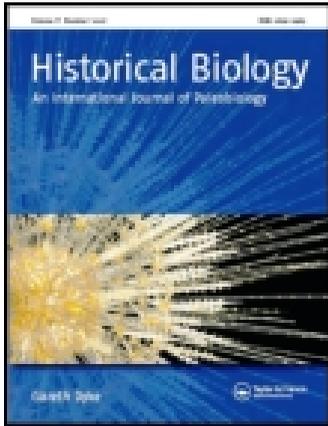


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The dentition of *Manidens condorensis* (Ornithischia; Heterodontosauridae) from the Jurassic Cañadón Asfalto Formation of Patagonia: morphology, heterodonty and the use of statistical methods for identifying isolated teeth

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The dentition of *Manidens condorensis* (Ornithischia; Heterodontosauridae) from the Jurassic Cañadón Asfalto Formation of Patagonia: morphology, heterodonty and the use of statistical methods for identifying isolated teeth

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The recently described *Manidens condorensis* is one of the most completely known taxa of the family Heterodontosauridae from the southern landmasses. However, some dental aspects are not well known due to preservational problems in the type material. This contribution reports new isolated teeth found in the Cañadón Asfalto Formation (Early-Middle Jurassic). These teeth are referred to *Manidens condorensis* based on the presence of autapomorphic characters of the unusual dentition of this taxon, such as the highly asymmetric tooth crowns and small crenulations on each denticles. The isolated crowns are well preserved and reveal the presence of undescribed and new autapomorphical features, including apical and basal wear facets on the occlusal surface of isolated crowns and a wear surface also in the caniniform tooth. We carried out statistical analyses (including morphogeometrical and discriminant analyses), using the holotype crowns as a morphological starting point, for characterising shape variation of the crowns along the toothrow and for identifying the position of isolated crowns. These analyses allow defining morphological regions within the postcaniniform toothrow and produce a metrically based discriminant function to predict the hypothetical position of future discoveries, providing a methodological framework that could be applied to other extinct heterodont dinosaurs.

Keywords: *Manidens condorensis*; teeth; morphometrics; heterodonty

1. Introduction

Among ornithischian dinosaurs, Heterodontosauridae has been regarded as one of the most phylogenetically problematic clades (Butler 2005; Norman et al. 2011; Sereno 2012). The controversy on the affinities of this group probably stems from the presence of morphological similarities between different groups of ornithischian dinosaurs and *Heterodontosaurus* (the best known heterodontosaurid), and the scarcity of morphological information is due to the incompleteness and rarity of other heterodontosaurid taxa. This situation led to phylogenetic hypotheses that postulated heterodontosaurids either as advanced ornithischians related to Ornithopoda (e.g. Sereno 1986), as sister taxon to Marginocephalia (Xu et al. 2006) or as one of the most basal ornithischian clades (e.g. Butler, Upchurch, et al. 2008, 2010; Zheng et al. 2009; Norman et al. 2011; Pol et al. 2011; Sereno 2012). Despite the debated affinities of this group of small-bodied cursorial dinosaurs, they have long been characterised by numerous apomorphies, such as a conspicuous caniniform and highly modified heterodont dentition in more evolved heterodontosaurids, which was traditionally regarded as an adaptation to herbivory (e.g. Galton 1973;

Weishampel 1984; Weishampel and Norman 1989). Actually, although several authors recently cast some doubts on the herbivorous diet on heterodontosaurids (Barrett 2000; Butler, Porro, et al. 2008, 2010, 2012), the currently accepted phylogenetic topologies of Heterodontosauridae and the morphological jaw characterisation of each species show a masticatory specialisation leading to a more efficient chewing mechanism within the group (Pol et al. 2011), and more basal species are related to an omnivorous diet and more evolved species to a herbivorous diet. Furthermore, their early appearance in the fossil record (at least in the Early Jurassic and possibly in the Late Triassic; see Báez and Marsicano 2001) places this group in a critical position for understanding the early diversification of Ornithischia and character evolution at the base of this clade (Butler, Upchurch, et al. 2008).

Until recently, Heterodontosauridae was considered to include only Early Jurassic forms from the Elliot Formation of South Africa (*Abrictosaurus consors* [Thulborn 1974], *Lycorhinus angustidens* [Haughton 1924; Thulborn 1970; Gow 1990], *Heterodontosaurus tucki* [Crompton and Charig 1962; Santa Luca 1980]), all of which have a very specialised masticatory apparatus. The temporal and geographical range of this dinosaur group was subsequently extended with the

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putative heterodontosaurid affinities of *Pisanosaurus mertii* (Casamiquela 1967; Bonaparte 1976) and the appearance of fragmentary heterodontosaurid material from the Late Triassic of Argentina (Báez and Marsicano 2001), as well as the possible heterodontosaurid affinities of *Echinodon becklesii* from the Early Cretaceous of England (e.g. Norman and Barrett 2002; Butler et al. 2012; Sereno 2012). Though the heterodontosaurid relationships of these animals were not unambiguously supported in all recent analyses, the discovery of four new species of undisputed heterodontosaurid affinities has modified the current understanding on the evolution of this group. Recent phylogenetic studies on Heterodontosauridae placed *Fruitadens haagarorum* (Butler et al. 2010, 2012), *Tianyulong confuciusi* (Zheng et al. 2009) and *Manidens condorensis* (Pol et al. 2011) as successive sister taxa of South African heterodontosaurids. More recently, Sereno (2012) described a new heterodontosaurid taxon from the Early Jurassic of South Africa, *Pegomastax africanus*, which was placed as a sister taxon of *Manidens condorensis*, and revised the taxonomy, evolution and masticatory function of heterodontosaurids. These new studies offered new data that changed our understanding of heterodontosaurid evolution, including the timing of their radiation, their biogeographic history, and the acquisition and development of adaptations to herbivory in their dentition.

