2011), as assumed for derived cerapodans (Nabavizadeh, 2020). However, the presence of a depressed lateral wall of the maxilla that extends along the jugal ventral to the “jugal boss”, and the shared presence of a low number of neurovascular foramina along the dentary and the maxilla, indicates the

presence of at least soft extraoral tissue surrounding the mouth (Morhardt, 2009). Additionally, some of the isolated teeth from the mid-posterior dentition of *Manidens* are polished on the non-occlusal face of the crown, which likely involved at least a lateral enclosure of the buccal cavity to prevent food from falling out of the mouth, while the same in the anterior dentition are more related to cropping (Becerra et al., 2018). If *Manidens* had immobile and fleshy soft extraoral tissues at least reaching to the posterior portion of the enlarged caniniform tooth, two possibilities might occur: 1) these likely stretched and then folded on themselves with each cycle of the jaw motion (Fig. 21C, red area); or 2) the extraoral soft tissues surrounded the mouth without forming a continuous sheet of tissue covering the dentition, and the corner of the mouth extended at least to the level of the last third of the postcaniniform dentition (Fig. 21C, red dot-line). In both cases, the extraoral soft tissues did not move as the muscular cheeks in mammals but still covered the postcaniniform teeth while the mouth was closed, which enabled moving the jaw and a wide gape without the length of the enlarged caniniforms affecting comfortable food intake.

Jaw Action

The areal extent of the attachment regions of the jaw musculature in *Manidens* indicates that the adductors were proportionally smaller than in *Heterodontosaurus* (e.g., Nabavizadeh, 2016, and references therein). Regardless of the morphology, arrangement, and wear of the dentition (Pol et al., 2011; Sereno, 2012; Butler et al., 2012; Becerra et al., 2014, 2018, 2020; Becerra and Pol, 2020), morphological and functional features of the skull in *Manidens* implies a skull that was less specialized towards high-fibre herbivory and extensive oral processing compared to *Heterodontosaurus*, and facultative omnivory. Jaw closure mechanics and the mechanical advantage of the jaw apparatus are strongly affected by the lowering of the jaw articulation and the elevation of the coronoid region (e.g., Nabavizadeh, 2016). A

lowered jaw articulation and increased height of the coronoid eminence can increase the length of the moment arm, **increase the relative bite force, and can be assessed with relative measures comparing** 2D skull schematics (Nabavizadeh, 2016). In *Manidens* (Fig. 22A), the jaw joint lowering below the occlusal line (0.09), coronoid height if compared to the jaw joint (0.12), and quadrate shaft length from the condyles to the mid-level of the lower temporal bar (0.22) are less marked than in *Heterodontosaurus* (0.163; 0.19; 0.25) (Fig. 22B), but more prominent than in *Tianyulong* (0.015 above the occlusal line; 0.029; 0.12) (Fig. 22C). The prominence and ventral curvature of the retroarticular process **indicates importance of the adductor** pterygoid musculature (Nabavizadeh, 2019). The moderate posterior prominence of the retroarticular process in *Manidens* (0.06) is less than *Heterodontosaurus* (0.10) but more than *Tianyulong* (0.03) (Fig. 22A–C), with the two first showing a similar ventral curvature **when** compared to *Tianyulong*, which **in contrast** presents a dorsal curvature of its brief retroarticular process. In addition, the sub-equally disposed quadrate condyles, **and the presence of a anteroposteriorly restricted and lateromedially narrow glenoid cavity in** *Manidens* allows only orthal motion of the jaw motion as in *Lesothosaurus* and *Tianyulong*, while some authors (e.g., Sereno, 2012) relate the different height of the quadrate condyles in *Heterodontosaurus* to the possibility of a transverse component in jaw motion.

Butler et al. (2012) compared hypothetical occlusion during jaw closure and basic lever arm mechanics between *Heterodontosaurus* and *Tianyulong* in a functional approach to the heterodontosaurid skull (with their conclusions on the latter species also functionally representing *Echinodon* and *Fruitadens*). The same approach can be used to compare the overall functional mechanics of the skull of *Manidens* with other heterodontosaurids (see Materials and Methods, and Fig. 22). In *Manidens*, the measured perpendicular distance value of the lower dentition to the jaw joint is 43.48% (or almost the half) the value of the upper dentition to the jaw joint (Fig. 22D), similar to that in *Tianyulong* (47.1%), while these

