Naturwissenschaften
DOI 10.1007/s00114-011-0780-5

ORIGINAL PAPER

A Middle Jurassic heterodontosaurid dinosaur from Patagonia and the evolution of heterodontosaurids

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Received: 9 October 2010 / Revised: 28 February 2011 / Accepted: 3 March 2011

Abstract Heterodontosauridae is a morphologically divergent group of dinosaurs that has recently been interpreted as one of the most basal clades of Ornithischia. Heterodontosaurid remains were previously known from the Early Jurassic of southern Africa, but recent discoveries and studies have significantly increased the geographical and temporal range for this clade. Here, we report a new ornithischian dinosaur from the Middle Jurassic Cañadón Asfalto Formation in central Patagonia, Argentina. This new taxon, *Manidens condorensis* gen. et sp. nov., includes well-preserved craniomandibular and postcranial remains and represents the only diagnostic ornithischian specimen yet discovered in the Jurassic of South America so far. Derived features of its anatomy indicate that *Manidens* belongs to Heterodontosauridae, as the sister taxon of *Heterodontosaurus* and other South African heterodontosaurids. The presence of posterior dentary teeth with high crowns but lacking extensive wear facets in *Manidens* suggests that this form represents an intermediate stage in the development of the remarkable adaptations to herbivory described for *Heterodontosaurus*. The dentition of *Manidens condorensis* also has autapomorphies, such as asymmetrically arranged denticles in posterior teeth and a mesially projected denticle in the posteriormost teeth. At an estimated total length of 60–75 cm, *Manidens* furthermore confirms the small size of basal heterodontosaurids.

Keywords Ornithschia · Gondwana · Jurassic · Cañadón Asfalto Formation · Heterodontosauridae

Introduction

The fossil record of ornithischian dinosaurs starts in the Late Triassic (Casamiquela 1967) and extends up to the end of the Cretaceous. However, the first 70 million years of ornithischian evolution are still poorly known (Butler et al. 2006, 2008a; Irmis et al. 2007), and our knowledge of early ornithschians is so far based almost entirely on fossils from a small number of geological units, such as the Elliot Formation of southern Africa (Knoll 2005; Butler et al. 2007; Irmis and Knoll 2008; Rauhut and Lopez-Arbarello 2008). One of the most conspicuous groups in Early Jurassic ornithischian assemblages is the Heterodontosauridae. Whilst it was long thought to represent an early and highly specialized lineage of derived clades of ornithischian dinosaurs, such as ornithopods (e.g. Sereno 1986, 1999; Weishampel and Witmer 1990; Norman et al. 2004a) or marginocephalians (Xu et al. 2006), recent research has reinterpreted this group as one of the most basal and

Communicated by Robert Reisz

Electronic supplementary material The online version of this article (doi:10.1007/s00114-011-0780-5) contains supplementary material, which is available to authorized users.

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successful radiation of ornithischians (Butler et al. 2007, 2008a). Furthermore, recent studies have demonstrated that this group was more widely distributed both geographically and stratigraphically than previously thought (Norman and Barrett 2002, Zheng et al. 2009, Butler et al. 2010). These studies have suddenly placed heterodontosaurids in a key position for understanding the origin and early evolution of ornithischian dinosaurs.

The Jurassic record of ornithischian dinosaurs from Gondwana is of special interest for our understanding of the early evolution of the group because basal members of the major lineages are found in the Late Triassic–Early Jurassic of southern Gondwana, indicating that the group as a whole might have originated here (Rauhut and Lopez-Arbarello 2008). However, the Jurassic ornithischian fossil record from Gondwana is currently restricted to the Early Jurassic of the Upper Elliot Formation of southern Africa (Knoll 2005) and the Late Jurassic Tendaguru Formation of Tanzania (Aberhan et al. 2002; Maier 2003; Rauhut and Lopez-Arbarello 2008). Apart from these units, Gondwanan ornithischians are only known from isolated remains (Barrett et al. 2008; Rauhut and Lopez-Arbarello 2008) and footprints (e.g. Moreno et al. 2004) that do not provide information for our understanding of the evolution of the group during the Jurassic.

The Cañadón Asfalto Formation of Chubut Province, Argentina, has yielded the most diverse and important Middle Jurassic terrestrial biota of Gondwana (Escapa et al. 2008). Vertebrate groups reported so far include basal members of every major lineage of terrestrial vertebrates to be expected in the Jurassic (Escapa et al. 2008), including a wealth of dinosaur remains (Bonaparte 1979, 1986; Rauhut 2003a, 2005; Escapa et al. 2008), pterosaurs (Rauhut et al. 2001; Cordoniú et al. 2010), turtles (Sterli 2008), mammals (Martin and Rauhut, 2005; Rauhut et al. 2002; Rougier et al. 2007a, b) and anurans (Báez and Nicoli 2008). Until recently, the dinosaur fauna was exclusively composed of sauropod and theropod saurischians, with only a single reported non-diagnostic specimen of an ornithischian (Rauhut and Lopez-Arbarello 2008). Here, we describe diagnostic ornithischian remains from a partially articulated skeleton found in this unit and evaluate its phylogenetic relationships and its significance for understanding the evolution of heterodontosaurid dinosaurs.

Systematic palaeontology

Dinosauria Owen, 1842
    Ornithischia Seeley, 1887
    Heterodontosauridae Kuhn, 1966
    Manidens condorensis gen. et sp. nov.

Etymology The genus name *Manidens*, from *manus* (Latin, hand) and *dens* (Latin, tooth), refers to the similarity of the posteriormost tooth to the human hand. The specific epithet *condorensis* refers to the nearby village of Cerro Cóndor, Chubut Province, Argentina.

Holotype MPEF-PV 3211 (Museo Paleontológico Egidio Feruglio, Trelew, Argentina), partial associated skeleton, including most elements of the skull and lower jaws, cervical, dorsal and sacral vertebrae, left scapula and coracoids, and almost complete pelvic girdles.