The dental anatomy and phylogenetic position of *Manidens condorensis* within Heterodontosauridae revealed a previously unknown stage on the evolution of this group of ornithischian dinosaurs (Pol et al. 2011). The heterodontosaurid species from the Southern Hemisphere (*Manidens*, *Pegomastax*, *Abrictosaurus*, *Heterodontosaurus* and *Lycorhinus*) differ remarkably from the species of the Northern Hemisphere (*Fruitadens*, *Echinodon* and *Tianyulong*) in their dentition and were recently clustered in the subclade Heterodontosaurinae by Sereno (2012). Although *Pisanosaurus* (Casamiquela 1967; Bonaparte 1976) and the fragmentary Triassic Argentinean material (Báez and Marsicano 2001) are actually regarded as dubious specimens (Sereno 2012), the interpretation of these fragmentary remains as heterodontosaurids could also represent the oldest record for the family (Bonaparte 1976; Báez and Marsicano 2001; Butler, Upchurch, et al. 2008, 2012). Furthermore, the South African heterodontosaurids have been characterised by the extensive and obliquely disposed wear facets that formed a wide occlusal surface (Hopson 1980; Norman et al. 2011; Sereno 2012), a similar feature is also present in *Pisanosaurus* and the fragmentary Triassic Argentinean material (Bonaparte 1976; Báez and Marsicano 2001). Although Sereno (1991) noted that the wear facets do not form a continuous surface between teeth such as *Heterodontosaurus*, the mentioned set of features suggests the presence of an orthal jaw movement with a transverse component and/or a rotation of the lower jaw along its long axis during occlusion, reflecting an advanced stage in the evolution of herbivory (Porro 2007; Holliday

and Witmer 2008; Norman et al. 2011; Sereno 2012). Although both *Pisanosaurus* and the Laguna Colorado specimens share several features with heterodontosaurids (Báez and Marsicano 2001; also see Sereno 1991, 2012; Butler, Upchurch, et al. 2008, 2012) and basal ornithischians (e.g. Irmis et al. 2007), further analysis and more complete specimens are needed to clarify their phylogenetic affinities. However, the taxa from the Northern Hemisphere, which include more recent species, have non-overlapping plesiomorphic crowns (i.e. leaf-shaped, mesiodistally symmetrical teeth with denticles disposed along the margin, similar height of crowns along the toothrow and absence of extensive wear facets [Norman and Barrett 2002; Zheng et al. 2009; Butler et al. 2010]).

In this context, the dental anatomy of *Manidens condorensis* has an important unique combination of characteristics. In the holotype MPEF-PV 3211, the lower postcaniniform toothrow has anteroposteriorly heterogeneous crowns in their height–width proportions that are mesiodistally imbricated, indicating an incipient evolutionary stage in the formation of a compact toothrow. This dental arrangement represents an intermediate stage between the plesiomorphic dentition of northern heterodontosaurids and the highly derived (but early appearing) dentition of some South African heterodontosaurids (e.g. *Heterodontosaurus*) that have a greater specialisation of their dental anatomy. The pattern of dental transformations related to the increasing adaptation to herbivory differs in heterodontosaurids and other ornithischian groups (Pol et al. 2011), underscoring the unique evolutionary path that led to the sophisticated chewing mechanism of heterodontosaurids.

Here, we describe new and well-preserved isolated teeth that have been found at the same locality and horizon as the holotype of *Manidens condorensis*. The detailed comparison between the new isolated teeth and the lower teeth of MPEF-PV 3211 revealed the presence of shared features (including several autapomorphies) that allow referral of the isolated teeth to this taxon. These new isolated teeth are much better preserved than those of the holotype and therefore provide new anatomical information to characterise the particular dentition of *Manidens condorensis*. Given the heterogeneous dentition of this taxon within the toothrow (represented by the lower postcaniniform crowns), we carried out statistical analyses to infer the position of each isolated tooth along the toothrow. This approach furthermore provides predictive functions that will be useful for future discoveries of isolated teeth of *Manidens condorensis*, and a methodological framework that could be applied to other extinct taxa with heterodont dentition.

1.1 Institutional abbreviation

MPEF-PV, Museo Paleontológico Egidio Feruglio, Trelew, Argentina.

2. Systematic paleontology

Dinosauria Owen, 1842

Ornithischia Seeley, 1887

Heterodontosauridae Kuhn, 1966

Manidens Pol, Rauhut and Becerra, 2011

Manidens condorensis Pol, Rauhut and Becerra, 2011

(Figures 1–2 and 6)

2.1 Holotype

MPEF-PV 3211, partial associated skeleton, including about 80% of the skull and lower jaws, vertebrae of cervical, dorsal and sacral regions, left scapula and coracoid, and almost complete pelvic girdles (Pol et al. 2011).

2.2 Referred material

MPEF-PV 1719, MPEF-PV 1786, MPEF-PV 1718, MPEF-PV 3810 and MPEF-PV 3811 were originally referred to this taxon by Pol et al. (2011) based on general similarities. MPEF-PV 3812, MPEF-PV 3813, MPEF-PV 3814, MPEF-PV 3815 and MPEF-PV 3816 are new referred remains. All of them are isolated teeth.

2.3 Locality and horizon

The holotype and referred material were collected from the microvertebrate locality Queso Rallado (Rauhut et al. 2002; Rougier, Martinelli, et al. 2007), approximately 5.5 km north-west of the Cerro Cóndor village (see also Pol et al. 2011, Supplementary Material, available online). These outcrops have been included within the Cañadón Asfalto Formation and this particular layer is a silicified mudstone within a series of mudstones and limestones, representing a lacustrine environment (Rougier, Garrido, et al. 2007). The Cañadón Asfalto Formation has traditionally been regarded as Callovian–Oxfordian based on the floral content of this unit (e.g. Tasch and Volkheimer 1970; Silva Nieto et al. 2002, 2003); however, recent radioisotopic dates of this unit yielded more ancient ages (ranging from the late Toarcian to the early Bathonian [Salani 2007; Cabaleri et al. 2010; Cúneo et al. 2013]). These older dates have also been supported by recent and detailed studies of the palynoflora of the Cañadón Asfalto (Volkheimer et al. 2009; Zavattieri et al. 2010; for additional discussion of the geology and age, see Cuneo et al., in press). The age of this unit is therefore currently regarded as ranging from the latest Early Jurassic to the Early-Middle Jurassic. Because the Queso Rallado locality is placed in the basal part of the formation, a late Early Jurassic age for *Manidens* is likely.

