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A heterodontosaurid ornithischian dinosaur from the Upper Triassic of Patagonia

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Resumen. UN DINOSAURIO ORNITISQUIO HETERODONTOSÁURIDO DEL TRIÁSICO SUPERIOR DE PATAGONIA. Restos fragmentarios de una nueva especie de heterodontosáurido, comparable a *Heterodontosaurus* Crompton y Charig, fueron descubiertos en concreciones de la Formación Laguna Colorada, una secuencia triásica continental aflorante en la provincia de Santa Cruz, Argentina. El material consiste en un fragmento de la parte posterior de una maxila izquierda con dentición, y, tentativamente, un caniniforme aislado con crenulaciones anteriores y posteriores. Los tres dientes maxilares preservados presentan facetas de desgaste planas, son columnares y se hallan muy próximos entre sí. Las superficies anteriores y posteriores de las coronas se hallan en contacto, rasgo considerado una sinapomorfía de *Heterodontosaurus* y *Lycorhinus* provenientes del Grupo Stormberg superior del sur de África, de edad jurásica temprana. Como en *H. tucki* Crompton and Charig, los dientes maxilares carecen de cíngulo o de constricción que separe corona de raíz y las facetas de desgaste de dientes adyacentes forman una superficie continua única. Sin embargo, los dientes maxilares posteriores presentan más numerosas y finas costillas en su superficie labial que los de *H. tucki*. Este nuevo registro de heterodontosáuridos extiende el rango temporal de este grupo de pequeños ornitisquios y, considerando la filogenia aceptada de los ornitisquios, indica una gran diversificación filética de estos últimos en el Triásico Tardío.

Abstract. Fragmentary remains of a new heterodontosaurid species, comparable to *Heterodontosaurus* Crompton and Charig, were discovered in concretions in the Laguna Colorada Formation, a Late Triassic continental sequence in Santa Cruz Province, Argentina. The material consists of a weathered, left posterior maxillary fragment with dentition, and, tentatively, an isolated caniniform with anterior and posterior serrations. The preserved three maxillary teeth bear flat wear facets, and are columnar and closely packed. The anterior and posterior surfaces of the crowns are in contact, a feature considered a synapomorphy of *Heterodontosaurus* and *Lycorhinus* from the Early Jurassic upper Stormberg Group of southern Africa. As in *Heterodontosaurus tucki* Crompton and Charig, the maxillary teeth lack a cingulum or a constriction separating crown and root, and the wear facets of adjoining teeth form a single, continuous surface. However, the posterior maxillary teeth bear more numerous and narrower ridges on their labial surfaces than those of *H. tucki*. This new record of a heterodontosaurid extends the temporal range of this group of small ornithischians and, considering the phylogeny of ornithischians as now understood, indicates an extensive phyletic diversification of these dinosaurs in the Late Triassic.

Key words. Dinosauria. Ornithischia. Heterodontosauridae. Triassic. Patagonia.

Palabras clave. Dinosauria. Ornithischia. Heterodontosauridae. Triásico. Patagonia.

Introduction

Unlike the well known Triassic continental sequences in west-central Argentina, which record taxonomically diverse fossil tetrapod assemblages (*e.g.*, Bonaparte, 1997; Caselli *et al.*, 2001), the outcrops of this age of the most southern part of South America have only yielded prosauropod dinosaurs (Casamiquela, 1977, 1980; Bonaparte and Vince, 1979) and ornithischian dinosaurs (Báez and Marsicano, 1998) to date. These dinosaur remains were discovered in beds that are part of the El Tranquilo Basin, south of the Deseado Massif in Santa Cruz Province, southern Patagonia (figure 1). The origin of this basin, as well as that of other Triassic depocenters in southern South America, is related to events associated with the pre-breakup of Gondwana (Uliana and Biddle, 1988). Triassic rocks in the El Tranquilo Basin are wholly continental and unconformably overlie Permian strata. The El Tranquilo Group, formerly known as the El Tranquilo Formation, was recently divided into the Cañadón Largo and the unconformably overlying Laguna Colorada Formation (Jalfin and Herbst,

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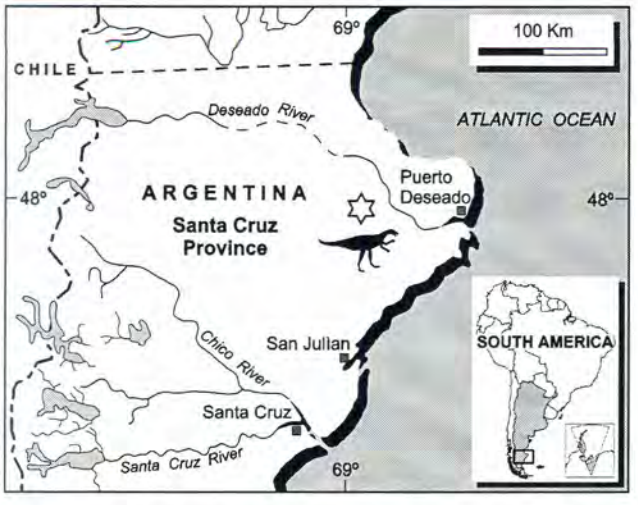