Referred material MPEF-PV 1719, 1786, 1718, 3810, 3811 isolated posterior teeth, from the same locality and horizon as the holotype.

Locality and horizon Queso Rallado locality within the Cañadón Asfalto Formation, 2.3 km west of the village of Cerro Cóndor, Chubut Province, Argentina. The bone-bearing layer is a silicified mudstone within a series of lacustrine mudstones and limestones (Rougier et al. 2007b). Further locality information is given in the Electronic supplementary material (ESM) and stratigraphic information can be found in Rougier et al. (2007b). GPS coordinates of this locality are deposited in the MPEF collections and are available upon request. The age of the Cañadón Asfalto Formation is usually given as Callovian–Oxfordian (e.g. Silva Nieto et al. 2002), but recent U–Pb radioisotopic age determinations (Cabaleri et al. 2010) and palynological research (Volkheimer et al. 2008) indicates that it is probably considerably older, with dates ranging from 171 ± 5 to 167 ± 4 Ma (Aalenian–Early Bathonian; Salani 2007; Cabaleri et al. 2010).

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; posterior teeth with asymmetric arrangement of denticles and with a mesial concavity in which the distal margin of the preceding tooth is lodged; posteriormost dentary tooth “hand-shaped”, with only one or two mesial denticles, the most anterior of which diverges mesially from the mesial margin of the crown; presence of small crenulations along the cutting margin of each denticle.

Description

The holotype has preserved most elements of the skull and lower jaws, most of the precaudal axial skeleton, including cervical, dorsal and sacral vertebrae, the left scapula and coracoid, and almost complete pelvic girdles (Fig. 1). Most of the elements of the skull roof are preserved, with the exception of the premaxillae, lacrimals, prefrontals and parietals, which could not be identified with confidence. Furthermore, the braincase is almost completely preserved, some fragments of the palate are present, and the mandible is only missing the predentary (*c* and *d* in Fig. 2), making the skull of *Manidens* one of the most complete heterodontosaurid skulls known. Skull elements were found mainly disarticulated, although some were found in articulation (most notably the almost complete right lower jaw and the left temporal region) or retained a close association (Figs. 1 and 2).

Despite the disarticulation of the skull, a few aspects of general skull shape and morphology can be evaluated. The length of the right mandible is 63 mm without the predentary, which might account for another 5–10 mm (based on *Heterodontosaurus*, in which the predentary accounts for approx. 10% of the length of the mandible). Because mandible length is similar to skull length in basal ornithischians, the skull of *Manidens* was most probably no more than 75 mm long and thus closely comparable in size to that of *Fruitadens*, one of the smallest known ornithischian dinosaurs, for which Butler et al. (2010: Fig. 3e) reconstructed a skull length of approximately 70 mm. The preserved jugal and postorbital demonstrate that the orbit was round and very large (Fig. 2), as in most basal ornithischians, and, together with the rather small maxilla, that the preorbital region of the skull was probably rather short. The lower temporal fenestra was much narrower than the orbit ventrally, but rapidly increased in anteroposterior length dorsally, as indicated by the very long posterior process of the postorbital and anterior branch of the squamosal (Fig. 2).

The maxilla has a posterodorsally sloping anterior margin, without a large anterior embayment for the reception of the enlarged dentary tooth, as it is present in all other known heterodontosaurids for which this element is known (*Tianyulong*: Zheng et al. 2009; *Fruitadens*: Butler et al. 2010; *Abrictosaurus*: Thulborn 1974; *Lycorhinus*: Gow 1975; *Heterodontosaurus*: Norman et al. 2004a), although the preservation of this area does not rule out the possibility of a considerably smaller embayment. The presence of such an embayment in *Echinodon* is uncertain (Norman and Barrett 2002). A well-developed buccal emargination is present and is separated from the large antorbital fossa by a horizontal ridge, which becomes more conspicuous posteriorly. This emargination seems to be more strongly developed than in *Echinodon* (Norman and Barrett 2002), *Tianyulong* (Zheng et al. 2009) and

