Heterodonty and double occlusion in Manidens condorensis: a unique adaptation in an Early Jurassic ornithischian improving masticatory efficiency

Article *in* The Science of Nature · August 2018

DOI: 10.1007/s00114-018-1569-6

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The Science of Nature (2018) 105:41
https://doi.org/10.1007/s00114-018-1569-6

SHORT COMMUNICATION

Heterodonty and double occlusion in *Manidens condorensis*: a unique adaptation in an Early Jurassic ornithischian improving masticatory efficiency

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Received: 27 March 2018 / Revised: 31 May 2018 / Accepted: 2 June 2018

Abstract

New materials of the ornithischian dinosaur *Manidens condorensis* highlight a strong heterodonty between the upper and lower dentitions and reveal a novel occlusion type previously unreported in herbivorous dinosaurs. The diamond-shaped maxillary teeth have prominent cingular entolophs in a V- to Z-shaped configuration that are absent in dentary teeth. These cingular entolophs bear denticles and serrations with vertical wear that is coplanar with the apical wear facets, supporting their involvement in chewing. The separated apical and basal wear in dentary teeth is consistent with the apical and cingular wear in maxillary teeth, indicating an alternate occlusion, an orthal jaw motion, and shearing interactions between marginal and cingular edges in a double occlusion. Measurements of the length and wear area along the marginal and cingular edges indicate that the latter are functionally equivalent to adding eight teeth to a maxillary toothrow of ten, almost doubling the lengths of cutting edges and the degree of intraoral processing, while maintaining a plesiomorphic skull anatomy, an adaptation to herbivory unique in Ornithischia.

Keywords *Manidens condorensis* · Ornithischia · Maxillary dentition · Heterodonty · Jaw mechanics

Introduction

The diversity of ornithischian dinosaurs was low before the Middle Jurassic in comparison with sauropodomorph and theropod clades (Irmis et al. 2007; Barrett et al. 2009). In contrast, ornithischians occupied herbivorous niches at low to intermediate highs of the vertical tiering during the second half of the Mesozoic and evolved the most sophisticated jaw mechanics among archosaurs (Cuthbertson et al., 2012; Williams et al. 2009; Sereno et al. 2010; Ösi et al. 2014; and references therein). Common craniomandibular adaptations of ornithischians to herbivory include a horny beak, an increase in number and decrease in size of teeth, the integration of individual teeth into sophisticated tooth batteries, medial displacement of the toothrow, ventral displacement of the jaw articulation, and increase of jaw adductor musculature and bite force (Nabavizadeh 2016; Strickson et al. 2016; MacLaren et al. 2017; and references therein). Heterodontosauridae represents the first radiation of ornithischians and possibly the first adapted to herbivory (Butler et al. 2008), including basal species with low, triangular, and well-spaced denticulated tooth crowns (Sereno 2012) and derived forms with tall and diamond-shaped teeth in a closely packed dentition, with oblique wear facets (Norman et al. 2011). *Manidens condorensis* from the late Early Jurassic of Argentina has been interpreted as a morphologically intermediate stage in the evolution of Heterodontosauridae in terms of its dentition (Pol et al. 2011; Becerra et al. 2014). Here, we report new materials that preserve its maxillary dentition and reveal an unreported occlusion pattern interpreted as an adaptation to herbivory that increases masticatory efficiency.

Communicated by: Sven Thatje

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00114-018-1569-6) contains supplementary material, which is available to authorized users.

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Published online: 14 June 2018

Materials and methods

All materials were recovered from the Cañadón Asfalto Formation (Pol et al. 2011) and are housed at Museo Paleontológico Egidio Feruglio (Trelew, Chubut). Microtomography in MPEF-PV 3211 and 3809 was conducted at Staatliche Naturwissenschaftliche Sammlungen Bayerns in Munich. DICOM datasets processing to 3D reconstructions was made with 3DSlicer version 4.3.0 (Fedorov et al. 2012). The measurement of chewing margins and wear facets in MPEF-PV 3809 was made with ImageJ (Schneider et al. 2012). More details are presented at the Online Resource 2.

Results

Teeth The dentary teeth of *Manidens* have an asymmetrical diamond-shaped outline, with the length of the mesial carina about 60% the distal carina, one to two denticles mesially and four to six distally, showing a mesial cavity and crenulated edges of the denticles (Online Resource 1). The dentary toothrow is notably heterodont in terms of size and shape including the presence of a large caniniform in the first tooth position (Pol et al. 2011).