Figure 1. Map of southern Patagonia showing location of the fossil site (indicated by a star) / *Mapa de la parte austral de Patagonia mostrando la localización del sitio fosilífero (indicado por una estrella).*

1995). Both units preserve abundant floral remains. Additionally, the Laguna Colorada Formation yields tetrapod remains.

This paper describes fragmentary remains referred to an heterodontosaurid ornithischian (Báez and Marsicano, 1997, 1998) that were collected from the same locality in the Laguna Colorada Formation as the articulated juveniles of the plateosaurid prosauropod *Mussaurus patagonicus* (Bonaparte and Vince, 1979). Also recovered from this site is part of the material that Casamiquela (1977, 1980) referred to *Plateosaurus* sp. and that is currently under revision (Bonaparte, personal communication, 1999). This heterodontosaurid constitutes the first unquestionable South American record of this group of small ornithischians, hitherto known from southern Africa, England, North America, and, possibly, China. Bonaparte (1976) proposed that the primitive Carnian ornithischian *Pisanosaurus* Casamiquela 1967 from western Argentina is an heterodontosaurid, but this conclusion is still controversial (Sereno, 1986; Weishampel and Witmer, 1990). In addition, this Late Triassic record from Patagonia extends the Early Jurassic stratigraphic range of heterodontosaurids further back in time, thus documenting a significant phyletic diversification of ornithischians earlier than previously known. This evidence also supports the suggestion that a substantial temporal gap separates the initial radiation of dinosaurs and their subsequent global dominance during the latest Triassic and Early Jurassic (Sereno, 1999).

Abbreviations. CPBA-V: Cátedra de Paleontología de la Facultad de Ciencias Exactas de la Universidad de Buenos Aires, Argentina; Colección de vertebrados. SAM K: South African Museum, Cape Town, Republic of South Africa. PVL: Colección Paleontología de Vertebrados del Instituto Miguel Lillo, Universidad Nacional de Tucumán, Argentina.

Geological context and age

The heterodontosaurid material described herein was recovered from the Laguna Colorada Formation, the upper unit of the El Tranquilo Group, in outcrops that surround an ephemeral lake locally known as Laguna Colorada (figure 1). The Laguna Colorada Formation consists of conglomerates, coarse to fine-grained sandstones, claystones and siltstones, which are mainly brownish-red and purple in color. This continental sequence exhibits fining-upward sedimentary cycles and has been interpreted as an alluvial succession developed in a fluvial environment of moderate-to-high sinuosity under seasonal climatic conditions (Jalfin and Herbst, 1995).

The Laguna Colorada Formation is exposed mostly in isolated depressions and margins of shallow ephemeral lakes, making it difficult to find an uninterrupted stratigraphical section for correlating the fossiliferous horizons. In addition, duplication of some locality names has produced confusion with respect to the fossil sites. Early fieldwork in the area by petroleum geologists in 1956 resulted in the discovery of two plant-bearing strata and an overlying level with concretions containing small vertebrate remains (Di Persia, 1956). These initial discoveries were made at Laguna Colorada, an ephemeral lake located 5 km north-east of the outcrop in which subsequent paleontological expeditions collected abundant fossil plants and remains of prosauropod dinosaurs (Herbst, 1961, 1965; Casamiquela, 1977, 1980). This latter vertebrate-bearing horizon also occurs at the margins of an ephemeral lake that was called successively Laguna La Colorada (Bonaparte, 1978), Laguna de la Isla (Casamiquela, 1980) and, confusingly, Laguna Colorada (Jalfin and Herbst, 1995). Recently, this locality was designated as the stratotype locality of the Laguna Colorada Formation (Jalfin and Herbst, 1995). The prosauropod remains occur as partially articulated bones and were collected from lutites of the middle section of this unit (Herbst, 1965; Bonaparte and Vince, 1979; Casamiquela, 1980). The heterodontosaurid material described herein is preserved in ferruginous dolomite concretions from a level slightly below the strata bearing *Mussaurus*.