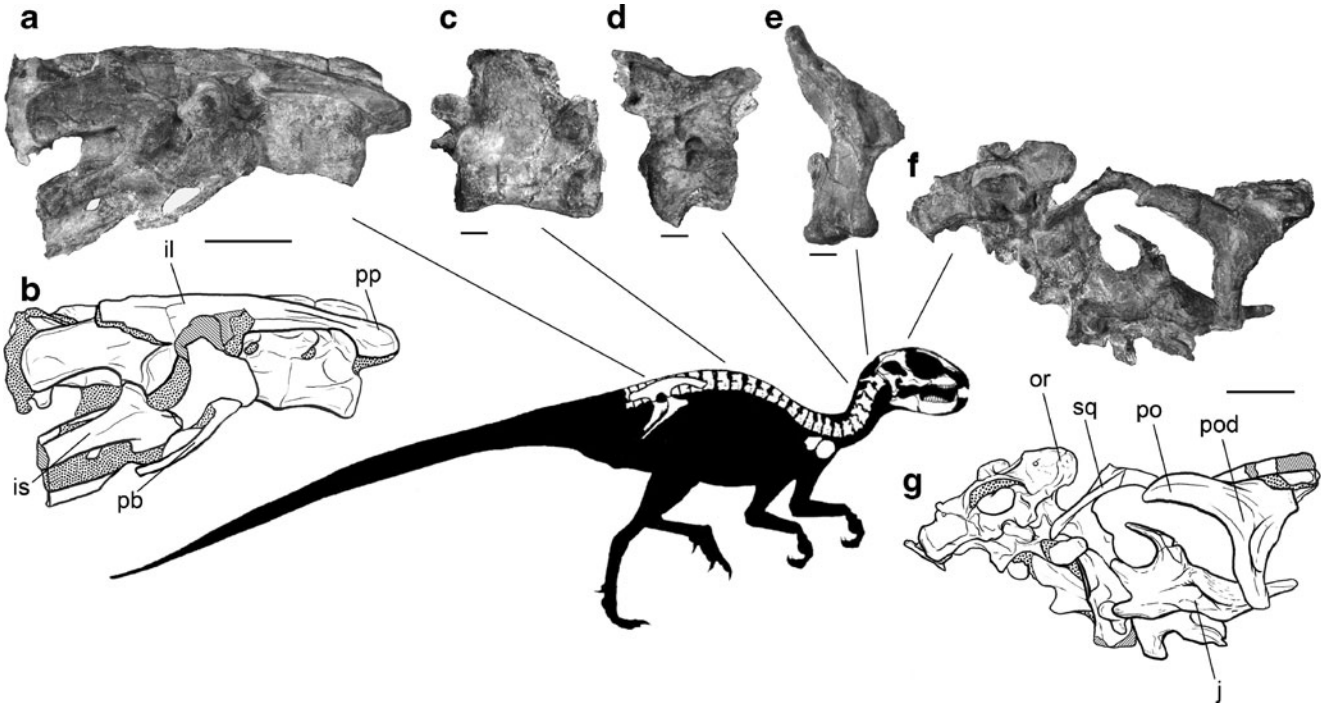

Fig. 1 Preserved elements of *M. condorensis* gen. et sp. nov. Outline reconstruction of the skeleton, indicating preserved elements, with photographs of selected skeletal elements of the type specimen (MPEF PV 3211). *a* Pelvic girdle, lateral. *b* Schematic drawing of pelvic girdle. *c* Dorsal vertebrae, lateral. *d* Cervical vertebrae, lateral. *e* Quadrate, anterior. *f* Temporal (lateral) and occipital (posterior) skull elements. *f* Schematic drawing of temporal and occipital region. *il* illium, *is* ischia, *j* jugal, *or* occipital region of the braincase, *pb* pubis, *po* postorbital, *pod* postorbital depression, *pp* preacetabular process, *sq* lateral shelf of the squamosal. *Dashed areas* represent broken surfaces and *dotted areas* represent sediment. *Scale bars* indicate 10 mm (*a*, *b*, *f*, *g*), 2 mm (*c*, *d*) and 1 mm (*e*)