distances are closer in value to one another in *Heterodontosaurus* (21.06%, see Butler et al., 2012, supplementary information). From a functional view point (following Greaves, 1974), these values indicate scissor-like occlusion during jaw closure in *Tianyulong* (the occlusion point moves anteriorly while jaws are closing), which may also have occurred in *Manidens*, instead of almost simultaneously occlude as inferred for *Heterodontosaurus* (Butler et al., 2012). However, the size heterodonty of the postcaniniform dentition (mid-teeth higher than the anterior and posterior teeth), which is absent in *Tianyulong* but present in *Manidens*, allows consideration of a rather modified scissor-like occlusion for the latter. When size heterodonty is considered, it can be noted that the anterior and mid-teeth likely occluded first and almost simultaneously (at least in the skull 2D reconstruction), while posteriorly placed teeth occluded shortly after. The relative length of the moment arm for Group 1 and Group 2 muscle resultants in *Manidens* are, however, intermediate in value between *Heterodontosaurus* and *Tianyulong* (Butler et al., 2012, supplementary information). The Group 1 muscles of *Manidens* (related to the strength of jaw adduction) develop a longer moment arm than in *Tianyulong* but shorter than in *Heterodontosaurus* (Fig. 22E; Butler et al., 2012, supplementary information), but are closer in value and in increased mechanical advantage to the jaws of the latter (Butler et al., 2012). The moment arm of the Group 1 muscles, increases when the jaw joint is depressed, a feature poorly developed in *Tianyulong*, better developed in *Manidens*, and maximized in *Heterodontosaurus* (Fig. 22). The Group 2 muscles in *Manidens* (related to closing the jaws at large gapes, see Butler et al., 2012 and references therein) have a shorter moment arm than in *Tianyulong* but longer than in *Heterodontosaurus*, and therefore an intermediate mechanical advantage between these latter species (Butler et al., 2012). Moment arms dimensions imply that there was strong jaw adduction and possibly a large gape in *Manidens*, which was weaker in jaw adduction but capable of a wider gape than *Heterodontosaurus*, and also stronger than *Tianyulong*, the latter

reaching larger gape angles and having rapid biting **with** weaker jaw adductions than *Manidens* or *Heterodontosaurus* (Butler et al., 2012).

The skull of *Manidens* displays a mosaic of morphological and functional traits related both to herbivory and a more generalist diet. The orthal motion of the jaws result in a scissor-like occlusion in *Manidens*. However, instead of having an occlusion point that moves anteriorly with the jaw closure (the primitive jaw condition, present in *Tianyulong*, *Echinodon* and *Fruitadens*), an almost simultaneous occlusion of anterior and middle dentitions occurs (similar to the derived condition present in *Heterodontosaurus*). Although the functional advantages of this modification over the primitive condition are to be tested, this slightly modified scissor-like occlusion is due to the toothrow height-width heterodont morphology of opposing dentitions (i.e., taller crowns in the mid-dentition reach the occlusion sooner in the masticatory cycle than lower crowns). On the other hand, the construction of the skull is functionally less likely to process high-fibre vegetation and produce extensive oral processing as in *Heterodontosaurus*, but likely to manipulate more soft vegetable items. All current data support a primarily herbivorous diet for *Manidens* with facultative omnivory, a diet already proposed for all heterodontosaurids by Barrett (2000), Porro et al. (2008), Butler et al. (2012), and Barrett et al. (2011) based on other lines of evidence.

CONCLUSION

Previously, our knowledge of the craniomandibular anatomy of Heterodontosauridae was largely restricted to that of the derived species *Heterodontosaurus* (Norman et al., 2011; Sereno, 2012), **with** other species being represented by incomplete or damaged skull remains. This description of the skull of the holotype specimen of *Manidens condorensis* MPEF-PV 3211 as well as referred specimens permits comparison of nearly all elements of the skull

with other species in Heterodontosauridae and Ornithischia. The use of micro-tomographic scans of all the fossil remains allowed identification and characterization of a nearly complete skull for *Manidens*, with features that could not be readily observed previously (Pol et al. 2011). We reinterpret the maxilla preserved in the holotype and various features of its anatomy are now corrected. The supraorbital described by Pol et al. (2011) is now correctly identified as a rib fragment, and the two supraorbital bones are identified inside the orbit and articulated with the lacrimal-prefrontal. The structure previously interpreted as the post-temporal fenestra is reinterpreted here as the cranioquadratic passage, whereas the actual post-temporal foramen is identified at the paroccipital-supraoccipital-parietal contact, as in *Heterodontosaurus* (Norman et al., 2011). The contacts between the nasals, prefrontals, and frontals are described, as well as the full extent of the nasals. The autapomorphies of the species are refined here, merging new data with those from previous studies, correcting or excluding some of the features previously considered as autapomorphic of *Manidens condorensis*. Given the rarity of heterodontosaurid specimens with complete skulls, this detailed description of the skull of *Manidens condorensis* substantially increases our knowledge on the skull anatomy for the clade. Of particular note are the presence of various features that document evolution within the heterodontosaurid lineage related to increasingly specialized herbivory. This detailed description also permits description of the attachment sites for the craniomandibular musculature, while CT scanning opens future potential research avenues such as biomechanical modelling of the skull.

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FIGURE CAPTIONS

FIGURE 1. *Manidens condorensis* Pol, Rauhut and Becerra, 2011 (holotype MPEF-PV 3211-11). Block of associated fossil remains comprising the skull snout and roof, and postcranial remains. Photographs (A–B) and 3D reconstructions (C–F) of the specimen in dorsal (B, D–E), and ventral (A, C, F) views of the skull roof. Scattered postcranial remains were transparented (grey) in the general view (C–D), and removed for the detail of the articulated and associated skull remains (E–F). **Abbreviations:** **f**, frontal; **l**, lacrimal; **ls**, laterosphenoid; **m**, maxilla (dorsal fragment); **n**, nasal; **p**, parietal, **pf**, prefrontal; **sup**, supraorbital; **vlpn**, ventrolateral process of the nasal. Scale bars equal to 1 cm. [planned for page width]