The age of the Laguna Colorada Formation is constrained by dates assigned to the underlying and overlying units. The underlying Cañadón Largo Formation is considered of Ladinian-Carnian age (Zavattieri, 1993; Zavattieri and Batten, 1996; Jalfin and Herbst, 1995), based on the study of its taxonomically rich macro- ("*Dicroidium* Flora") and micro-

floras (Ipswich Microflora). Granitoid complexes intrude the Laguna Colorada Formation in a locality near the tetrapod fossil site. These complexes were dated in 203±2 Ma by a detailed Rb-Sr whole-rock study (Pankhurst *et al.*, 1993), thus giving a Hettangian-Sinemurian age for the intrusive event. This evidence is in agreement with the Late Triassic (probably Norian) age of the Laguna Colorada Formation proposed on the basis of its floral content (Bonetti, 1964; Jalfin and Herbst, 1995; Spalletti *et al.*, 1999). Furthermore, elements of the "*Dicroidium* Flora" were recorded in beds of the Laguna Colorada Formation, both above and below the bone-bearing concretion horizon. These plant assemblages differ strikingly from those recorded in the Liassic Roca Blanca Formation that discordantly overlies the Laguna Colorada Formation and is exposed in the same region (Herbst, 1961, 1965).

Systematic paleontology

The heterosaurid material consists of isolated remains that are preserved in concretions of 5-15 cm in diameter. One of these concretions contained a maxillary fragment that could be detached from the matrix and probably represents a new species. Other concretions from the same horizon contained an isolated vertebra and unidentified bone fragments, not described herein.

DINOSAURIA Owen, 1842
ORNITHISCHIA Seeley, 1888
ORNITHOPODA Marsh, 1866
HETERODONTOSAURIDAE Romer, 1966
cf. ***Heterodontosaurus*** Crompton and Charig, 1962

Type Species. *Heterodontosaurus tucki* Crompton and Charig, 1962.

cf. ***Heterodontosaurus*** sp.
Figures 2.A-F, 3.A-B and 4.A-B

Referred material. CPBA-V-14091: posterior left maxillary fragment with teeth (a) and natural external mold (b). CPBA-V-14092: a concretion containing a caniniform tooth with serrated cutting edges.

Occurrence. Laguna Colorada (=Laguna La Colorada of Bonaparte and Vince, 1979 = Laguna de la Isla of Casamiquela, 1980; *non* Laguna Colorada of Panza, 1995), stratotype locality of the Laguna Colorada Formation, Late Triassic (Norian?) (Jalfin and Herbst, 1995), central Santa Cruz Province, Patagonia, Argentina.

Description. The specimen CPBA-V-14091a corresponds to the incomplete, posterior part of a left maxilla at the level of its contact with the jugal (figure 2). This maxillary fragment, which is 14.5 mm long, preserves four teeth. The teeth are heavily worn, suggesting that the fragment belongs to a mature individual. In lateral view, the specimen is elongated and truncated at both the anterior and posterior ends (figures 2.A-2.B). The posterior half of the fragment curves gently downward, reaching a point clearly ventral with respect to the level of the margins of the alveoli. The labial surface of the maxilla is dorsoventrally convex and, although extensively weathered, it transitions smoothly onto a longitudinal groove along the dorsal margin of the element, which may represent the articular contact for the jugal. The alveoli lie medially of the lateral surface of the maxilla. Lingually, the maxilla forms a horizontal shelf, the width of which diminishes posteriorly; owing to this change of width, the cross-section of the fragment also decreases caudally. A distinct, but low, longitudinal ridge extends along the shelf, close and parallel to the tooth row (figures 2.E-2.F).

Four closely packed teeth are present. The anteriormost tooth of this series is sectioned longitudinally and preserves only its posterior half. The next two teeth are complete but badly weathered, whereas the last tooth of the row is notably smaller than the other teeth and broken through at its base. Posterior to the last tooth, the remaining maxilla does not show evidence of additional teeth or alveoli; this suggests that the preserved teeth form the posterior end of the maxillary tooth row. There is no evidence of replacement teeth. The teeth are high-crowned and curve gently lingually. They are columnar owing to the absence of a cingulum or a constriction to separate crown and root (figures 2.A-2.D). The labial and lingual surfaces of the crowns are poorly preserved and were damaged during preparation; therefore, the presence of ridges or grooves on their labial surfaces cannot be ascertained. However, a natural external impression of the maxilla is preserved on another fragment of the enclosing concretion (CPBA-V-14091b). On this piece of rock a thin layer of the enamel that covered the distal half of the labial surface of each crown is clearly evident (figure 3.A). Examination of a peel of this enameled surface (figure 3.B) revealed the presence of several vertical ridges at irregular intervals on the distal half of each crown, giving a striated appearance to the teeth. The preserved posterior portion of the first tooth of the series bears three ridges. Seven ridges are present on the anterior two thirds of the second tooth, those of the central region of the tooth being more closely spaced than those at the anterior and posterior regions. On the anterior part of the succeeding tooth four ridges are barely visible. All these ridges are very thin and sharply defined; we were unable to distinguish between primary and secondary ridges. These ridges may have supported distal denticles that were obliterated by wear.