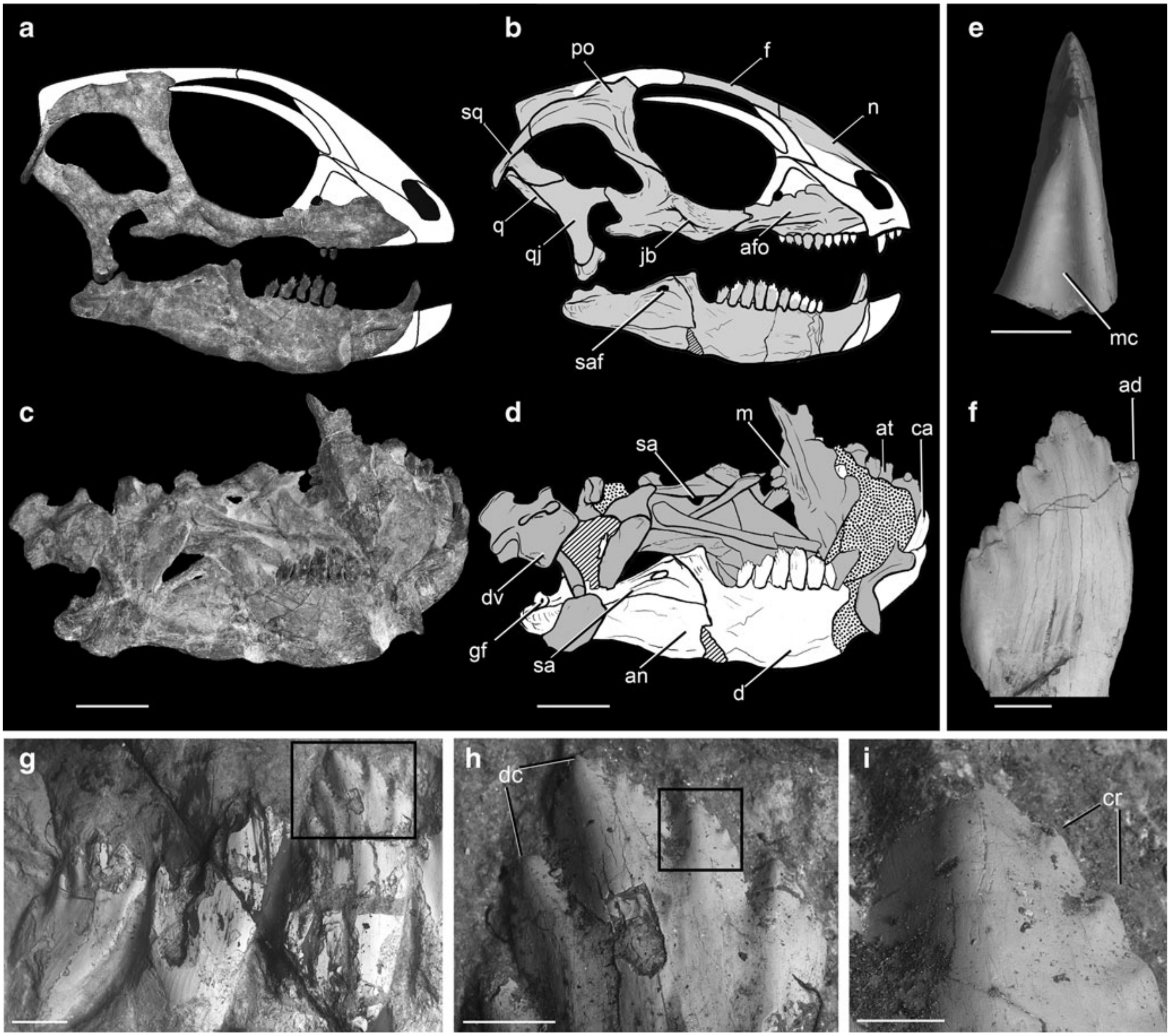

Fig. 2 Anatomical details of the craniomandibular and dental remains of *M. condorensis* gen. et sp. nov. *a* Photographs of preserved cranial and mandibular elements of the holotype (MPEF-PV 3211) superimposed on a skull reconstruction in lateral view. *b* Reconstruction of the skull and mandible in lateral view. *c* Photograph of right lower jaw and associated elements of the holotype (MPEF-PV 3211). *d* Interpretative drawing of right lower jaw in lateral view (right maxilla, left lower jaw and other bones shaded in *grey*); *dashed areas* represent broken surfaces and *dotted areas* represent sediment. *e–h* SEM images of posterior mandibular tooth in mesial (*e*) and bucal (*f–i*) views corresponding to MPEF-PV 3810 (*e*), MPEF-PV 3811 (*f*) and holotype MPEF-PV 3211 (*g–i*). *ad* anteriormost denticle mesially offset, *afo* antorbital fossa, *an* angular, *at* anterior teeth of left dentary, *ca* caniniform, *cr* crenulations, *d* dentary, *dc* denticles, *dv* dorsal vertebra, *f* frontal, *g* glenoid fossa, *jb* jugal boss, *m* maxilla, *mc* mesial cavity, *n* nasal, *po* postorbital *q* quadrate, *qj* quadratojugal, *sq* squamosal, *sa* surangular, *saf* anterior surangular foramen. *Scale bars* indicate 10 mm (*a–d*), 1 mm (*e–g*), 0.5 mm (*h*) and 0.1 mm (*i*)

Fruitadens (Butler et al. 2010), but similar to the condition in *Lycorhinus* (Gow 1975) and *Heterodontosaurus* (SAM K337). The antorbital fenestra was very small and placed in the posterodorsal margin of the antorbial fossa of the maxilla, as in *Lesothosaurus* (Sereno 1991), *Heterodontosaurus* (Norman et al. 2004a) and other basal ornithischians (Norman et al. 2004a, b; Barrett et al. 2005). The anterior ramus of the jugal is slender and formed most of the ventral margin of the orbit (Fig. 2). At the junction with the postorbital ramus, a pronounced lateral boss is present, as in *Heterodontosaurus* (Norman et al. 2004a) and, probably, *Abrictosaurus* (Thulborn 1974). However, in contrast to the former taxon, in which the boss is ventrally placed, it is found at the dorsal margin of the bone in *Manidens* (*a* and *b* in Fig. 2). A jugal boss seems to be absent in *Tianyulong*, although the posterior part of the jugal is missing in this taxon (Zheng et al. 2009). The postorbital process of the jugal flexes abruptly posteriorly at the beginning of the articular facet for the postorbital (Fig. 1). The posterior process of the jugal is short, much higher than the anterior process, and bifurcates posteriorly, forming a wide angle between the two processes (*a* and *b* in Fig. 2), also resembling the condition in *Heterodontosaurus* (Norman et al. 2004a). Although a bifurcated posterior end of the jugal is also present in other basal ornithischians (Barrett and Han 2009) and saurischians (e.g. Sereno and Novas 1993), the two processes usually form a narrower angle and both contact the quadratojugal, whereas only the dorsal process contacts the quadratojugal in *Heterodontosaurus* and *Manidens*. The postorbital is triradiate and has a very long posterior and very short anterior process. A well-developed lateral boss is present at the posterodorsal margin of the orbit just below the junction between the anterior and ventral rami of the postorbital, as in *Lesothosaurus* (Sereno 1991) and many saurischians (e.g. Sereno and Novas 1993). Posterior to this boss, the postorbital of *Manidens* has a depression, resembling the condition of *Heterodontosaurus tucki* (SAM K337). The posterior end of a stout, rod-like palpebral is preserved above the anterior process of the left postorbital, indicating that this bone was very long and probably transversed the whole length of the orbit, in contrast to the situation in *Heterodontosaurus*, but as in some other ornithischians, such as *Agilisaurus* (Peng 1992; Barrett et al. 2005). The squamosal has a long, straight lateral shelf dorsally above its ventral process, considerably more developed than a similar structure in *Heterodontosaurus* (Norman et al. 2004a). Anterior to this shelf, the long anterior process of the squamosal flexes notably ventrally to meet the posterior process of the postorbital, indicating that the main body of the squamosal was considerably tilted, as in *Heterodontosaurus* (Norman et al. 2004a), *Lesothosaurus* (Sereno 1991) and *Hypsilophodon* (Galton 1974). The left and right nasals and frontals are fused at their midline sutures without any visible suture, but apparently not with each other. The nasals are flat and gradually widen posteriorly. Their lateral margins are slightly thickened, as is the case in *Heterodontosaurus* (Butler et al. 2008b). The frontal has a considerably widened, strongly rimmed ventral facet for the forebrain. The quadrate is slender and only slightly flexed posteriorly. The quadrate foramen is developed as a large embayment in the lateral flange of the bone, as in *Hypsilophodon* (Galton 1974) and iguanodontians. The lateral condyle for the articulation with the lower jaw is much larger than the medial condyle, as in other heterodontosaurids and ceratopsians (Butler et al. 2010).