FIGURE 2. *Manidens condorensis* Pol, Rauhut and Becerra, 2011 (holotype MPEF-PV 3211-10). Block of associated fossil remains comprising the lower jaws in articulation and associated right maxilla, right jugal and elements of the palate. Scattered postcranial remains were transparented (grey). Photographs (A–B) and 3D reconstructions (C–D) of the specimen in lateral right (A, C) and left (B, D) views of the lower jaws. **Abbreviations:** **an**, angular; **ar**, articular; **co**, coronoid; **d**, dentary; **ep**, right ectopterygoid; **j**, right jugal; **m**, right maxilla; **pa**, prearticular; **pl**, fragment of the right palatine; **pt**, pterygoid (distal region of the ventral process); **q**, left quadrate (condylar region); **sa**, surangular; **sp**, splenial; teeth in orange. Scale bars equal to 1 cm. [planned for page width]

FIGURE 3. *Manidens condorensis* Pol, Rauhut and Becerra, 2011 (holotype MPEF-PV 3211-9). Block of associated fossil remains comprising the left temporal region, left pterygoid elements, and the basicranium. Scattered postcranial remains were transparented (grey). Photographs (A–B) and 3D reconstructions (C–D) of the specimen in medial (A, C) and lateral (B, D) views of the temporal bones. **Abbreviations:** **bc**, basicranium and occipital

region; **ep**, ectopterygoid; **j**, jugal; **po**, postorbital; **q**, quadrate; **qj**, quadratojugal; **sq**, squamosal. Scale bars equal to 1 cm. [planned for page width]

FIGURE 4. *Manidens condorensis* Pol, Rauhut and Becerra, 2011. Right maxilla of the holotype MPEF-PV 3211-10 and left maxilla of the specimen MPEF-PV 3809 referred to *Manidens condorensis* (Becerra et al., 2018) in lateral (**A**, **C**, **I**), medial (**B**, **D**, **J–K**), dorsal (**E**, **L**), ventral (**F**), posterolateral (**G**), and posteromedial (**H**) views. Details highlight the maxillary-jugal-ectopterygoid articulation region (**G–H**), the presence of neurovascular foramina (**I**), alveolar foramina (**J**), the medial suture region of the anterior process of the maxilla (**K**), and the antorbital fenestra in dorsal view marking the narrow slit communicating the antorbital region with an internal pneumatic space in the maxilla (**L**). **Abbreviations:** **adm**p, anterodorsal maxillary process (ascending process of the maxilla); **af**, antorbital fenestra; **afo**, antorbital fossa; **alf**, alveolar foramen; **amp**, anterior maxillary process; **ch**, choana; **dia**, diastema; **fo**, additional foramen; **I**, lacrimal (fragment); **md**, maxillary lateral depression; **m-ec**, maxilla-ectopterygoid articulation region (and part of the jugal-maxilla articulation); **m-j**, maxilla-jugal articulation region; **m-m**, intermaxillary articulation region; **mn**, maxillary notch; **npr**, nasopalatine ridge; **nvf**, neurovascular foramen; **pdmp**, posterodorsal maxillary process; **plmp**, posterolateral maxillary process; **pm**, premaxilla (fragment); **pm-m**, premaxilla-maxilla articulation region; **pn**, pneumatic space; **snf**, subnarial fenestra (and fossa); **v-m**, vomer-maxilla articulation region. **Scales** in **A–F**, **G–H**, **J–K**, **I**, and **L** equal to 0.5 cm. [planned for page width]

FIGURE 5. *Manidens condorensis* Pol, Rauhut and Becerra, 2011 (holotype MPEF-PV 3211-11). Preserved snout region (**A–B**), with details of the nasals in articulation (**C–F**, **S**), left prefrontal (**G–J**), right prefrontal (**K–N**), left lacrimal (**O–P**), right lacrimal (**Q–R**), and the composite nasal-lacrimal-prefrontal articulation region (**T**), in dorsal (**A**, **C**, **G**, **K**), ventral (**B**, **D**, **H**, **L**), lateral right (**E**, **M**, **Q**), lateral left (**F**, **I**, **O**, **T**), medial (**J**, **N**, **P**, **R**), and

anterodorsal (S) views. In A–B, other skull bones were maintained in articulation but transparented. Note that C–T, the fragmented portions of each bone were accommodated in a more natural position to assure a better interpretation. In O, Q, both lacrimals show a detail in ventrolateral view to face the opening of the lacrimal foramen. **Abbreviations:** ?pm-n, possible premaxilla-nasal articulation region; **dlr**, dorsolateral ridge of the nasal; **f**, frontal; **fo**, foramen; **fs**, fossa; **ins**, internasal sulcus; **l**, lacrimal; **lfo**, lacrimal foramen; **lfs**, lacrimal fossa; **l-j**, lacrimal-jugal articulation region; **l-pf**, lacrimal-prefrontal articulation region; **m**, maxilla (fragment); **n**, nasal; **nc**, nasal cavity; **nf**, narial fossa; **n-f**, nasal-frontal articulation region; **n-l**, nasal-lacrimal articulation region; **n-pf**, nasal-prefrontal articulation region; **pf**, prefrontal; **pf-f**, prefrontal-frontal articulation region; **pf-so**, prefrontal-supraorbital articulation region; **so**, supraorbital. Scales in A–B and C–F equal to 1cm; and in G–N, O–R, S–T equal to 0.5 cm. [planned for page width]