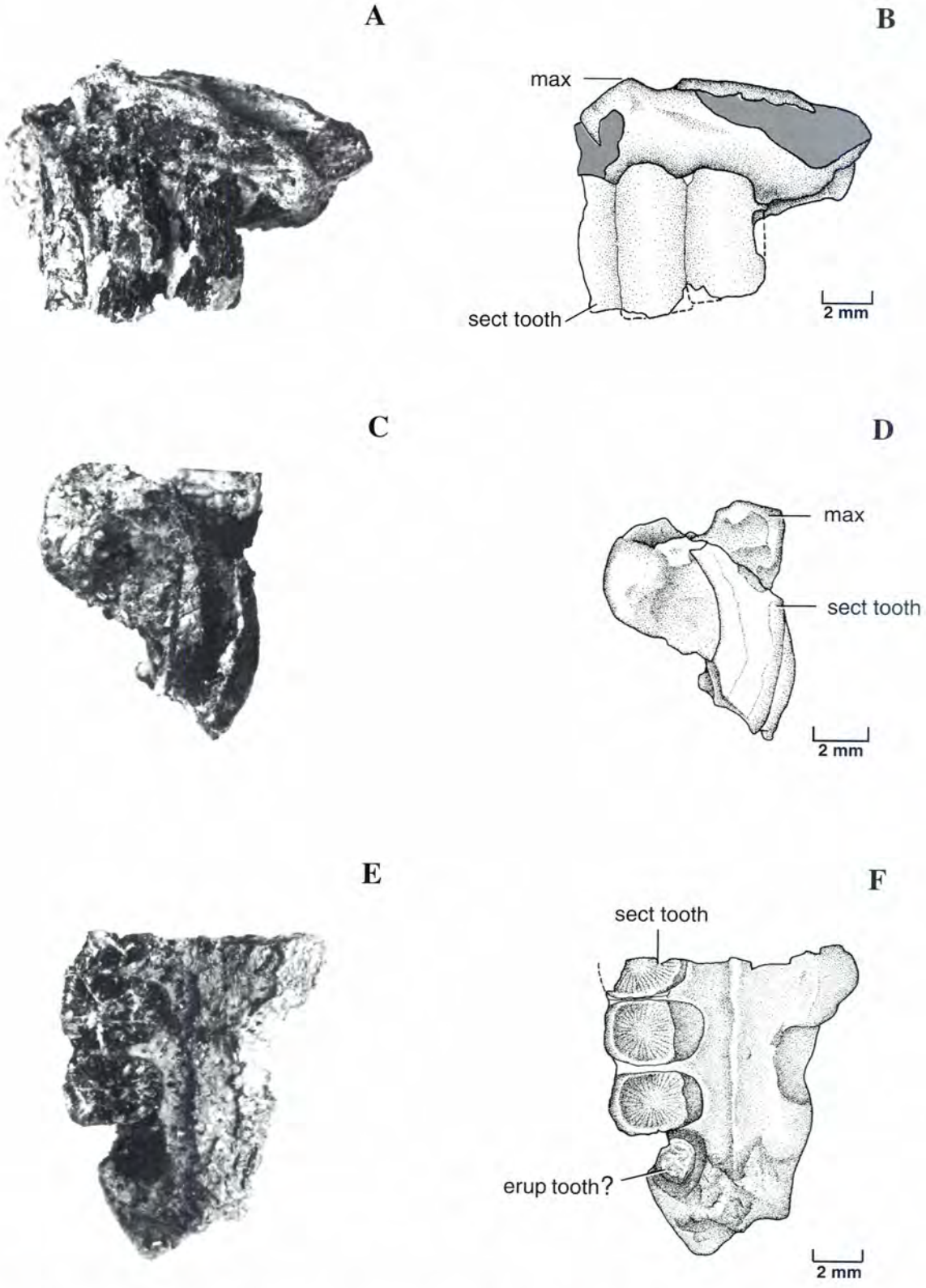

Figure 2. A-F, *Heterodontosaurus* sp., CPBA-V-14091a, posterior left maxillary fragment / *parte posterior de fragmento maxilar izquierdo*.A, photograph in labial view / *fotografía en vista labial*; **B,** drawing in labial view / *dibujo en vista labial*; **C,** photograph in anterior view / *fotografía en vista anterior*; **D,** drawing in anterior view / *dibujo en vista anterior*; **E,** photograph in ventral view / *fotografía en vista ventral*; **F,** drawing in ventral view / *dibujo en vista ventral*. Grey areas indicate broken bone / *Las áreas grises indican roturas del hueso*. Abbreviations / *Abreviaturas*: **erup tooth?**, erupting tooth? / *diente en erupción?*; **max,** maxilla / *maxilar*; **sect tooth,** sectioned tooth / *diente seccionado*.