2.4 Emended diagnosis

Small heterodontosaurid (estimated body length of approximately 50–60 cm) with the following autapomorphies: jugal with strongly developed, dorsally placed lateral boss; dorsal part of the postorbital process of the jugal very slender and flexes abruptly posteriorly at the beginning of the articular facet for the postorbital; forebrain facet on the ventral surface of the frontal enlarged and with significantly raised margins; external mandibular fenestra absent; posterior teeth with asymmetric arrangement of denticles and with a mesial concavity in which the distal margin of the preceding tooth is lodged (as in cerapodan ornithischians; e.g. Chinnery et al. 1998; Rauhut 2001; Galton 2007); the posteriormost dentary tooth ‘hand shaped’ in lateral view, with only one or two mesial denticles, the most anterior of which diverges mesially from the mesial margin of the crown (acting like a ‘thumb’ in the ‘hand-shaped’ crown) and four to five distal denticles apically to distally oriented (acting like the remaining ‘fingers’ in the ‘hand-shaped’ crown); the presence of small crenulations along the cutting margin of each denticle, exclusively formed by the enamel (the underlying dentine is unaltered); antorbital fossa reaches the jugal anterior process, deviating below the jugal boss; mesial denticulate margin approximately 60% of the length of the distal margin; apical and basal wear facets on the labial surface of the dentary crowns that are vertically oriented.

2.5 Referral of isolated teeth to *Manidens condorensis*

The new isolated teeth and those of the dentary of the holotype of *Manidens condorensis* (MPEF-PV3211) share several diagnostic morphological characters. These include mesiodistally asymmetrical, labiolingually compressed and leaf-shaped crowns that bear a central, conspicuous apicobasal ridge and a few slightly developed apicobasal ridges on both surfaces of the crown. These ridges originate at the base of each denticle, extend basally along the surface of the crown and disappear before reaching its base. The margin of the crowns has morphologically subequal denticles that are apicodistally or distally oriented (except the mesialmost denticle). In addition, the isolated teeth share the dental autapomorphies of *Manidens condorensis* noted by Pol et al. (2011), such as the presence of a mesial groove, delimited by two ridges, denticles asymmetrically disposed on the tooth margin (with one or two mesial denticles and four to six distal denticles), the mesialmost denticle mesially projected above the mesial margin and small enamel crenulations on the margins of the denticles. The presence of these features allows us to refer these crowns to *Manidens condorensis* (crown pictures showed in Pol et al. 2011, Figure 2(e)–(i)) and the presence of wear facets allows us to infer some aspects of the masticatory

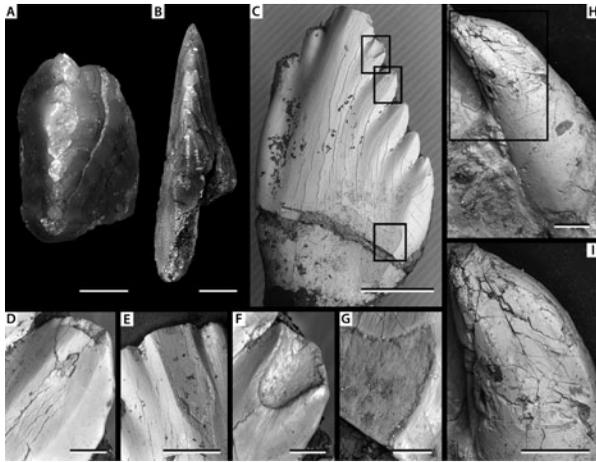


Figure 1. Main morphological features of the crowns of *Manidens condorensis*. (A) Occlusal view of MPEF-PV 3813; (B) distal view of specimen MPEF-PV1719; (C) occlusal surface of crown of MPEF-PV3812, boxes show the areas with wear facets with detailed the SEM images (D, F and G); (D) detail of apical wear facet of MPEF-PV 3812, in which the dentine is not exposed; (E) detail of apical planar wear facet of MPEF-PV 1786, both enamel and dentine are worn; (F) detail of apical concave wear facet of MPEF-PV 3812, exposing both enamel and dentine, (G), basal planar wear surface of MPEF-PV 3812; (H and I) lower caniniform tooth of the holotype MPEF-PV 3211. Scale: 1 mm.

movement, in this case predominantly orthal. Finally, due to the absence of a lingual view of dentary crowns and the lack of adequately preserved crowns in the maxilla of MPEF-PV 3211, the identification to the maxillary or dentary toothrow of isolated crowns is not possible at the moment.

2.6 New anatomical information on the dentition of *Manidens condorensis*

The well-preserved isolated teeth provide new information on the dentition of *Manidens condorensis*. These teeth show that the labial and lingual surfaces of the crown differ in their basal extension, the development of their apicobasal ridges and the basal extension of the apicobasal ridges. In occlusal view, both surfaces of the crown are mesiodistally convex (related to the development of the central ridges; Figure 1(A)), and the surface that is more basally extended is also slightly apicobasally concave in distal view (related to a basally bulbous crown; Figure 1(B)). Finally, and more importantly, the isolated crowns reveal new autapomorphic features related to the presence of unusually developed wear facets. Two distinct types of wear facets are present in the more basally extended surface of the preserved teeth: one is located apically on the crown (on the denticles) and the other is a flat wear facet located at the base of the crown (Figure 1(C)–(G)). The apical wear facets extend on the surface of the