FIGURE 6. *Manidens condorensis* Pol, Rauhut and Becerra, 2011 (holotype MPEF-PV 3211-11). Preserved frontoparietal region of the skull and supraorbitals (A–B), with details of the frontals (C–D, M–N) and parietal fragments (E–L, O) in dorsal (A, C, E, I, K), ventral (B, D, H, J, L), right lateral (F), posterodorsal (G, N), posterolateral (M), and anterolateral (O) views. Note that C–H and M–O, the fragmented portions of each bone and the sagittal crest of the parietals were accommodated in a more natural position to assure a better interpretation. **Abbreviations:** **e**, eye socket; **ec**, encephalon cast; **f**, frontal; **fl**, frontal lobes (cast); **f-p**, frontal-parietal articulation region; **l**, lacrimal; **ls**, laterosphenoid; **n**, notch; **nc**, nuchal crest; **n-f**, nasal-frontal articulation region; **ol**, olfactory lobes (cast); **ot**, olfactory tracts; **p**, parietal (fragments); **pf**, prefrontal; **pf-f**, prefrontal-frontal articulation region; **po-f**, postorbital-frontal articulation region; **sc**, sagittal crest; **so**, supraorbital; **stfs**, supratemporal fossa. Scales in A–B, C–D and E–H equal to 1cm; and in I–O equals to 0.5 cm. [planned for page width]

FIGURE 7. *Manidens condorensis* Pol, Rauhut and Becerra, 2011 (holotype MPEF-PV 3211-11). Digitally isolated right (A–B) and left (C–F) supraorbitals and left laterosphenoid (G–I) in dorsal (A, E, I), ventral (B, F), lateral (C, H) and medial (D, G) views.

Abbreviations: ?rmcv, possible opening for the rostral middle cerebral vein; ac, antotic crest; CN.V, possible contribution of the laterosphenoid to the margin of the external opening of the trigeminal nerve; fo, foramen; fs, fossa; h-ls, head (capitate process) of the laterosphenoid; l-so, lacrimal-supraorbital articulation region; ls-po, laterosphenoid-postorbital articulation region; pf-so, prefrontal-supraorbital articulation region. Scales equal to 0.5 cm. [planned for page width]

FIGURE 8. *Manidens condorensis* Pol, Rauhut and Becerra, 2011 (holotype MPEF-PV 3211). Preserved bones representing the left dorsal temporal bar (postorbital and squamosal) in articulation and association with other (transparented) temporal bones (MPEF-PV 3211-9; A–B), and the isolated right postorbital (MPEF-PV 3211-7; K–P) in lateral (A, C, L, Q), medial (B, D, K, S), anterior (E, M, W), posterior (H, P, V), dorsal (F, N, T), ventral (G, O, U), and posterodorsal (R) views. Note in I–J, the microCT images represent a cross-section of the base of the ventral process of the right postorbital, showing the fine porous bone structure of the cortical bone at the edge of the lateral process facing the orbit. In K–P, the fragmented portions comprising the right postorbital were accommodated in a more natural position to assure a better interpretation. **Abbreviations:** ap, brief anterior process of the postorbital; aps, anterior process of the squamosal; bc, basicranium; e, eye socket; ep, left ectopterygoid; f-po, frontal-postorbital articulation region; j, jugal; lc, lateral crest of the squamosal at the quadratojugal-squamosal articulation region; lfs, lateral fossa of the postorbital; lp, lateral process of the postorbital; lr, lateral rim of the squamosal; ls-po, laterosphenoid-postorbital articulation region; mlp, medial laminar process of the squamosal; mp, medial process of the postorbital; mr, medial rim of the postorbital; nc, nuchal crest; po, postorbital; po-j,

postorbital-jugal articulation region; **poqp**, postquadratic process of the squamosal; **po-sq**, postorbital-squamosal articulation region; **pp**, posterior process of the postorbital; **prqp**, prequadratic process of the squamosal; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **qj-sq**, quadratojugal-squamosal articulation region; **q-sq**, quadrate-squamosal articulation region; **sfe**, supratemporal fenestra; **sq**, squamosal; **sq-op**, squamosal-opisthotic (paroccipital process) articulation region; **sq-p**, squamosal-parietal articulation region; **vp**, ventral process of the postorbital. Scales equal to 0.5 cm. [planned for page width]