Figure 3. A-B, *Heterodontosaurus* sp., CPBA-V-14091b. **A,** photograph of natural mold of maxilla in lateral view, showing patches of enamel / *fotografía de un molde natural de la maxila en vista lateral, mostrando restos de esmalte*; **B,** peel of impression of the labial surface of teeth, showing the longitudinal ridges (dusted with ammonium chloride) / *"peel" de la impresión de la superficie labial de los dientes, mostrando la costulación longitudinal (impregnado con cloruro de amonio).* Scale bar: 2 mm / *Escala: 2 mm.*

As mentioned above, the maxilla is broken at the level of the most anterior tooth preserved, making it possible to observe the long root of this tooth, which extends deeply into the maxilla (figures 2.C-2.D). Both crown and root form a continuous lingually directed curve. The anterior three teeth are quadrangular in cross-section and are nearly equal in size. In contrast, the most posterior tooth has a round cross-section. Because of this shape and its very small size, it might be an erupting tooth (figures 2.E-2.F). In lateral view, the second preserved tooth is 6.6 mm high, and has an apical anteroposterior width of 3.1 mm and a proximal anteroposterior width of 2.7 mm. Its occlusal surface is 3.2 mm long anteroposteriorly and 3.1 mm wide labiolingually.

The occlusal surface of each tooth is slightly oblique, facing ventrally and lingually. Adjacent tooth margins are flat for close apposition (figures 2.E-2.F) and the wear facets are roughly on the same level, resulting in a continuous occlusal surface along the tooth row.

A nearly complete, large caniniform tooth was discovered in a separate concretion (CPBA-V-14092) from the bed in which the maxillary fragment was collected (figures 4.A-4.B). This tooth was tentatively assigned to the same heterodontosaurid taxon represented by the maxillary fragment (Báez and Marsicano, 1997, 1998). The tooth is preserved in two fragments of rock, one containing most of the canine and the other its distal tip; a third portion of the concretion preserves the external impression of part of the tooth. The preserved part of the tooth has a total height of 25 mm and a maximum width of 6.6 mm. This tooth is slightly recurved and transversely compressed, with anterior and posterior cutting edges. Both cutting edges bear small but distinct serrations (about three per millimeter). However, because parts of the edges are damaged, the serrations are preserved discontinuously along the distal 3/4 of the tooth length. The tip is rounded and a thin layer of enamel covers the labial and lingual surfaces of the tooth. Given the absence of clear association or positional information, we were unable to identify this tooth as upper or lower with certainty. Nevertheless, its overall shape resembles that of the dentary caniniform of *Heterodontosaurus tucki* better than the premaxillary tusk of the same species based on comparisons with the holotype (SAM K 337).

Discussion. Báez and Marsicano (1997, 1998) considered that the presence of high-crowned cheek teeth in the maxillary fragment, wear facets that lie in a single plane, and a caniniform tooth with serrated cutting edges suggest that these remains from the Laguna Colorada Formation represent a heterodontosaurid. These features were considered diagnostic of the heterodontosaurid clade in recent phylogenetic analyses of ornithischian relationships (Sereno, 1986, 1999; Weishampel and Witmer, 1990). These studies placed heterodontosaurids as the sister-group to higher ornithopods (Sereno, 1986, 1999; Weishampel and Heinrich, 1992).

Three monotypic genera from the Lower Jurassic of southern Africa (Weishampel and Witmer, 1990) currently comprise Heterodontosauridae (=Heterodontosauria Sereno, 1986), apart from the putative heterodontosaurids *Pisanosaurus* (Carnian of Argentina) (Bonaparte, 1976) and *Echinodon* (Lower Cretaceous of England) (Sereno, 1986; Barrett, 1999). These three genera, mainly based on cranial and dental characters, are *Abrictosaurus* Hopson, 1975, *Heterodontosaurus* Crompton and Charig, 1962, and *Lycorhinus* Haughton, 1924. Other heterodontosaurid genera have been erected (Young, 1982; Broom, 1911) but their taxonomic status is dubious (Weishampel and Witmer, 1990). In addition, remains of a very small heterodontosaurid were discovered in the

Early Jurassic Kayenta Formation of Arizona, but this material has not yet been described (Attridge *et al.*, 1985; Sereno, 1986; Sues *et al.*, 1994).