denticles and are mostly flat to slightly concave and vertically oriented. The facets expose only the enamel or both enamel and dentine, depending on the stage of wear. The facets of the different denticles of the same crown are coplanar to each other, suggesting that they were produced by tooth–tooth occlusion (Figure 1(C)–(E)). A few facets have the dentine surface slightly apicobasally concave, which may have been produced by differential wear by food abrasion (Figure 1(F); see Costa and Greaves 1981). The basal wear facets are also interpreted as being caused by tooth–tooth occlusion, as they form a simple, laterodistally oriented planar surface (Figure 1(G)). The isolated crowns and the holotype crowns show insufficient evidence to identify maxillary and dentary crowns, and almost all isolated crowns reveal the presence of wear facets (and evidence for dental occlusion) in the apicobasally higher side of the crown. Based on the observed asymmetry in the available teeth and the fact that asymmetric teeth can be inversely oriented in the mandible and maxilla among ornithischians (specular disposition of features on the faces of opposing crowns, being the lingual face of maxillary crowns similar to the labial face of dentary crowns and the labial face of maxillary crowns similar to the lingual face of dentary crowns; e.g. *Dryosaurus lettowvorbecky* Norman, 2004; *Hypsilophodon foxii* Galton, 1974), here we assume that the apicobasally higher face represents the surface that came into contact with the opposing teeth during the occlusion (because is generally worn), and that there is no marked morphological differentiation between the maxillary and dentary crowns. With this, to save words to refer to each surface of the crown during this study, and counting on that the differentiation of maxillary and dentary crowns remains unsolved (including also the differentiation in lingual and labial views of each crown), the worn surface of the crown is here named as ‘occlusal surface’, whereas the opposite unworn surface is here called ‘non-occlusal surface’, rather than labial or lingual. Finally, the Scanning Electron Microscope images of the caniniform tooth MPEF-PV 3211 revealed the presence of a planar and continuous worn surface that is labiomessially oriented. This facet is limited mesially by a smooth border and both basally and apically by a fracture (Figure 1(H)–(I)). Apically worn caniniforms have been reported for *Lycorhinus* and *Heterodontosaurus* (Gow 1990; Norman et al. 2011), but Sereno (2012) cast doubts on this particular feature. In *Manidens*, the wear surface is planar, continuous and does not reach the apex of the crown (contrasting with the alleged wear facets of the other taxa). Given that, in other heterodontosaurids, the dentary caniniform tooth is lodged posterior to the premaxillary caniniform tooth during occlusion, this facet might reflect tooth-to-tooth occlusion of the caniniform teeth at least during some part of the mastication cycle.

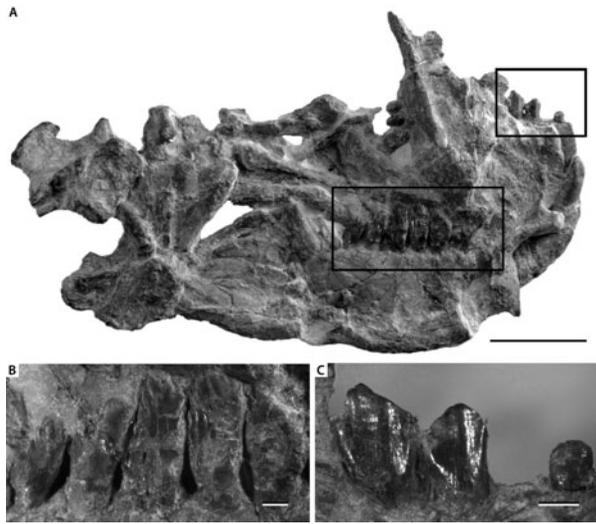


Figure 2. Dental material preserved in the holotype of *Manidens condorensis* (MPEF-PV 3211). (A) General view, boxes show the crowns detailed in B and C; (B) last five dentary postcaniniform crowns; (C) first three dentary postcaniniform crowns. Scales in A, 1 cm; B and C, 1 mm. Mesial to the right, all images in labial view (mentioned also as occlusal surface).

3. Materials and methods

The specimens used in this study include the best preserved postcaniniform crowns of the dentary of the holotype of *Manidens condorensis* (MPEF-PV 3211; Figure 2), which are the second, third, seventh and ninth postcaniniform teeth, and all the referred isolated crowns (MPEF-PV 1719, MPEF-PV 1786, MPEF-PV 1718, MPEF-PV 3810, MPEF-PV 3811, MPEF-PV 3812, MPEF-PV 3813, MPEF-PV 3814, MPEF-PV 3815 and MPEF-PV 3816; see Supplementary Material, available online).

For the geometric morphometric analysis (GMA), the photos were first treated with MakeFan6 software (Sheets 2003) to draw guidelines to help in the determination of landmarks and semilandmarks. The specimen image files (TPS files) were generated using tpsUTIL 1.46 (Rohlf 2010a). The digitalization and scaling of landmarks and semilandmarks were performed out using tpsDIG 2.16 (Rohlf 2010b). Landmark and semilandmark configurations were superimposed using generalised procrustes analysis (GPA; Goodall 1991; Rohlf 1999) to eliminate the distorting effects caused by different factors (translation, scaling, rotation), following the least squares criterion (the sum of the squared distances between the corresponding points is minimised). The semilandmarks were slid using the minimum bending energy criterion (Bookstein 1997), which consist of sliding the semilandmarks until the strain energy is minimised, softening the deformation between curves (Pérez et al. 2006). The aligned coordinates of landmarks and semilandmarks of all specimens were compared using a thin-plate spline function (Bookstein 1989). The partial deformation (partial warps) and

principal components (relative warps) were calculated using tpsRELW 1.49 (Rohlf 2010c). Further details of this analysis are given in the Supplementary Material, available online.

The discriminant analysis (DA) was carried out using the Infostat free version program (Di Rienzo et al. 2011). The measurements of each metrical variable used in the DA were obtained using a digital caliper (accuracy 0.01 mm).