The maxillary dentition of the holotype of *Manidens* (MPEF-PV 3211) was 3D reconstructed based on micro-CT data (Fig. 1a, b; Online Resource 1). A new isolated maxilla (MPEF-PV 3809) preserves ten maxillary teeth and replacement teeth (Fig. 1c–e; Online Resource 1) and can be referred to *Manidens condorensis* on the basis of autapomorphies in tooth morphology.

Wear has erased the apical features of the anterior maxillary teeth in MPEF-PV 3211 (M2–M5) and 3809 (M3–M4), but these are present in MPEF-PV 3818, an isolated, apicobasally tall, and slender crown (Fig. 1b, d–f). Some teeth in MPEF-PV 3211 (M6–M8) and 3809 (M5–M10) show two to three denticles symmetrically distributed around the apical denticle, each forming a rather low apex (Fig. 1b–e). The mesial cavity is present from M5 onwards in both specimens (Fig. 1c, Online Resource 1), although all the maxillary dentition is closely packed, in contrast to the dentary dentition (Becerra et al. 2014). In both specimens, an oblique distal ectoloph is evident from position M4 onwards and an oblique distal entoloph from M3 onwards (Fig. 1d, e; Online Resource 1). A mesial entoloph appears from positions M5–M6, obliquely oriented in M6 and almost horizontally in M7–M8 in MPEF-PV 3211, and similarly oblique for M5–M7 and horizontal for M8–M10 in MPEF-PV 3809 (Fig. 1b, d–e). Cingular entolophs are apically oriented and extend over half of the crown, gradually changing from a V- to a Z-shaped configuration; their mesiodistal length and medial prominence increase posteriorly (Fig. 1d, e). Additionally, the cingular entolophs in MPEF-PV 3809 and isolated maxillary teeth bear ornamentations, with large denticles at the mesial entolophs (two to three denticles in M5–M6), and small serrations at the distal entolophs (M5–M7). Maxillary and dentary cheek dentitions share the same size heterodonty (Becerra et al. 2014). Maxillary teeth have thickened enamel over the cutting edge of the denticles instead of crenulated margins, evident in isolated teeth (Online Resource 1). Isolated teeth show up to seven denticles in their mesial entoloph and an extra mesial ectoloph that morphologically varies from a rounded prominence to a denticulated edge (Fig. 1g, h), features possibly increasing posteriorly along the toothrow (Online Resource 1).

Manidens differs from other heterodontosaurids and ornithischians in the marked morphological differentiation between the upper and lower toothrows (Fig. 1i, j). The symmetric distribution of denticles of the diamond-shaped maxillary dentition of *Manidens* is shared with *Echinodon*, while the asymmetric hand-shaped dentary teeth are similar to those of *Pegomastax* (Sereno 2012). Cingular protuberances were reported in other heterodontosaurids: distal ectolophs in *Lycorhinus angustidens*, and slight ectolophs in *Tianyulong*, the posterior teeth of *Echinodon*, and the largest crowns of *Fruitadens* (Sereno 2012, and references therein). Outside Heterodontosauridae, some species of Thyreophora, basal Ornithopoda, Pachycephalosauria, and basal Ceratopsia have evolved cingular edges in their dentition (exhaustive comparison in Online Resource 2). Nevertheless, upper and lower tooth rows in these species are morphologically similar and specularly arranged (Weishampel et al. 2004).

Wear facets Wear on dentary teeth of *Manidens* is characterized by a near vertical orientation of distinct apical and basal facets (Becerra et al. 2014), identified in the type specimen and isolated teeth (Online Resource 1). Apical wear facets face posteriorly in distal denticles and the crown apex, and anteriorly in the facets of mesial denticles. Basal wear facets are also located either distally or mesially on the base of the crown and are coplanar with the apical facets.

Wear facets on maxillary teeth are present at the apical and lingual cingular margins. As in dentary teeth (Becerra et al. 2014), the facets are almost vertically oriented (67°/77° for apical/cingular wear with respect to the horizontal plane) and are flat to concave, depending on the degree of development (Fig. 1d, e). Anterior teeth have apical wear facets larger than the cingular facets, but in posterior teeth, the apical facets are smaller than those of the cingular entolophs. The wear facets show a step at their basal enamel-dentine boundary (trailing edge) and a continuous transition at their apical limit (leading edge) (Online Resource 1). As in dentary teeth, apical and basal wear facets located on the distal half of the crown face slightly posteriorly, while those on the mesial half face anteriorly (Fig. 2a–f). Additional wear is present at the non-occlusal surface of some of the dentary and maxillary teeth (Online Resource 1).