In *Abrictosaurus*, the anterior and posterior margins of adjacent cheek teeth are well separated, the blade-like crowns are relatively low and bear narrow basal cingula, and the wear facets (one large facet per tooth) are steeply inclined labiolingually. A neck sets off each crown from the slender root (Thulborn, 1974; Hopson, 1975; Weishampel and Witmer, 1990). These features rule out the possibility that the heterodontosaurid from Patagonia might be referable to *Abrictosaurus*. It is also noteworthy that the only caniniform tooth attributed to the latter genus has serrations that are restricted to the anterior margin (Thulborn, 1970; Charig and Crompton, 1974; Hopson, 1975). In *Lycorhinus* (= *Lanasaurus*) the laterally compressed upper crowns taper gradually into the roots (Gow, 1975), although lingually and labially the crowns stand out from the roots (Gow, 1990). The anterior and posterior margins of the posteromedially inclined crowns slightly overlap (Weishampel and Witmer, 1990). Each crown bears anterior and posterior wear facets that are of somewhat different orientation, but create an overall occlusal surface that is highly inclined as in *Abrictosaurus* (Hopson, 1975; Gow, 1990; Weishampel and Witmer, 1990). The teeth preserved on the maxilla from the Laguna Colorada Formation are columnar owing to the absence of distinction between crown and root, and adjacent crown margins are squared for close apposition. Contiguous crowns are practically in contact throughout their lengths. These features argue against referral of this material to *Lycorhinus* and, conversely, closely ally it to *Heterodontosaurus*. As in *Heterodontosaurus*, the heterodontosaurid from the Laguna Colorada Formation has closely packed, very high-crowned upper cheek teeth, lacking a cingular swelling or a constriction between crown and root. Also as in this South African genus, the enamel only covers the distal half of the labial surface of each maxillary tooth. However, this portion bears more numerous and narrower ridges than the corresponding teeth in the holotype of the type species of the genus, *H. tucki*. In the latter species, the labial surface of each maxillary tooth bears three prominent ridges -anterior, central and posterior- separated by well-defined concave areas. Additional ridges intercalated between these main ridges occur in the most anterior maxillary teeth only, which are laterally compressed (Crompton and Charig, 1962; Charig and Crompton, 1974). These features of *H. tucki* contrast with the condition in the material from the Laguna Colorada Formation. It is also noteworthy that the individual represented by the maxilla appears to have been of approximately the same size as the holotype of *H. tucki* (SAM K 337), considered to belong to an individual of advanced age (Hopson, 1975). Thus, it is unlikely that these dif-