4. Morphological variation in the toothrow of *Manidens condorensis*

The heterodont dentition of *Manidens condorensis* includes a lower caniniform teeth and a morphologically variable postcaniniform toothrow that is almost completely preserved in the dentary of the holotype material. The tooth count is at least 11 in the dentaries, including the hypertrophied anterior caniniform (a low tooth count as in other heterodontosaurids [Pol et al. 2011], including the closely related taxon *Pegomastax* [Serenio 2012]). The caniniform is the largest tooth of the dentary. It is a stout element, with a recurved apex, and is slightly compressed labiolingually. This tooth seems to lack marginal serrations, in contrast to the caniniform teeth of the South African heterodontosaurids *Heterodontosaurus*, *Lycorhinus*, *Abriictosaurus* and *Pegomastax* (Charig and Crompton 1974; Hopson 1975; Serenio 2012). However, an unserrated carina is present distally, but apparently not mesially, although the apical wear opens the possibility that a short carina might have been present along the apical part. The postcaniniform crowns vary transitionally along the toothrow in shape, size and proportions. Basically, the first three postcaniniform crowns are rhomboidal-shaped small crowns, but distal to these elements the crowns increase in size rapidly and become mesiodistally expanded. The teeth in the middle of the toothrow are higher apicobasally than broad mesiodistally, with the highest tooth crowns being more than 1.5 times higher than broad. Especially, high tooth crowns were traditionally considered to be a synapomorphy of heterodontosaurids (e.g. Weishampel and Witmer 1990; Norman et al. 2004), but the crowns are considerably lower in the basal heterodontosaurids *Echinodon*, *Fruitadens*, *Tianyulong* and an unnamed taxon from the Early Jurassic Kayenta Formation (Norman and Barrett 2002; Zheng et al. 2009; Butler et al. 2010, 2012; Serenio 2012), so that such a high crown height/crown width ratio represents a synapomorphy shared by *Manidens* and the South African forms (Heterodontosaurinae *sensu* Serenio 2012). Finally, the last two crowns decrease in height, but not in mesiodistal width. Due to preservation, the maxillary toothrow in MPEF-PV 3211 includes only four apically incomplete crowns, which are labially and mesially worn. The

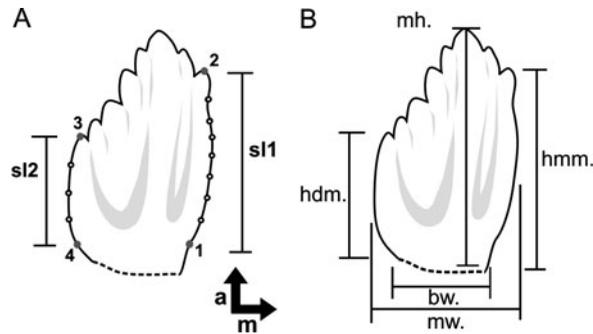


Figure 3. (A) Definition of landmarks and semilandmarks for the morphogeometrical analysis, including schematic representation of landmarks (grey) and semilandmarks (white) position: 1, basalmost point of the mesial margin; 2, apex of the first denticle; 3, apex of the last denticle; 4, basalmost point of the distal margin; sl1 and sl2, semilandmarks describing the margin between two landmarks. (B) Variables measured on each crown for the DA: hdm, height distal margin; mh, maximum height; hmm, height mesial margin; bw, basal width; mw, maximum width; a, apical; m mesial. The arrows represent a view of the occlusal surface of the crown.

preserved maxillary crowns vary slightly in height. On the basis of the available information, we assume that the observed variation within the dentary tooththrow was also present in the maxillary tooththrow. Thus, the lower tooththrow present in MPEF-PV 3211 is here used as a proxy for representing the shape variation for both maxillary and dentary tooththrows.

The variation of these characteristics along the tooththrow is also observed in isolated crowns referred to *Manidens condorensis*, and could therefore provide useful information to identify their position. This is of particular interest, given that the isolated crowns are much better preserved than those of the holotype (see Figure 2), so that a detailed identification of the position of these teeth will improve our knowledge on the available morphological information on the peculiar dentition of *Manidens condorensis*. In the following section, we use morphometric data to perform two statistical analyses to test the identification of the position of the new isolated teeth using the postcaniniform mandibular teeth of the holotype as a reference.

5. Morphometric characterisation of the tooththrow of *Manidens condorensis*

Although we only have 14 teeth (data points) for the two statistical analyses (including the isolated teeth and those of the holotype), our aim is to provide a quantitative approach to characterise the different regions of the postcaniniform tooththrow, rather than achieving the values of statistical significance for the inference made upon these variables (for which a much larger sample would be needed). We first conducted an exploratory GMA, which aims to search for the existence of morphological clusters.

Second, we conducted DA with metrical variables to re-evaluate the nature of the clusters of teeth identified in the GMA. Third, we obtained a canonical function, which will allow identifying the position of future findings of isolated teeth based on the morphometric data.

5.1 Geometric morphometric analysis

The described transitional change within the tooththrow of the holotype is reflected in the morphological variation in the proportions of the isolated teeth here reported, as each of these isolated crowns shares features with only a few crowns of the holotype. The differences between specimens were measured by defining landmarks and semilandmarks. The combination of these variables in the studied specimen is used to define a 2D morphospace on the basis of the shape variation (Bookstein 1991, 1997; Richtsmeier et al. 2002). Based on the premise that the similarity between isolated teeth and those attached to the dentary of the holotype will be reflected in the location of the specimens in the morphospace, this method should show morphological clusters that would relate crown morphology and dental position along the tooththrow. The GPA method ensures that the variation explained by size is excluded from the total variance, thus reducing the variance to that explained by shape differences.

The landmarks and semilandmarks were defined following a mesiodistal arrangement within the crown. Four landmarks and 10 semilandmarks were used, which summarise the morphological information available from the occlusal (apicobasally higher) surface of the crown (Figure 3(A)). Theoretically, each landmark and group of semilandmarks should represent homologous structures. In this particular analysis, the homology of each point corresponds to a positional homology within the tooth (see Figure 3(A)). Although the isolated crowns are excellently preserved, some of the holotype crowns have a damaged apex and only have their labial (occlusal) surface exposed (Figure 2(B)). Because of this, we did not define a landmark for the tooth apex or on the non-occlusal surface of the crowns.