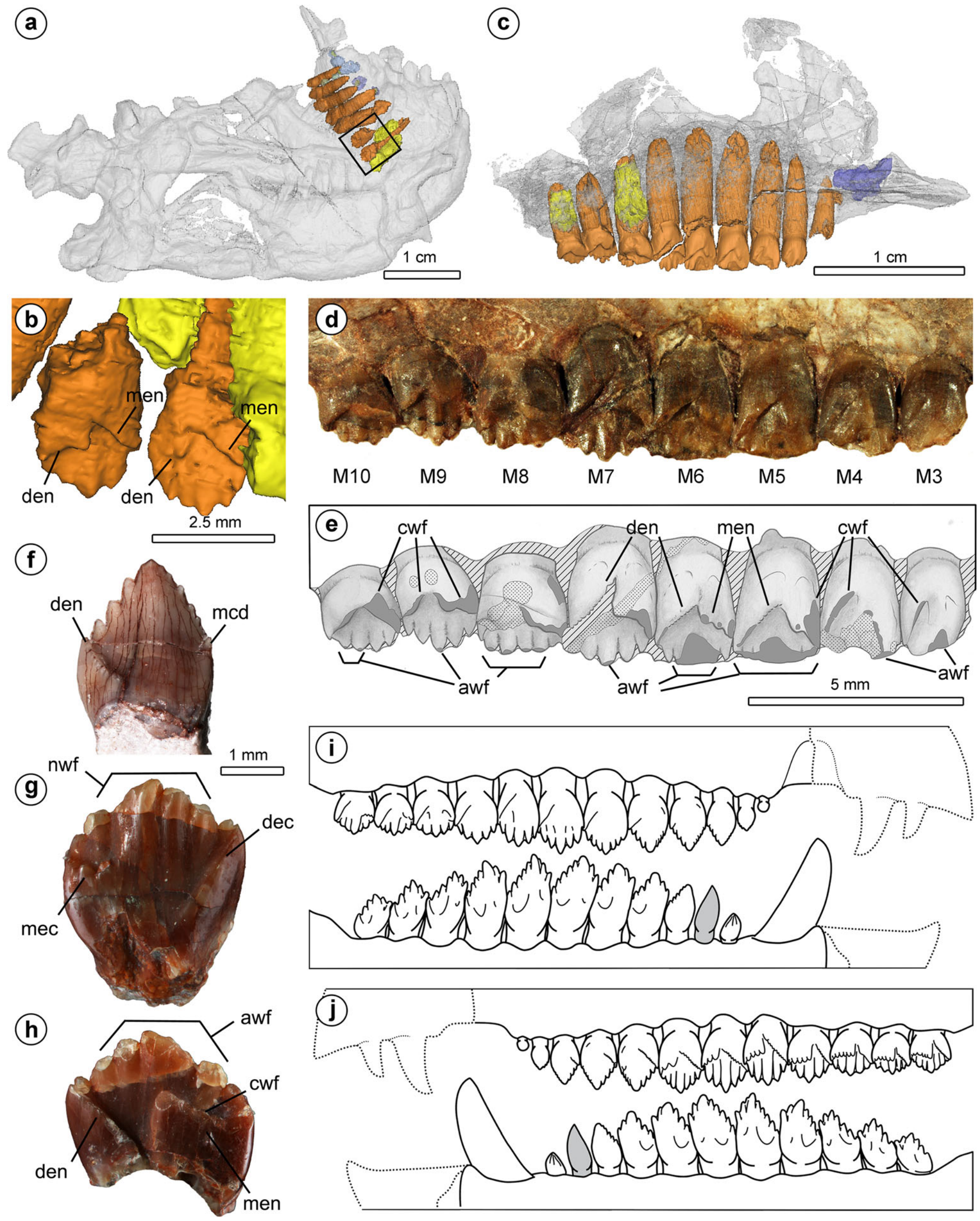

Fig. 1 **a**, **c** 3D reconstructions of MPEF-PV 3211 and MPEF-PV 3809 in right and medial views highlighting the functional (orange/darker gray) and replacement maxillary teeth (yellow/brighter gray). **b** Maxillary teeth M7–M8 of MPEF-PV 3211 in lingual view. **d**, **e** Dentition of MPEF-PV 3809 in lingual view. **f** MPEF-PV 3818 in lingual view. **g**, **h** MPEF-PV 3820 in labial and lingual views, respectively. Additional isolated maxillary teeth in Online Resource 1. **i**, **j** Hypothetic reconstruction of dentition in *Manidens condorensis* in **q** labial and **r** lingual views, based on this work and unpublished information (MPEF-PV 3808, gray caniniform; Becerra et al., in prep.). Abbreviations: awf, apical wear facet; cwf, cingular wear facet; dec, distal ectoloph; den, distal entoloph; mcd, mesial cingular denticle; mec, mesial ectoloph; men, mesial entoloph; nwf, wear at the non-functional face

Discussion

Scratch orientation in wear facets of maxillary (apical and cingular) and dentary (apical) teeth (with angles ranging around 80–105° and variable lengths), together with the leading and trailing edges located apically and basally in these facets, support a simple orthal jaw closure (Fig. 2e, f, Online Resource 1). Wear at the non-occlusal surface of teeth, with smoothened boundaries and few randomly oriented scratches, is likely due to food abrasion (Fig. 2a, Online Resource 1). No wear was identified within the paracingular fossa (Fig. 2a), indicating that the apex of the antagonistic crown did not fit within this fossa (as the cusp-basin occlusion of tribosphenic mammals). The different orientation of wear facets in mesial and distal regions in maxillary and dentary crowns indicates an imbricating, and, probably, precise occlusion of the opposing toothrows (Fig. 2e). The coplanar orientation of apical and basal wear facets indicates that the apical carinae of dentary teeth occluded with the apical and cingular margins of maxillary teeth, forming a double sequential occlusion (Fig. 2f). Thus, in addition to the shearing motion of apex-apex contact, the apical carinae of dentary teeth formed a second shearing interaction with the cingular entolophs of maxillary teeth during the same masticatory cycle, a feature previously unknown in other dinosaurs.