In the braincase, the foramen magnum has been dorsoventrally flattened by deformation, but it was originally larger than the stout, semicircular occipital condyle (Fig. 1). The paroccipital processes are dorsoventrally high, relatively short and have rounded lateral margins. The post-temporal fenestra is developed as a large foramen within the paroccipital process, well separated from the exoccipital–squamosal suture, as in *Heterodontosaurus* (Norman et al. 2004a) and *Gasparinisaura* (Coria and Salgado 1996). The basal tubera are separated by a wide notch below the condyle. The basisphenoid is wide and short, with a well-developed ventral basisphenoid recess, resembling the condition in some basal theropods (Raath 1985; Rauhut 2003b).

No external mandibular fenestra is present in the lower jaw (Fig. 2), unlike the situation in *Heterodontosaurus* and *Tianyulong* (Norman et al. 2004a; Zheng et al. 2009) and most other basal ornithischians (e.g. Haubold 1990; Sereno 1991; Butler et al. 2007), but similar to *Abrictosaurus* (Thulborn 1974), *Scelidosaurus* (Owen 1863) and more derived cerapodans. The dentary is robust and dorsoventrally high, in contrast to the more slender dentaries in other heterodontosaurids (Thulborn 1974; Norman and Barrett 2002; Norman et al. 2004a; Zheng et al. 2009; Butler et al. 2010). It has a strongly enlarged, caniniform first dentary tooth typical of many heterodontosaurids (Norman et al. 2004a; Zheng et al. 2009; Butler et al. 2010). The dorsal part of its posterior end extends posterodorsally to form the anterior margin of the coronoid process, as in all ornithischians. The latter is a well-developed, triangular eminence that rises to about 160% of the height of the dentary at the tooth row, which is less than in *Tianyulong* (Zheng et al. 2009) and *Abrictosaurus* (Thulborn 1974), although this is mainly due to the unusual robustness of the dentary. The surangular forms the entire posterior part of the process in lateral view, and there is an enlarged anterior surangular foramen near its dorsal margin, just posterior to the apex of the coronoid process (Fig. 2). Posteriorly, the surangular becomes rapidly lower towards the jaw articulation, which is located considerably ventral to the level of the tooth row as in *Heterodontosaurus* and derived ornithopods (Weishampel 1984). The glenoid facet is developed as an elongate concavity, which is considerably longer anteroposteriorly than the distal quadrate head and is delimited anteriorly by a well-developed, triangular dorsal projection of the surangular. The retroarticular process is a stout, posteroventrally directed process with a median ridge along its posterodorsal surface resembling the condition of some ornithopods, such as *Thescelosaurus* (Galton 1997). As in most ornithischians, this process is shorter than the mandibular glenoid articulation.

The dentition is strongly heterodont. The exact tooth count cannot be established due to overlap and incompleteness of some of the elements. However, the lower dentition is composed of at least 11 teeth, including the hypertrophied anterior caniniform of the dentary (*c* and *d* in Fig. 2)

This number is slightly lower than in *Heterodontosaurus* and *Abrictosaurus*, which have 13 dentary teeth (Norman et al. 2004a), but higher than in *Tianyulong* (nine dentary teeth; Zheng et al. 2009) and comparable to *Fruitadens* (9–11 dentary teeth; Butler et al. 2010). The caniniform is a stout, recurved pointed tooth that seems to lack marginal denticles, as in *Fruitadens* (Butler et al. 2010), but in contrast to the situation in *Heterodontosaurus*, *Lycorhinus* and *Abrictosaurus* (Charig and Crompton 1974; Hopson 1975). The first three post-caniniform teeth are very small and well spaced from each other (but poorly preserved in MPEF-PV 3211; *d* in Fig. 2). The subsequent dentary teeth rapidly increase in size posteriorly and become mesiodistally expanded, but the distal-most two teeth slightly decrease in size so that the highest tooth crowns are situated at the mid-length of the posterior region of the tooth row (*c* and *d* in Fig. 2), similar to the situation in *Fruitadens* (Butler et al. 2010) and *Abrictosaurus* (Thulborn 1974). In contrast, although there is also an increase in tooth size from the first to the third post-canine tooth in *Tianyulong* and *Heterodontosaurus*, the decrease in at least the mesiodistal size of the posteriormost teeth in these taxa is much less marked (Hopson 1980; Norman et al. 2004a; Zheng et al. 2009). The crowns of posterior teeth are asymmetrical, unlike the much more symmetrical dentary teeth of other heterodontosaurids (Thulborn 1974; Charig and Crompton 1974; Hopson 1975; Norman and Barrett 2002; Zheng et al. 2009; Butler et al. 2010). They are leaf-shaped, lateromedially compressed and have a weakly developed central ridge on the lingual and labial surfaces (*f* and *g* in Fig. 2), more marked than in *Fruitadens* (Butler et al. 2010), but apparently less conspicuous than in *Heterodontosaurus* (Hopson 1980). Unlike the situation in *Echinodon* (Norman and Barrett 2002), *Tianyulong* (Zheng et al. 2009) and *Fruitadens* (Butler et al. 2010), the tooth crowns are considerably higher than wide, comparable to the situation in *Lycorhinus* (Hopson 1975) and *Heterodontosaurus* (Hopson 1980; Norman et al. 2004a). The margins of the crowns bear well-developed denticles, usually one or two mesial to the apex and four or five distal to the apex, creating the aforementioned asymmetry in the tooth crown (*f* and *g* in Fig. 2). The margin of each denticle bears small crenulations, which are likely formed exclusively by ridges on the enamel (*g*–*i* in Fig. 2), and have not been reported in any other heterodontosaurid so far, although subdivided denticles are present in some other ornithischians (Bakker et al. 1990; Rauhut 2002). All crowns have a gentle distal curvature that is more conspicuous in the apical region (*f*–*h* in Fig. 2). Both the number of denticles and the apical curvature of the crown vary along the tooth row. The posteriormost dentary tooth has a distinct "hand-like" appearance, with the anteriormost denticle being offset mesially from the mesial margin (*f* in Fig. 2). The posteriormost six asymmetric teeth are higher and tightly appressed against each other, unlike the more widely spaced teeth in *Tianyulong* (Zheng et al. 2009) and *Fruitadens* (Butler et al. 2010), but similar to the situation in *Lycorhinus* (Hopson 1975) and *Heterodontosaurus* (Hopson 1980; Norman et al. 2004a, b). Each crown bears a mesial groove, delimited by two ridges (*e* in Fig. 2), which houses the distal margin of the preceding tooth, as in the closely packed dental batteries of more derived ornithischians.