5.1.1 Results

The results of the GMA show that the first two components explain 89.5% of the total variance among the specimens, determining three different clusters (Figure 4). The first component (Rel1 in Figure 4) explains 76.97% of the total variance. This variation implies towards positive values of this axis, the relative increase of the mesiodistal width (an increase in the distance between landmarks 1 and 4, and 2 and 3), a decrease in the distance between landmarks 1 and 2, and a decrease in the mesial projection of mesial denticle (captured by semilandmarks between landmarks 1

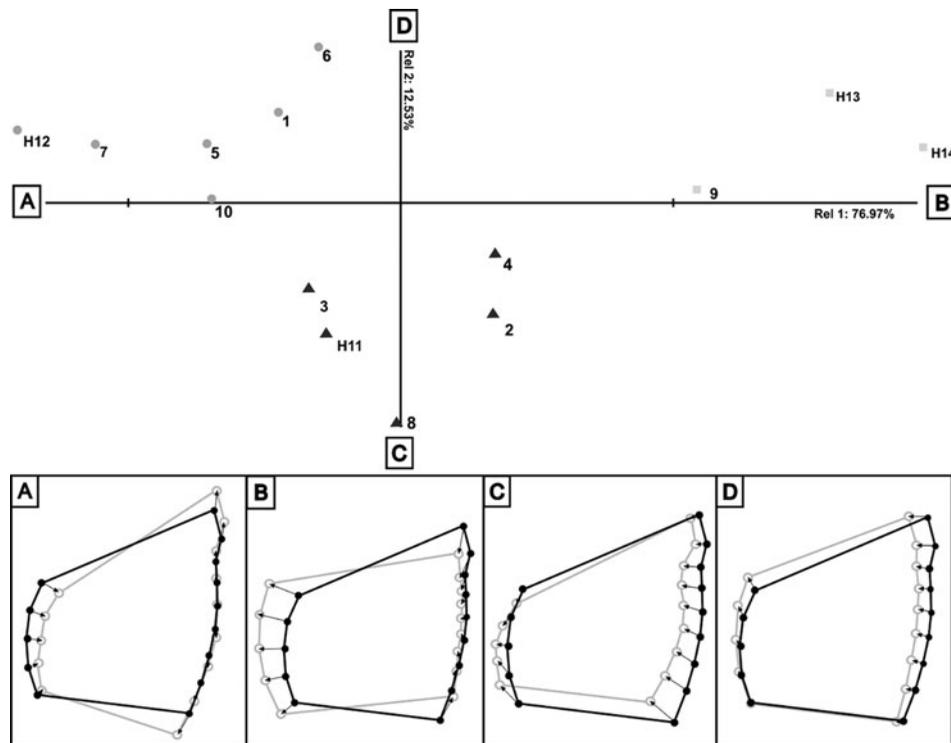


Figure 4. Morphometric analysis results, modified to clarify the three different groups. A–D show the shape of most extreme values of each axis in grey (A and B in axis X, C and D in axis Y) and the consensus in black (shape in the origin), the vectors show the morphological change: 1, MPEF-1718; 2, MPEF-1719; 3, MPEF-1786; 4, MPEF-3810; 5, MPEF-3811; 6, MPEF-3812; 7, MPEF-3813; 8, MPEF-3814; 9, MPEF-3815; 10, MPEF-3816; H11, holotype, ninth crown; H12, holotype, seventh crown; H13, holotype, third crown; H14, holotype, second crown.

and 2; see Figure 4(A),(B)). On the basis of the information provided only by this component, there is a clearly separated group formed by the anterior teeth of the holotype (H13, H14; Figure 4) and one of the isolated teeth (9; Figure 4). The other teeth of the holotype (H11 and H12; Figure 4) are located towards negative values of this axis, showing the change from the lower and wider anterior crowns, to the higher and narrower crowns of the medial and posterior portion of the lower toothrow of *Manidens*. Most of the isolated crowns (1–8 and 10) are located along the first component (Rel1) between the mid to posterior teeth of the holotype (H11 and H12).

The second component (Rel2 in Figure 4) explains 12.53% of the total variance. This variation includes the posterior projection of the apical region of the crown (landmarks 2 and 3) with respect to the base of the crown (landmarks 1 and 4) and the increase in the height of the distal margin (hdm) of the crown (progressive separation of landmarks 3 and 4).

5.1.2 Morphological clusters

Based on these results and the location of all teeth along these two axes, the specimens analysed are classified into three different groups or morphological clusters. This

clustering is mainly explained by the difference in height of the mesial margin (hmm) and hdm of the crowns, which vary markedly along the toothrow of *Manidens*. In the left sector of the graphic, the crowns are higher than wide and have the mesial margin apicobasally higher than the distal margin (circles in Figure 4). Towards the right, the crowns are wider than high (with a smaller difference between the hdm and hmm; triangles in Figure 4). Finally, the low crowns with distal and mesial margins that are subequal in height are located at the right end of the graphic (squares in Figure 4).

The location of the crowns of the holotype in this graph helps allocating the isolated teeth into three distinct clusters that are morphometrically distinguishable. These clusters are referred herein as anterior crowns (squares in Figure 4), middle crowns (circles in Figure 4), and posteriorly placed crowns (triangles in Figure 4), representing the three regions of the toothrow observed in the crowns of the holotype.

The groups defined from the GMA can be further analysed through DA based on the simple morphometric measures to test if simple measurements can be used to easily identify the position of isolated teeth, which would be useful for the new discoveries of isolated teeth of *Manidens condorensis*.

5.2 Discriminant analysis

DA uses the clusters identified through the GMA and a set of simple morphometric measures to test if the latter are informative to infer the position of isolated teeth in the toothrow of *Manidens* (using as comparative source those teeth found in the dentary of the holotype). Working with more easily measurable variables facilitates expanding these results to determine the position of future discoveries.

The metrical variables of the occlusal surface of the crown used for the DA are basic height and width linear dimensions of different regions of the crown (Figure 3(B)). For the two apically incomplete anterior crowns on the holotype lower toothrow (Figure 2(C)), the values of maximum height (mh) could not be measured. To circumvent this problem, we carried out a sensitivity analysis by varying the estimated mh value of the incomplete crowns extending up to 0.5 mm beyond the preserved apical region, to test how the uncertainty on the height of these elements (20% and 24% of the preserved length of the crown) affects the results of the DA. The results of these measured variations were tested in multiple DAs and we corroborated that it does not affect the significance of the identification and the contribution of each variable to the delimitation of clusters.