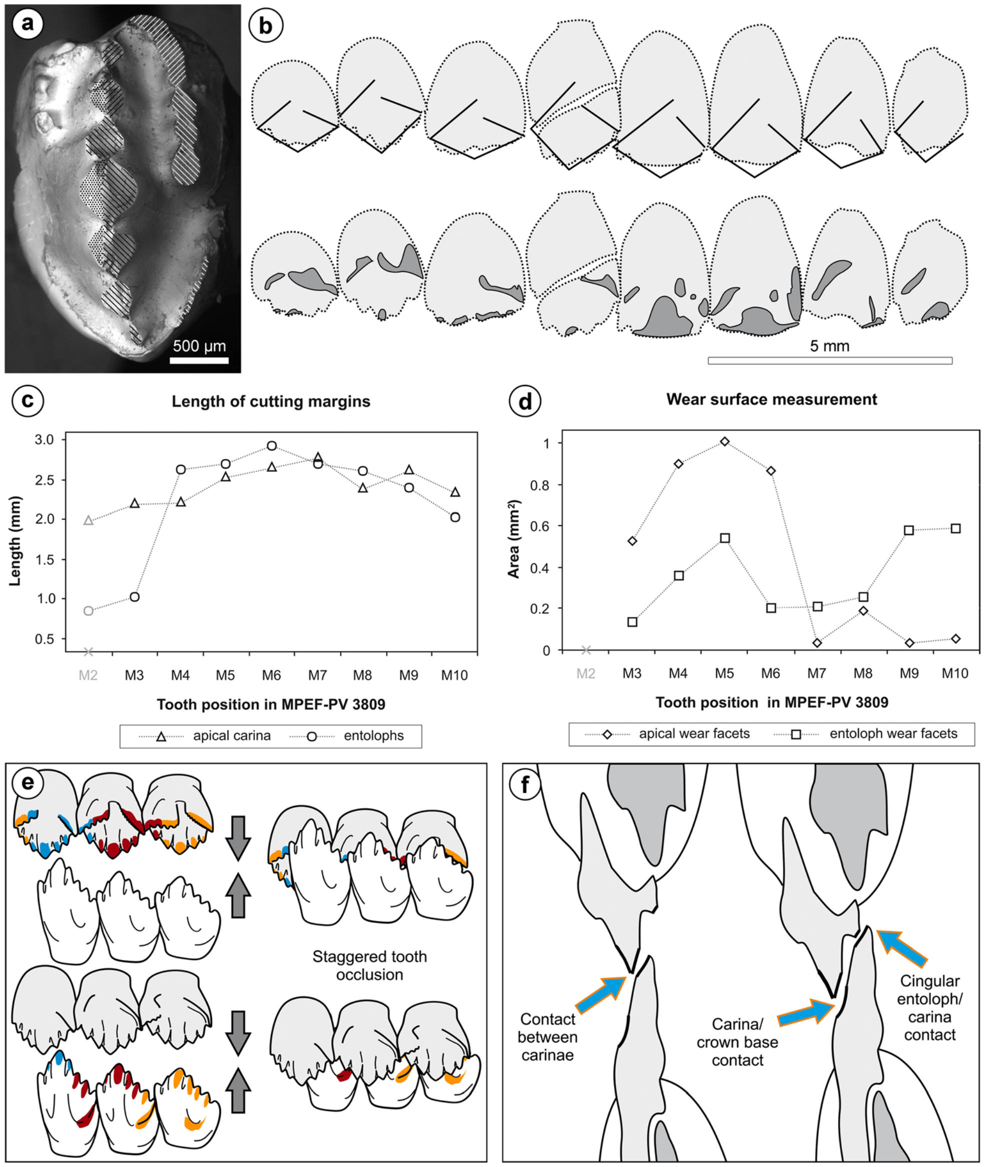

Fig. 2 **a** SEM imaging of MPEF-PV 3820 in occlusal view. lines indicate the interaction facets with two antagonistic teeth, dots indicate food abrasion facets, and hues differentiate apical from cingular wear. **b** Schematics of the dentition of MPEF-PV 3809, lines and dark areas representing the length and wear facet measurements as they were taken. **c**, **d** Plots depicting measured values of length (**c**) and wear area (**d**) on each tooth position, with hypothetic values for M2. **e** Hypothetical staggered tooth occlusion based on wear development (contact of different opposing tooth in blue, red, and yellow or hues of gray), with **f** two shearing interactions at the same masticatory cycle in a double occlusion

The double shearing mechanism of *Manidens* improves the masticatory efficiency of the toothrow. The length of shearing apical margins of the upper toothrow is subequal to the length of shearing margins of the entoloph (21.76 versus 19.83 mm; Fig. 2b, c). Similarly, the area of the apical wear facets is 3.615 mm^2 and that of the cingular wear facets is 2.895 mm^2 (80.1% of the apical wear; Fig. 2b, d). Thus, both the length and area of the occlusal surface provided by the cingular entolophs in *Manidens* almost double the masticatory efficiency by adding a shear power equivalent to 6.4 to 8.2 additional teeth (based on the sum of marginal area or length) if only the apical carina was functional (Online Resource 3).