FIGURE 9. *Manidens condorensis* Pol, Rauhut and Becerra, 2011 (holotype MPEF-PV 3211). Bones comprising the ventral temporal bar from the left side of the skull (MPEF-PV 3211-9; **A, C–F, K–L**), **dissarticulated** jugal (MPEF-PV 3211-10; **B, G–J**), and quadratojugal (MPEF-PV 3211-6; **photographs, M–N**) from the right and side of the skull in association with other (transparented) skull bones (**A–B**), in lateral (**A, C, H, K, N**), medial (**B, F, J, L–M**), dorsal (**E, G**), and ventral (**D, I**) views. Note in **C–F** that the fragmented portions comprising the left jugal were accommodated in a more natural position to assure a better interpretation. **Abbreviations:** **a**, angular; **adp**, anterodorsal process of the jugal; **ap**, anterior process of the quadratojugal; **ar**, articular; **avp**, anteroventral (**laminar**) process of the jugal; **bc**, basicranium; **co**, coronoid; **dp**, dorsal (posterodorsal) process of the jugal; **dv**, dorsal vertebra; **ep**, **left** ectopterygoid; **ep-j**, ectopterygoid-jugal articulation region; **fo**, lateral foramen of the jugal; **j**, jugal; **jb**, lateral process of the jugal or “**jugal boss**”; **j-qj**, jugal-quadratojugal articulation region; **l-j**, lacrimal-jugal articulation region; **mc**, medial ventral crest of the quadratojugal; **mdc**, medial dorsal crest of the quadratojugal; **mg**, medial groove; **m-j**, maxilla-jugal articulation region; **pa**, prearticular; **pdp**, posterodorsal process of the quadratojugal; **po-j**, postorbital-jugal articulation region; **pp**, posterior process of the jugal; **pt**, **left** pterygoid; **pvp**, posteroventral process of the quadratojugal; **q**, quadrate; **qj**, quadratojugal; **qj-q**, quadratojugal-quadrate articulation region; **sa**, surangular; **so**,

postorbital; **sq**, squamosal; **sq-qj**, squamosal-quadratojugal articulation region; **vmp**, ventromedial process of the jugal; **vp**, ventral process of the jugal (jugal flange). Scales equal to 0.5 cm. [planned for page width]

FIGURE 10. *Manidens condorensis* Pol, Rauhut and Becerra, 2011 (holotype MPEF-PV 3211). Quadrate from the left side of the skull in articulation and association with other (transparented) cranial bones (MPEF-PV 3211-9, and condylar region in MPEF-PV 3211-10; **A–H**) and isolated right quadrate (MPEF-PV 3211-5; **I–N**), in lateral (**A, C, I**), medial (**B, F, L**), anterior (**D, J**), posterior (**E, K**), dorsal (**G, M**), and ventral (**H, N**) views. Note that in **A–H**, the condylar region and the rest of the quadrate are preserved as separated fragments in different fossil blocks, and were accommodated in a more natural position to assure a better interpretation. The red dot-lines represent the missing portions of the left quadrate (**C–E**); black dot-lines shape the paraquadratic foramen (**A, C**); blue dot-lines mark the space within the quadrate-squamosal articulation (**B**). **Abbreviations:** **ads**, anterodorsal sulcus for the posterior margin of the prequadratic process of the squamosal and the posterodorsal process of the quadratojugal; **ar**, articular; **bc**, basicranium; **cs**, quadrate condylar shaft; **dv**, dorsal vertebra; **ec**, ectopterygoid; **j**, jugal; **lc**, lateral condyle of the quadrate; **ldc**, laterodorsal crest of the quadrate; **lvp**, lateroventral (lateral) process of the quadrate; **mc**, medial condyle of the quadrate; **pa**, prearticular; **pmc**, posteromedial crest of the quadrate; **pqfo**, paraquadratic foramen; **pt**, pterygoid; **pt-q**, pterygoid-quadrate articulation region; **pvc**, posteroventral crest at the condylar region of the quadrate; **q**, quadrate; **qh**, quadrate head; **qj**, quadratojugal; **qj-q**, quadratojugal-quadrate articulation region; **q-sq**, quadrate squamosal articulation region; **qw**, pterygoid wing of the quadrate; **sa**, surangular; **sj**, space within the quadrate-squamosal articulation, likely a synovial joint; **sq**, squamosal. Scale equals to 1 cm in **A–B**, and 0.5 cm in **C–N**. [planned for page width]

FIGURE 11. *Manidens condorensis* Pol, Rauhut and Becerra, 2011 (holotype MPEF-PV 3211). Left pterygoid (**A, C–F**), both ectopterygoids (**B, G–R**), and a fragment of the right palate (**B**), in association with other (transparented) skull bones. Most of the pterygoid was separated with the left ectopterygoid and the remainder of the specimen MPEF-PV 3211-9, while the distal end of the pterygoid flange and the right ectopterygoid are preserved with the remainder of specimen MPEF-PV 3211-10. Elements are in lateral (**C, I, O**), medial (**A, E, L, R**), dorsal (**B, F, H, N**), ventral (**D, G, M**), anterior (**K, Q**), and posterior (**J, P**) views. Note that in **C–F**, the fragmented portions of the pterygoid were accommodated in a more natural position to assure a better interpretation. **Abbreviations:** ?**pt-pt**, possible interpterygoid contact region; **alh**, anterolateral wing-like half of the ectopterygoid (laterodorsally oriented); **ap**, anterior process of the pterygoid; **ar**, articular; **avp**, anteroventral process of the ectopterygoid; **bc**, basicranium; **bsp**, basisphenoidal process of the pterygoid; **ca**, caniniform tooth of the dentary; **co**, coronoid; **d**, dentary; **dv**, dorsal vertebra; **ec**, ectopterygoid; **ec-j**, ectopterygoid-jugal articulation region; **ec-m**, ectopterygoid-maxilla articulation region; **j**, jugal; **mc**, medially oriented crest; **mr**, medial rim reinforcing the pterygoid mid-portion; **pa**, palatine (fragment); **pa-ec**, palatine-ectopterygoid articulation region; **ph**, posterior half of the ectopterygoid (posteroventrally oriented); **pt**, pterygoid; **pt-ec**, pterygoid-ectopterygoid articulation region; **ptf**, pterygoid flange; **pt-q**, pterygoid-quadrato articulation region; **ptw**, quadrato wing of the pterygoid; **q**, quadrato; **qj**, quadratojugal; **sa**, surangular. Scales equal to 1 cm in **A–B**, and 0.5 cm in **C–R**. [planned for page width]