The cervical vertebrae are shorter than the dorsal vertebrae and have short and stout diapophyses and parapophyses. Strongly elongate hypertrophied epipophyses are present in the preserved anterior cervicals, as in *Heterodontosaurus* (Santa Luca 1980). Cervical and dorsal neural spines are anteroposteriorly elongate and low. There are six sacral vertebrae, the neural spines of which form a continuous sheet of bone over the ilium. An anterior caudal vertebra has a low elongate centrum with well-developed chevron facets.

Only the left coracoid and proximal portion of the scapula are preserved. The coracoid has a well-developed, hook-like posteroventral process that is separated from the glenoid cavity by a wide notch. The pelvic girdle is complete, with the exception of the distal ends of the pubes and ischia (Fig. 1). The ilium is low and elongate, with a preacetabular process that accounts for approximately 50% of the total length of the bone. A longitudinal ridge extends along the lateral surface of the preacetabular process, but is less well-developed than in *Heterodontosaurus* (Santa Luca 1980). Unlike the latter taxon and other basal ornithischians, in which the pubic peduncle is longer than the ischial peduncle, the former is subequal in length or even slightly shorter than the latter in *Manidens*. As in all ornithischians, the pubis is opisthopubic with a very slender posteroventral shaft (Fig. 1). The prepubic process is short, only little extending beyond the pubic peduncle of the ilium anteriorly, and robust. A small obturator foramen is present below the acetabulum. The ischium is more robust than the pubis and has an extensive medial suture along its shafts, which are rectangular in cross-section. Not enough of the shaft is preserved to establish the presence or absence of an obturator process.

Discussion

To test the phylogenetic relationships of the new taxon, we included it in a slightly modified version of the data matrix of Butler et al. (2010), which focuses on the interrelationships of basal ornithischian clades and includes the most extensive taxon sampling of heterodontosaurids published to date. The final data matrix included 51 taxa and 230 characters (see ESM) and was analysed using equally weighted parsimony in TNT, version 1.1 (Goloboff et al. 2008a, b). We performed a traditional heuristic search with 1,000 replicates with random addition sequences followed by tree bissection–reconnection (TBR) branch swapping, followed by a second round of TBR.

The analysis resulted in 216 MPTs with a length of 551 steps, the strict consensus of which (Fig. 3) is well resolved for basal ornithischians. In particular, the results show phylogenetic relationships for heterodontosaurids that have both evolutionary and biogeographic implications for the group. *M. condorensis* was found to be a heterodontosaurid more closely related to Early Jurassic southern African forms than to the later northern representatives of the clade. The position of *Manidens* within Heterodontosauridae is supported by the presence of three of the six unambiguous synapomorphies of this clade [lateral condyle of quadrate larger than medial (character 63.2), coronoid process well-developed (character 101.1), enlarged caniniform anterior dentary tooth (character 124.1)]. The clade of *Manidens* and the Early Jurassic taxa from South Africa clusters all heterodontosaurids from Gondwana (node 2 in Fig. 3) and is supported by two unambiguous synapomorphies [lack of alveolar foramina (character 126.1) and apicobasally high mid-dentary and maxillary tooth crowns (character 228.0)] and one ambiguous synapomorphy [angular occupying more than half the depth of the mandible at the level of the coronoid process (character 230.1)]. However, *Manidens* is placed as the sister taxon of the South African clade (node 1 in Fig. 3) since it lacks the unambiguous synapomorphy of this group [systematic development of wear facets along the entire tooth row (character 222.1)]. See ESM for a full list of synapomorphic characters of each clade. The discovery of *Manidens* in the Middle Jurassic of Patagonia and the phylogenetic hypothesis presented here have important implications for understanding several evolutionary aspects of heterodontosaurids, including the pace and mode of their radiation and biogeographic history, the evolution of body size and the evolution of their adaptations to herbivory.

Radiation and distribution of Heterodontosauridae

Given the wide geographic range of other Early–Middle Jurassic dinosaurs, such as basal theropods and sauropodomorphs (Weishampel et al. 2004; Smith et al. 2007), the