The unique characteristics of the jaw mechanics of *Manidens* (plesiomorphic orthal occlusion and a double cutting edge) were achieved through minor morphological modifications that almost double the masticatory efficiency, ultimately reducing the energy spent in tooth formation and mandibular motion. This deviates from previous evolutionary trends in Ornithischia (Sereno 1997; Bell et al. 2009; Erickson et al. 2012; and references therein), in which improvements in mastication efficiency were commonly achieved through the development of dental batteries, the increase in rostral length of the skull, or by acquiring a complex jaw motion. These new data of the dentition of *Manidens* reveal previously unrecognized functional and morphological adaptations in Heterodontosauridae during the first radiation of ornithischians in the Early Jurassic, adding to the already diverse array of herbivorous adaptations known in ornithischian dinosaurs.

Acknowledgements Dr. Y. Herrera (UNLP), the institution and staff from the Staatliche Naturwissenschaftliche Sammlungen Bayerns (Munich), and the reviewers are thanked.

Funding information The Deutscher Akademischer Austauschdienst (DAAD) financed the travel for M.G.B. to Germany (ID 57130097); fieldwork and research were supported by Agencia Nacional de Promoción Científica y Técnica to D.P. (ANPCyT, PICT 1288 and 0808), Deutsche Forschungsgemeinschaft to O.W.M.R. (DFG, RA1012/9-1), and National Science Fundation to Dr. G. Rougier (NSF, DEB 0946430 and DEB 1068089).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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