FIGURE 12. *Manidens condorensis* Pol, Rauhut and Becerra, 2011 (holotype MPEF-PV 3211-9). Occipital and ventral regions of the braincase (basicranium), in association with other (transparented) skull bones of the left temporal region (**A**), in dorsal (**A, E**), ventral (**B**), and details on **B**), lateral right (**C**) and left (**D**), and posterior (**F**) views. Note that due to extreme fusion, all occipital and ventral bones of the braincase could not be separated, but

these were colored based on external features. Dot-lines indicate the osteological correlate for the rostral tympanic recess (yellow); dorsal tympanic recess (green); caudal tympanic recess (blue); incomplete margin of the preotic pendant and cranial openings (black); and casts of the braincase (violet). **Abbreviations:** ?**cr.if**, crista interfenestralis; ?**pn**, small fossa likely related to a pneumatic recess; ?**ptfe**, likely location of the posttemporal fenestra; **afo**, accessory foramen; **bbp**, basiptyergoid process; **bc**, basicranium; **bo**, basioccipital; **bpr**, basiptyergoid recess; **bs**, basisphenoid; **bs.sp**, basisphenoidal septum; **bt**, basal tubera; **btc**, basisphenoidal transversal crest; **CN.V**, passage for the trigeminal nerve (V); **CN.VII**, passage for the facial nerve; **CN.XI-XII**, passages for the accessory (XI) and hypoglossal (XII) nerves; **cqp**, cranioquadratic passage; **ct**, crista tuberalis; **ctr**, caudal tympanic recess; **dtr**, dorsal tympanic recess; **ec**, ectopterygoid; **eo**, exoccipital; **eoc**, exoccipital crest; **fe.met**, foramen metoticum; **fe.ov**, fenestra ovalis; **fe.psr**, fenestra pseudorotunda; **fm**, foramen magnum; **ica**, ventral opening of the pituitary fossa for the internal carotid artery; **j**, jugal; **j.fo**, jugular foramen; **mnc**, median nuchal crest; **oc**, occipital condyle; **osc**, otosphenoidal crest; **pfo**, pituitary fossa; **po**, postorbital; **pop**, paroccipital process; **pro**, prootic; **prp**, preotic pendant; **ps**, presphenoid (cultriform process); **p-so.e**, eminence likely marking the parietal-supraoccipital contact; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **rtr**, rostral tympanic recess; **rtr-d**, posterodorsal diverticulum of the dorsal tympanic recess confluent with the otic foramen; **so**, supraoccipital; **sq**, squamosal; **ssr**, subsellar recess. **Scales equal** to 1cm. [planned for page width]

FIGURE 13. *Manidens condorensis* Pol, Rauhut and Becerra, 2011 (holotype MPEF-PV 3211-10). Right (**A, D**) and left (**B, F**) lower jaws in lateral (**A–B**) and medial (**C, F**) views, with a detail on the articular (**C, E**) in dorsal view. Note that all jaw bones were not accommodated in this figure, making evident the displacement of the dentary fragments and the right articular from their natural positions. **Abbreviations:** **a**, angular; **ar**, articular; **asfo**, anterior surangular foramen; **asfs**, anterior surangular fossa; **ca**, caniniform dentary tooth; **co**,

coronoid; **co.pap**; coronoid posterior alar process; **cp**, coronoid process of the dentary; **d**, dentary; **dea**, dorsal eminence of the articular; **emfo**, external mandibular fossa; **gf**, glenoid fossa for the quadrate-articular articulation; **imfs**, internal mandibular fossa; **lc**, lateral crest of the articular; **lfs**, lateral fossa of the articular; **mc**, medial crest of the retroarticular process; **mcrp**, median crest of the retroarticular process; **mfs**, medial fossa of the retroarticular process; **pa**, prearticular; **psfo**, posterior surangular foramen; **rp**, retroarticular process; **sa**, surangular; **sp**, splenial. Scales equal to 1 cm in **A–B, D** and **F**; and 0.5 cm in **C** and **E**.
[planned for page width]

FIGURE 14. *Manidens condorensis* Pol, Rauhut and Becerra, 2011. Right (**A–C, E, G**) and left (**F, H, I–J**) dentaries and coronoids of the holotype MPEF-PV 3211-10 in lateral (**A, I**), medial (**B, J**), dorsal (**E, F**), and ventral (**G, H**) views; with details of the laterodorsal aspect of the dentary showing a row of neurovascular foramina anterior to the dentary foramen (**C**), and a picture of the the striated lateral face of the coronoid eminence of the dentary in specimen MPEF-PV 3808 (**D**). Note that in all 3D reconstructions, the fragments of each dentary were accommodated in a more natural position to assure a better interpretation.