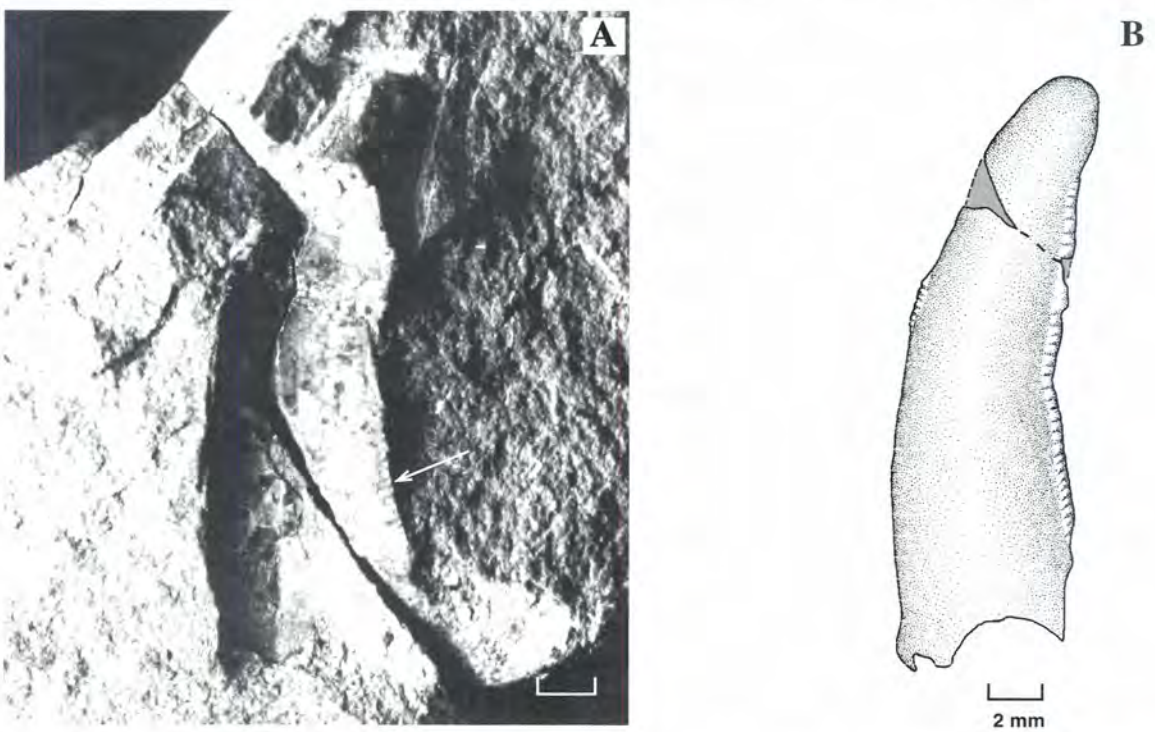

Figure 4. A-B, *Heterodontosaurus* sp., CPBA-V-14092, caniniform tooth / *diente caniniforme*. A, photograph in lateral view; serrations indicated by arrow / *fotografía en vista lateral; crenulaciones indicadas por la flecha*; **B,** composite diagrammatic drawing in lateral view / *dibujo diagramático compuesto en vista lateral.*

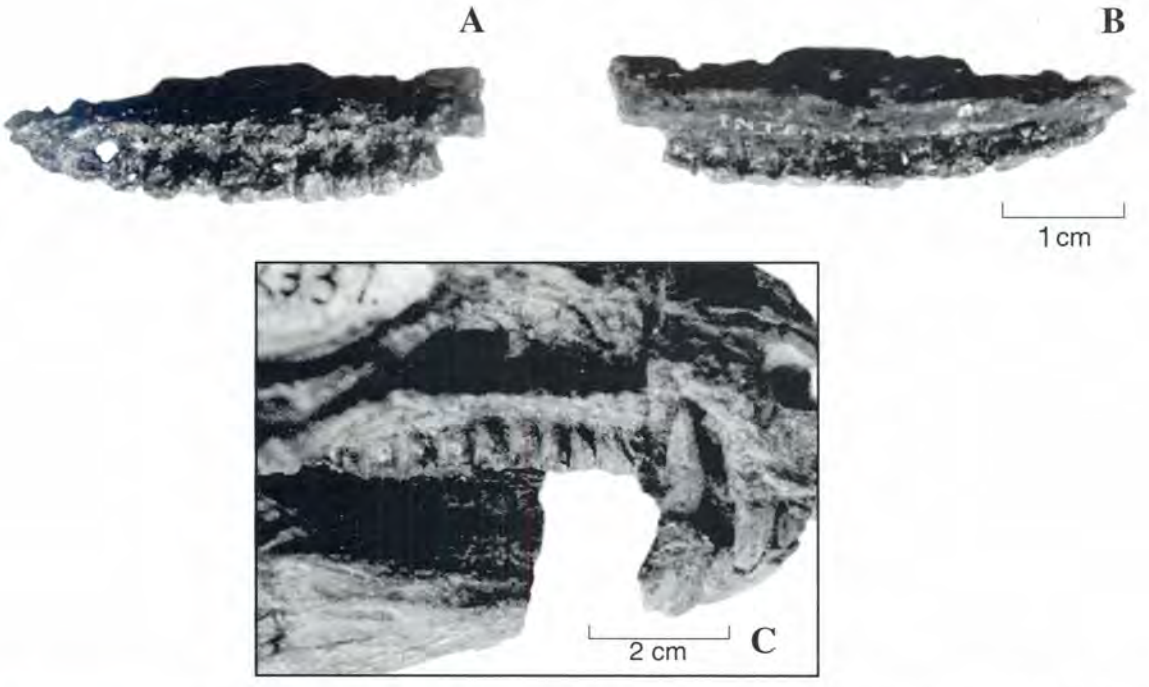

Figure 5. ***Pisanosaurus mertii*** Casamiquela, PVL 2577 (holotype / *holotipo*). **A,** right maxillary dentition in lateral (labial) view / *dentición maxilar derecha en vista lateral (labial)*; **B,** right maxillary dentition in medial (lingual) view / *dentición maxilar derecha en vista medial (lingual)*. ***Heterodontosaurus tucki*** Crompton and Charig, SAM 337 (holotype / *holotipo*). **C,** detail of right maxilla with teeth in lateral view / *detalle del maxilar derecho con dientes en vista lateral*.

ferent features may be due to different developmental stages. Although the highly fragmentary nature and poor preservation of the material described herein prevents further comparisons, the preservation of significant dental features suggests that it represents a new species of *Heterodontosaurus*. However, it cannot be ruled out that discovery of additional material might provide data to warrant a generic distinction.