On the basis of this result, we used the maximum preserved height, ignoring the apical incompleteness of these two anterior crowns. All new variables were measured in both the holotype and the isolated crowns. The values of each metrical variable are detailed in the Supplementary Material, available online.

5.2.1 Results

The first canonical axis of the DA explains 63.13% of the total variance (eigenvalue, Table 1(C)) and it shows a clear separation of two cloud points: the crowns placed in the middle and anterior region of the holotype toothrow, on the one hand (circles and squares in Figure 5(B)), and the crowns placed in the posterior region of the holotype, on the other hand (triangles in Figure 5(B)). The clustering of the isolated crowns with those of the holotype in the DA (Figure 5B) is consistent with that of the GMA (Figure 4). All the measured variables contribute to the first canonical axis, but the largest contribution is given by maximum width (mw) and mh (see Figure 5(A)). The mw relates directly to the values of this canonical axis, but the mh does so inversely (Figure 5(A)). This means that crowns with high positive values for the canonical axis 1 have the

Table 1. DA results.

A. Centroids in the discriminant space					
Groups	Axis 1	Axis 2			
1	-1.07	3.02			
2	-1.83	-1.26			
3	2.84	0.3			
B. Canonical discriminant functions					
	1	2			
Constant	-1.32	3.78			
mh	-7.48	-0.85			
bw	1.45	1.84			
mw	7.85	-1.26			
hmm	3.2	-1.68			
hdm	-2.68	1.97			
C. Eigenvalues					
Eigenvalues	%	Accumulated %			
5.8	63.13	63.13			
3.39	36.87	100			
D. Cross-classification table					
Group	1	2	3	Total	Error (%)
1	3	0	0	3	0
2	0	6	0	6	0
3	0	0	5	5	0
Total	3	6	5	14	0

Notes: A, centroid coordinates of each cluster in the discriminant space; B, coefficient values for the canonical function; C, variance percentage explained by each canonical axis or eigenvalues; D, resulting table showing how many specimens of each group were correctly assigned. Group 1, 'anterior region' crowns; group 2, 'middle region' crowns; group 3, 'posterior region' crowns.

characters not considered in the morphometric analyses. This anterior crown is labiolingually narrow and the mesial cavity is barely developed, both apically and labiolingually. The mesial cavity does not reach the base of the first denticle, which is consistent with the well-spaced arrangement of anterior crowns in the lower tooththrow of the holotype of *Manidens*. The anterior teeth have two mesial denticles and four distal denticles, less than in middle and posterior teeth. The mesial denticles are less prominent in anterior teeth than in middle and posterior teeth and the mesialmost denticle is projected apically. The apex of the anterior tooth (MPEF-PV 3815) is more clearly separated from the marginal denticles than in middle and posterior teeth (Figure 6(B),(D)). The ridge of the occlusal surface extending basally from the apex is broader than in middle and posterior teeth, approximately occupying the mesial half of the occlusal surface of the crown. Finally, the apical region of the crowns of anterior teeth is not posteriorly recurved as in the middle and posterior regions. These differences help characterising the morphological features of the anterior crowns of *Manidens condorensis*.

6.2 Middle region

The teeth included in this group have a similarly high ratio of mh to mw (DA) as the anterior crowns, but differ from them in a larger difference between the hmm and hdm (GMA). These teeth also have the largest apicobasal height of the lower tooththrow (considering both the maximum crown height and the hmm).

The crowns of the middle region also differ from other teeth in characters not considered by the morphometric analyses, such as having the apicobasally highest crowns and a deeper mesial cavity than all other elements of the tooththrow (Figure 6(E)–(G)). The development of a deep mesial cavity is related to the tight marginal contact between adjacent crowns in the middle region of the tooththrow. The apicobasally high crowns of the middle region also have more denticles on their distal margin than other teeth. There are five well-developed denticles and an incipiently developed denticle that is partially merged with the apex of the tooth (e.g. MPEF-PV 3813; see Supplementary Material, available online). The mesial margin of the teeth of the medial region bears two denticles, as well as an incipiently developed denticle that is partially merged with the apex of the tooth (e.g. MPEF-PV 3813; see Supplementary Material, available online). The two mesial denticles of these teeth are well spaced from each other and differ in shape and size. The basalmost of these two denticles is more conspicuous in comparison with those of anterior teeth and projects apically (with only a slightly developed mesial deflection), whereas the other denticle is small, as those of anterior teeth.

6.3 Posterior region

The crowns of the posterior region have a lower ratio of crown height/bw than preceding elements of the tooththrow (DA). The mesial margin is apicobasally higher than the distal margin, but not as much as in the crowns of the middle region (GMA). The crowns of the posterior region