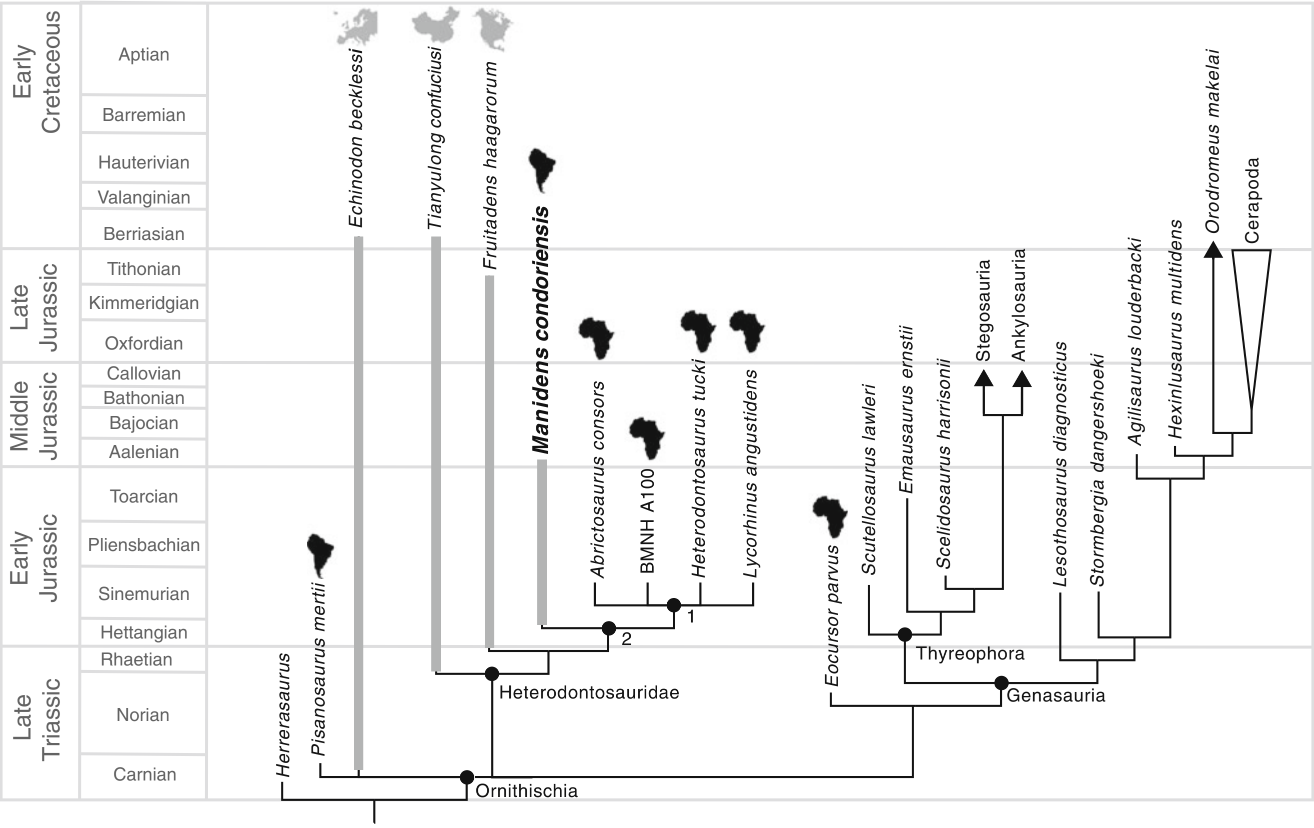

Fig. 3 Results of the phylogenetic analysis showing the proposed interrelationships of *M. condorensis* within ornithischians. The phylogenetic tree is plotted against geological time to calibrate the phylogeny and highlight the extensive ghost lineages in basal heterodontosaurids (*grey lines*). Derived clades of Ornithischia have been collapsed into single taxonomic units for clarity. For details of phylogenetic analysis, see text and ESM

apparent restriction of derived heterodontosaurids to southern Gondwana is somewhat surprising. Furthermore, the fact that the two most basal heterodontosaurids, *Fruitadens* and *Tianyulong*, are currently only known from the Northern Hemisphere (though in much higher stratigraphic levels) seems to contradict the hypothesis that the early ornithischian radiation took place in southern Gondwana (Rauhut and Lopez-Arbarello 2008). However, the phylogenetic uncertainty on the position of some forms, such as *Echinodon* from the Middle Purbeck Beds (Berriasian) of southern England (see Sereno 1997; Norman and Barrett 2002), fragmentary remains from the Late Triassic of southern Patagonia (Báez and Marsicano 2001) and the undescribed remains from the Kayenta Formation (Attridge et al. 1985; Sues et al. 1994; Sereno 1997), precludes the assessment of a robust biogeographic scenario for heterodontosaurids. Furthermore, the minute size of some heterodontosaurids (see below) and the generally poor Early and Middle Jurassic fossil record may explain their disparate distribution. Thus, future finds may change our view of both heterodontosaurid and basal ornithischian evolution and biogeography.

However, based on the currently available information, the phylogenetic analysis indicates that there was an early radiation of heterodontosaurids at least in the Early Jurassic and probably in the Late Triassic (as suggested by the remains from this time found in southern Patagonia; Báez and Marsicano 2001). The phylogenetic position of Early Jurassic forms indicates that several lineages must have been generated in this initial radiation of Heterodontosauridae, including the lineages leading towards *Tianyulong* and *Fruitadens* and the derived and probably endemic clade from southern Gondwana (node 2 in Fig. 3). The occurrence of *Manidens* in the Middle Jurassic of central Patagonia demonstrates that this clade still persisted at least into the Middle Jurassic. The initial radiation of heterodontosaurids (and the phylogenetic positions of *Tianyulong* and *Fruitadens*, and probably *Echinodon*) implies at least two other long-lived lineages of heterodontosaurids (Fig. 3). These mark a major mismatch between the phylogenetic topology obtained for heterodontosaurids and the order of appearance of taxa in the fossil record (see ESM), which further underlines the extremely poor fossil record of this clade. The undescribed form from the Kayenta Formation indicates that the group might have achieved a Pangean distribution by the Early Jurassic. Thus, it is expected that future discoveries will show an even higher diversity and wider geographic distribution of heterodontosaurids in the Early Jurassic (and possibly also in the Late Triassic).