It is pertinent to point out that several dental character-states distinguish the Patagonian species from *Pisanosaurus mertii* Casamiquela of central western Argentina, although discussion of the heterodontosaurid affinities of the latter are outside the scope of this paper. Personal observations of the holotype of *P. mertii* (PVL 2577) revealed that the maxillary teeth have a constriction between crown and root and that the crowns are distinctly angled lingually (figure 5.A-5.B) as indicated by Bonaparte (1976). They are not closely packed hence the wear facets do not form a continuous surface as in *Heterodontosaurus*. The external surfaces of the maxillary teeth lack ridges, unlike *H. tucki* (figure 5.C) and the Patagonian heterodontosaurid, although this absence was interpreted as the result of wear (Bonaparte, 1976).

Paleogeographic and evolutionary significance

Heterodontosaurid dinosaurs were recorded in scattered localities of the Northern and Southern Hemispheres in strata regarded of Early Jurassic age, although a late-surviving representative (*Echinodon*) may be present in the Lower Cretaceous of England (Sereno, 1986; Barrett, 1999). All described heterodontosaurid taxa are from the upper Stormberg Group of southern Africa. *Abrictosaurus* and *Lycorhinus* are known from the upper Elliot Formation, whereas *Heterodontosaurus* was recorded in this unit and in the overlying Clarens Formation. However, heterodontosaurids have also been reported from the Kayenta Formation of southwestern North America (Attridge *et al.*, 1985; Sereno, 1986), considered of late Sinemurian-Pliensbachian age (Peterson, 1994; Sues *et al.*, 1994). Putative heterodontosaurid remains have also been described from the Lower Lufeng Formation of China (Young, 1982), but their taxonomic allocation remains doubtful (Weishampel and Witmer, 1990). The Liassic age of the heterodontosaurid-bearing strata of southern Africa is widely accepted at present (*e.g.*, Sues *et al.*, 1994; Gow, 2000). This chronological assignment is based on the close similarity of the tetrapod assemblages recovered from these beds and those from the Kayenta Formation and other Liassic sequences in the Northern Hemisphere (Olsen and Galton, 1984; Shubin *et al.*, 1994), although more refined global correlations and faunal comparisons are needed.

The discovery of a heterodontosaurid dinosaur in Patagonia furnishes additional evidence of the widespread distribution of terrestrial tetrapods in Late Triassic-Early Jurassic times. The configuration of the Pangean landmasses during the late Paleozoic-early Mesozoic (Golonka *et al.*, 1994) made dispersal of these vertebrates possible.

Current paleogeographic reconstructions show that prominent mountain ranges extended across southwestern Gondwana in the Permo-Triassic, intervening between Africa and Patagonia (Cox, 1992; Visser, 1993; Veevers *et al.*, 1994). The presence of *Heterodontosaurus*, or a closely related form, in southern Patagonia suggests that by the Late Triassic those highlands were not high enough to act as an effective faunistic barrier. It is noteworthy that some predrift reconstructions of western Gondwana depict Patagonia significantly close to southern Africa, although it rotated dextrally away from Africa during the initial separation of East Antarctica from Africa and South America in the Early Jurassic (Dalziel and Grunow, 1992; Marshall, 1994; Richards *et al.*, 1996).

The Late Triassic age of the Patagonian heterodontosaurid implies an earlier origin of heterodontosaurids than previously recorded. This also suggests an earlier split of the bird-hipped dinosaurs into the armoured thyreophorans and unarmoured neornithischians during the Late Triassic according to the present understanding of dinosaur phylogeny (Sereno, 1999). Moreover, *Heterodontosaurus*, far from being a basal heterodontosaurid, has been considered, together with *Lycorhinus*, more derived than *Abrictosaurus* in features interpreted as specialized for an strictly herbivorous diet (Sereno, 1986; Crompton and Attridge, 1986; Weishampel and Witmer, 1990). It is noteworthy that, apart from *Pisanosaurus* (Casamiquela, 1967; Bonaparte 1976) from the Carnian Ischigualasto Formation (Rogers *et al.*, 1993), placed as the sister-taxon of all other ornithischians by some authors, most putative ornithischians from sequences of unquestionable Late Triassic age are documented by isolated teeth (Sereno, 1991, Hunt and Lucas, 1994). These teeth differ significantly from those of the known Triassic ornithischians from Argentina in lacking the specializations for dealing effectively with plant matter that may have been acquired independently in *Pisanosaurus* and heterodontosaurids. This evidence attests that basal cladogenesis of ornithischian dinosaurs was well under way before the end of the Triassic, although the fossil record has failed to document this early diversification to date.

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