Abbreviations: **alr**, anterolateral slight ridge; **ca**, caniniform tooth of the dentary; **co.pap**, coronoid posterior alar process; **co-sa**, coronoid-surangular articulation region; **cp**, coronoid process of the dentary; **d**, dentary; **dfo**, dentary foramen; **d-pa**, dentary-prearticular articulation region; **d-sa**, dentary-surangular articulation region; **d-sp**, dentary-splenial articulation region; **imfs**, internal mandibular fossa; **nvf**, neurovascular foramina; **pvp**, posteroventral process of the dentary; **str**, striated dorsolateral surface of the coronoid eminence of the dentary. Scale bar equals to 0.5 cm in **C**, 0.1 cm in **D**, and 1 cm in **A–B** and **E–J**. [planned for page width]

FIGURE 15. *Manidens condorensis* Pol, Rauhut and Becerra, 2011 (holotype MPEF-PV 3211-10). Postdentary bones of the right (**A–B**) and left (**C–D**) lower jaws in medial (**A, C**)

and lateral (**B, D**) views. Note that the articular of the right lower jaw was accommodated in a more natural position to assure a better interpretation; and that the splenial (**A, C**), prearticular (**B, D**), and surangular (**D**) were presented as transparent elements to ease a better interpretation of the articulation of all postdentary bones. In **A–B**, the missing regions of the prearticular and surangular posteriorly were 2D reconstructed as dot-lined areas with color fill following the better preserved bones of the left jaw. **Abbreviations:** **a**, angular; **asfo**, anterior surangular foramen; **asfs**, anterior surangular fossa; **avsfo**, anteroventral surangular foramen; **co**, coronoid; **co.pap**, coronoid posterior alar process; **d**, dentary; **gf**, glenoid facet for the quadrate-articular articulation; **lc**, lateral crest of the articular; **lfs**, lateral fossa of the articular; **mc**, medial crest of the articular; **mfs**, medial fossa of the articular; **pa**, prearticular; **pvp**, posteroventral process of the dentary; **rp**, retroarticular process; **sa**, surangular; **sp**, splenial. Scale equals to 1 cm. [planned for page width]

FIGURE 16. *Manidens condorensis* Pol, Rauhut and Becerra, 2011 (specimen MPEF-PV 3819). Isolated tooth referred to *Manidens condorensis*, identified as a premaxillary tooth based on morphology (**A–B**); with views of the crown (**C–H**), and details on the enamel surface (**I**), and marginal ornamentation (**J–K**). Isolated tooth in labial (**A, C, J–K**; mesial at right), lingual (**B, D, H–I**; mesial at left), apical (**E**; mesial is upwards), distal (**F**; labial at right) and mesial (**G**; lingual at right) views. **Abbreviations:** **dt**, denticle; **ec**, enamel crenulations; **wle**, wave-like relief of the enamel surface. Scales equal to 0.1 cm in **A–H**; and 0.01 cm in **I–K**. [planned for page width]

FIGURE 17. *Manidens condorensis* Pol, Rauhut and Becerra, 2011. Skull and lower jaw reconstruction in 3D and schematics, in lateral (**A–B**), medial (**C**), dorsal (**D**) and posterior (**E**) views. Note that in **A**, the better preserved skull bones of MPEF-PV 3211 were used to achieve the 3D reconstruction: the fragments of the nasal, prefrontal, frontal, jugal quadrate, pterygoid, dentary and the entire articular were accommodated to its most natural position; the

used maxilla corresponds to MPEF-PV 3809; the parietal and basicranium were modelled based on the preserved remains; and the lower jaw corresponds to a specular image of the right jaw. **In B–E, the missing regions are in light grey; skull spaces and foramina are in darker grey and black. Abbreviations:** **a**, angular; **af**, antorbital fenestra; **afo**, accessory foramen; **afs**, antorbital fossa; **ar**, articular; **asfo**, anterior surangular foramen; **avsfo**, anteroventral surangular foramen; **bo**, basioccipital; **bpp**, basisphenoidal process; **bs**, basisphenoid; **co**, coronoid; **cqp**, cranioquadratic passage; **d**, dentary; **dfo**, dentary foramen (and associated foramina arranged in a row); **ep**, ectopterygoid; **f**, frontal; **fo**, foramen; **gf**, glenoid fossa; **j**, jugal; **jb**, lateral process of the jugal or “jugal boss”; **l**, lacrimal; **lfo**, lacrimal foramen; **ls**, laterosphenoid; **mx**, maxilla; **n**, nasal; **oc**, occipital condyle; **p**, parietal; **pa**, prearticular; **pap**, paroccipital process; **pa-sa.fo**, prearticular-surangular foramen; **pf**, prefrontal; **po**, postorbital; **pqfo**, paraquadratic foramen; **pqfo**, paraquadratic foramen; **pro-op**; prootic-opisthotic complex; **prp**, preotic pendant; **psfo**, posterior surangular foramen; **pt**, pterygoid; **ptfe**, posttemporal fenestra; **q**, quadrate; **qc**, quadrate condyles; **qj**, quadratojugal; **rp**, retroarticular process; **sa**, surangular; **sofo**, supraorbital foramen; **sp**, splenial; **spo**, supraorbital; **sq**, squamosal. Scale equals to 1cm. [planned for page width]