Ontogenetic stage and body size

One of the aspects of the evolution of Heterodontosauridae that was recently emphasized is that post-Early Jurassic forms represent some of the smallest ornithischian dinosaurs, including the smallest known adult ornithischian to date (i.e. *Fruitadens*; Butler et al. 2010). This is confirmed by the find of *Manidens*: Based on the closely comparable size of the cranial remains, this taxon was probably in the same size range as *Fruitadens*, for which Butler et al. (2010) estimated a total body length of 65–75 cm and a mass of <1 kg. One important question, of course, is whether the type of *Manidens* represents a juvenile or an adult or subadult individual. Butler et al. (2008b) demonstrated that ontogenetic changes in *Heterodontosaurus* included a relative lengthening of the snout, an increase of the number of teeth and the fusion of several sutures in the skull, such as the nasal–nasal suture. Although the relatively large orbits, short snout and low number of teeth in *Manidens* (in comparison with adult *Heterodontosaurus*) might thus be taken as indications that the type specimen represents a juvenile, there are several aspects that argue against this interpretation. First, the number of teeth in the dentary of *Manidens* (11) is lower than that of large individuals of *Heterodontosaurus* (13; Norman et al. 2004a), but it is comparable to or even higher than that in the basal heterodontosaurids *Tianyulong* (9) and *Fruitadens* (9–11), which are of comparable size (Zheng et al. 2009; Butler et al. 2010). Second, the interfrontal and internasal contacts in the type specimen of *Manidens* are fused without any visible suture, which, according to Butler et al. (2008b), would indicate that it is not a juvenile. Finally, the neural arches of the presacral vertebrae in the type specimen are also fused to their respective centra without any visible suture. Butler (2010: 676) discussed the timing of neurocentral fusion in ornithischians and came to the conclusion that "neurocentral fusion may only have occurred in the very oldest individuals of basal ornithischian species." Thus, the type specimen might not only represent a sexually mature, but even an old individual (see also Brochu 1996; Irmis 2007).

Given that other basal ornithischians, such as *Pisanosaurus* (Bonaparte 1976), *Eocursor* (Butler 2010), *Lesothosaurus* (Sereno 1991; Knoll 2002) and *Scutellosaurus* (Colbert 1981) are slightly larger animals, there seems to have been a tendency towards miniaturization in basal heterodontosaurids. The "juvenile" characters of small heterodontosaurids, such as the low number of teeth and the large orbit and short snout, might thus be explained as a result of heterochrony, which seems to have played a role in miniaturization in other reptiles as well, such as lepidosaurs (Rieppel 1984). The same process might have played a role in the evolution of maniraptoran theropods, as well, in which small forms also display large orbits (e.g. Turner et al. 2007).

Evolution of herbivory in Heterodontosauridae

The discovery of *Manidens* and the phylogenetic hypothesis presented here indicate a trend towards greater sophistication in the adaptations to herbivory within the phylogeny of Heterodontosauridae. As Butler et al. (2010) noted, three adaptations to herbivory are present in *Heterodontosaurus*, including closely packed teeth, high tooth crowns, and extensive wear facets on the maxillary and dentary teeth. Basal heterodontosaurids, such as *Tianyulong* and *Fruitadens*, lack these adaptations and bear lower crowns that are more widely spaced and lack extensive wear facets. The new taxon fills the gap between the basal forms and the derived South African clade of *Heterodontosaurus* in having high and closely appressed crowns but lacking extensive wear facets. Thus, the pattern of character acquisition in heterodontosaurids indicates that an increase in tooth crown height preceded the development of extensive wear facets in this clade (Fig. 3). This is in marked contrast to the evolutionary pattern observed in other groups of ornithischian dinosaurs in which the evolution of sophisticated chewing mechanisms (involving intensive wear on the teeth) predated the increase in relative crown height and the appearance of high tooth batteries in iguanodontians (Weishampel 1984) and ceratopsians (You and Dodson 2004; Xu et al. 2006). The evolution of herbivory in these other groups of dinosaurs resembles the pattern of character acquisition present in other groups of vertebrates (e.g. Cenozoic herbivorous mammals; Pascual 1996), placing the evolution of herbivory in heterodontosaurids as a distinct case among amniotes. It is noteworthy that this increased sophistication of the dietary adaptations in the southern African heterodontosaurids, which might account for their relative diversity in the Elliot Formation, does not contradict the idea that the more generalized dentition of basal heterodontosaurids favoured their longevity as evolutionary lineages (Butler et al. 2010).

The discovery of a heterodontosaurid in the Middle Jurassic of Patagonia underlines the recently recognized diversity of the clade, increases the recently extended geographical and temporal range of this clade, and shows that heterodontosaurids remained a component of herbivorous dinosaurian faunas of Gondwana at least until the Middle Jurassic. Given the general rarity of small terrestrial vertebrates in many Jurassic localities, the absence or rarity of heterodontosaurids might represent an artefact of the fossil record. The relative diversity and abundance of these animals in comparison to that of large-bodied dinosaurs was probably higher than previously suspected and will likely be further appreciated in light of future discoveries.

Acknowledgements We thank Guillermo Rougier for collecting the specimen described here. Fieldwork was only possible with the friendly support of the Farias family, the Subsecretaría de Cultura of the Chubut province and the School number 31 at Cerro Cóndor. Leandro Canessa carried out the very delicate preparation of the type specimen and Pablo Puerta and Leandro Canessa prepared the isolated teeth. Fieldwork was supported by the project "Paleontological Exploration of Patagonia" (Fundación Antorchas and University of Louisville) and NSF DEB-0946430 for the study of Mesozoic mammals from South America (to Guillermo Rougier). This research was conducted with the support of ANPCYT (grant PICT 1756) and international collaboration grant CONICET-Chinese Academy of Sciences to DP, and DFG (grant RA 1012/9-1) to OR. Access to SEM lab was possible thanks to ALUAR Aluminio Argentino, and the technical help of Mr. Jaime Groizard is deeply appreciated. R. Butler is deeply thanked for providing constructive comments and discussion about this specimen. Line drawings of 2 have been conducted by Mr. Jorge Gonzalez. Ms. Sheena Kaal is thanked for access to comparative specimens of *Heterodontosaurus* at the Iziko-South African Museum to DP. Mr. Zheng Xiao-Ting is thanked for access to comparative specimens of *Tianyulong* at the Shandong Tianyu Museum of Nature to DP. Ms. Zhang Xiaomei is also thanked for her help, and Dr. Xu Xing is thanked for providing access to other relevant comparative material. Critical comments by Richard Butler and four anonymous reviewers have considerably helped to improve the manuscript.

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