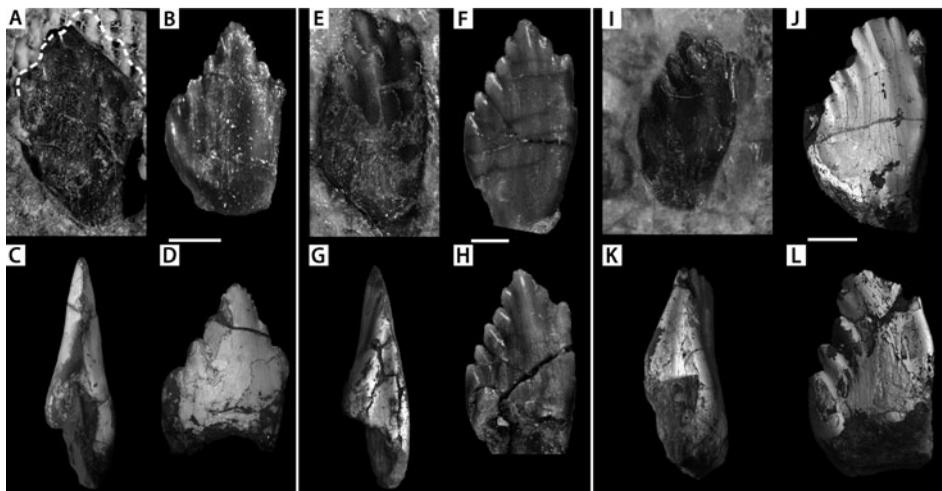


Figure 6. Pictures of representative specimens of the defined regions using GMA and DA analyses; anterior (A–D), middle (E–H) and posterior region (I–L), including isolated and holotype crowns. Some images were rotated to allow orientation. (A) Third holotype crown preserved, labial view, the punctuated line represents the non-preserved apical region; (B–D) specimen MPEF-3815 in occlusal surface, mesial and non-occlusal surface view, respectively; (E) seventh holotype crown preserved in labial (occlusal surface) view; (F–H) specimen MPEF-1719 in occlusal surface, mesial and non-occlusal surface view, respectively; (I) ninth holotype crown preserved in labial (occlusal surface) view; (J and K), specimen MPEF-1786 occlusal surface and mesial views; (L) specimen MPEF-1718 in non-occlusal surface view. Scales: 1 mm. In mesial view, occlusal surface on right; in non-occlusal and occlusal surface view, mesial on right.

also differ from other elements of the toothrow in characters not considered by the morphometric analyses, such as having the labiolingually broadest mesial cavity (Figure 6(K)). The number of denticles on the distal margin of the posterior teeth is either five or four, and they differ from those of the anterior and middle region in being more distally projected and in having deeper interdenticular slits. There are two well-developed mesial denticles in the posterior teeth. These also differ from those of other regions in having deeper interdenticular slits, and the basalmost denticle of the posteriormost teeth has an apicommesial projection (MPEF-PV 3211; Figure 6(I)). The posterior region of the dentition of *Manidens* has the strongest imbrication of adjacent crowns, which is favoured by both the remarkably broad mesial cavity (Figure 6(K)) and the anterior projection of the basalmost mesial denticle and the posterior convexity of the distal margin of the crown (Figure 6(L)).

7. Applicability to new discoveries

The statistical analyses carried out help assigning isolated crowns to a hypothetical position within the toothrow. The DA also formulates a discriminant function that maximises the explained variance to form the previously obtained clusters using the defined metrical variables as a starting point. This discriminant function indicates the contribution of each variable to the explained variance in each canonical axis (obtained from the eigenvectors; see Table 1(B)). The simple metric variables used in this analysis can easily be measured in new isolated lower teeth of *Manidens* to determinate its coordinates in each canonical axis from the canonical function (see Table 1). This will provide a quantitative justification for identifying the approximate position along the toothrow.

The component of the variance explained by canonical axis 1 can be determined by the following equation:

$$Z_x = -1.32 - (7.48 \times mh) + (1.45 \times bw) + (7.85 \times mw) \\ + (3.2 \times hmm) - (2.68 \times hdm).$$

And the component of the variance explained by canonical axis 2 can be determined by the following equation:

$$Z_y = 3.78 - (0.85 \times mh) + (1.84 \times bw) - (1.26 \times mw) \\ - (1.68 \times hmm) + (1.97 \times hdm).$$

8. Discussion

The morphological variation along the postcaniniform toothrow of *Manidens condorensis* (Becerra et al. 2011;

Pol et al. 2011) is clearly transitional (i.e. anteroposterior variation of height and width of the crowns), but the morphological and statistical analyses carried out here allow to go further and distinguish three morphologically distinct regions. This division of the dentary toothrow is not only useful for descriptive purposes but also enables the assignment of isolated crowns of *Manidens* to the anterior, middle or posterior regions of the toothrow, based on the morphometric characteristics. Although the use of statistical analyses for identifying the position of isolated crowns provides only a hypothesis based on the currently available evidence, it is worth noting that we have reached consistent results using three different approaches: the identification of discrete morphological characters, the use of landmarks and semilandmarks in geometric morphometrics and simple metric measures in the DA. Furthermore, the DA also provided a canonical function that will facilitate the identification of the position of new isolated teeth of *Manidens condorensis*. Finally, depending on the statistical method, the three regions of the postcaniniform toothrow of *Manidens condorensis* can be distinguished by the ratio of mh to mw (DA) or by the difference between hmm and hdm (GMA). This opens the possibility of applying one or the other method depending on the measures or landmarks that are available in incompletely preserved teeth.

Based on these results, working with statistical methods on isolated teeth can increase knowledge of a particular species or even operate as a tool for taxonomic assignments at higher levels. In an example, the study of isolated teeth dinosaur taxa provides difficulties in terms of their taxonomic assignment and, in many cases, such elements can only be referred to higher taxonomic groups (e.g. Currie et al. 1990; Chinnery et al. 1998; Barrett and Wang 2007; Ruiz-Omeñaca et al. 2010; Saegusa and Tomida 2011). However, the highly variable dental morphology of ornithischian taxa allows in some cases (with the corresponding morphological comparison) reaching the identification of isolated crowns up to the species level, although many of these taxa are highly incomplete and either have uncertain phylogenetic affinities or have been subsequently regarded as *nomina dubia* (e.g. *Alocodon kuehnei*, *Trimucrodon cuneatus*, *Phyllodon henkeli* [Thulborn 1973], *Siluosaurus zhangqiani* [Dong 1997], *Iguanodon ottingeri* [Galton and Jensen 1979]). A similar approach with useful results have been conducted by Smith et al. (2005) on identifying higher taxonomic levels for isolated theropod teeth, showing the applicability of this approach even if teeth are not diagnostic at the species level (as in the case of theropods).

Finally, in some ornithischian groups (as well as other groups of extinct archosaurs), there is a marked variation in the proportions and morphology of the crowns along the toothrow (e.g. *Heterodontosaurus*, *Abrictosaurus*, *Lycorhinus*, *Lesothosaurus*, *Gasparinisaura*, *Orodromeus*, *Hyp-*

silophodon). The quantitative approach developed in this contribution for the study of isolated teeth of *Manidens condorensis*, therefore, has the potential of being applied in other heterodont taxa for inferring the position of isolated crowns. In many cases (such as the one of *Manidens*), this can help achieving a more complete and thorough knowledge on the dentition of some ornithischian dinosaurs, providing critical data for understanding the paleoecology and evolution of one of the two major groups of herbivorous dinosaurs.

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