FIGURE 18. *Manidens condorensis* Pol, Rauhut and Becerra, 2011. Inferred muscular origins and insertions for the pterygoid (**A**, dorsomedial view), basisphenoid (**B**, anterodorsal view), and laterosphenoid (**C**, lateroventral view). **Abbreviations:** **MLPt**, **m. levator pterygoideus**; **MPPt**, **m. protractor pterygoideus**; **MTP**, **m. tensor periorbitae** (**m. levator bulbi**). **Scales equal** to 0.5 cm. [planned for page width]

FIGURE 19. *Manidens condorensis* Pol, Rauhut and Becerra, 2011. Inferred muscular origins and insertions for the pterygoid (**A**, posteromedial view), quadrate (**B**, anterior view), and temporal region (**C–F**, in dorsolateral, dorsal, lateral and medial views respectively). **Abbreviations:** **lv**, distinctive temporal fossa in the frontals for a large vascular structure

(marked with dot-lines); **MAMEM**, m. adductor mandibulae externus medialis; **MAMEP**, m. adductor mandibulae externus profundus; **MAMES**, m. adductor mandibulae externus superficialis; **MAMP**, m. adductor mandibulae posterior; **MDM**, m. depressor mandibulae; **MPs**, m. pseudotemporalis; **MPtD**, m. pterygoideus dorsalis; **MPtV**, m. pterygoideus ventralis. Scales equal to 0.5 cm. [planned for page width]

FIGURE 20. *Manidens condorensis* Pol, Rauhut and Becerra, 2011. Inferred muscular insertions for the postdentary region of the right (**A–D**, **F**, **G**) and left (**E**, **H–I**) lower jaws in dorsomedial (**A**), dorsolateral (**B**), posteromedial (**F**), ventrolateral (**H**) and lateral (**I**) views, with details of the coronoid (**C**, medial view) and articular (**D**, medial view; **E**, lateral view; **G**, dorsal view). **Abbreviations:** **MAMEM**, m. adductor mandibulae externus medialis; **MAMEP**, m. adductor mandibulae externus profundus; **MAMES**, m. adductor mandibulae externus superficialis; **MAMP**, m. adductor mandibulae posterior; **MDM**, m. depressor mandibulae; **MPs**, m. pseudotemporalis; **MPtD**, m. pterygoideus dorsalis; **MPtV**, m. pterygoideus ventralis. Scales equal to 0.5 cm. [planned for page width]

FIGURE 21. *Manidens condorensis* Pol, Rauhut and Becerra, 2011. **Skull reconstruction with attempted** reconstruction of cranial musculature based on the inferred muscle origins and insertions (**A–D**, grey areas), with a likely reconstruction of the soft extraoral tissues covering the lateral aspect of the postcaniniform dentition (**C**, red areas considering a complete covering of the postcaniniform teeth; red dot-line marks a more likely posterior positioning of the mouth commissure until reaching the posterior region of the postcaniniform dentition) for the postdentary region. **Abbreviations:** **MAMEM**, m. adductor mandibulae externus medialis; **MAMEP**, m. adductor mandibulae externus profundus; **MAMES**, m. adductor mandibulae externus superficialis; **MAMP**, m. adductor mandibulae posterior; **MDM**, m. depressor mandibulae; **MPs**, m. pseudotemporalis; **MPtD**, m. pterygoideus dorsalis; **MPtV**, m. pterygoideus ventralis. Scale equals 0.5 cm. [planned for page width]

FIGURE 22. Skull reconstructions of *Manidens* (A, D–E), *Heterodontosaurus* (B) and *Tianyulong* (C) scaled to the same basal skull length and illustrating the morphological and mechanical differing between most complete heterodontosaurid skulls (modified from Butler et al., 2012, supplementary information). In A–C, quantified morphological variation of the quadrate shaft length (darker grey), height of the coronoid region to the jaw joint (mid-grey), height of the occlusal line to the jaw joint (lighter grey), and length of the retroarticular region (black) (based on observations of Nabavizadeh, 2016, 2019); the measured values were divided by the jaw length to ease comparison between taxa (following Butler et al., 2012). In D, the contact between upper and lower tooth rows during jaw closure is measured in the skull reconstruction (Greaves, 1974; Butler et al., 2012). Following the authors, the jaws were set at 15° between the tooth rows and the perpendicular distance was measured between the occlusal surface (red lines) and the jaw joint for the upper (lighter grey) and lower (darker grey) tooth rows. The measures were compared with results from Butler et al. (2012). In E, the moment arm lengths for Group 1 and 2 muscles are estimated based on the skull reconstruction (following Butler et al., 2012). Gray arrows indicate orientation of muscle vectors for Group 1 and Group 2 muscles, while red lines indicate perpendicular moment arms between these muscle groups and the jaw joint. Moment arms were scaled by mandibular length to produce relative moment arm length for each muscle group, as performed by Butler et al. (2012) to skull reconstructions of *Heterodontosaurus* and *Tianyulong*. Scale equals to 0.5 cm in D–E. [planned for page width]