

A MEDIUM-SIZED ORNITHOPOD (DINOSAURIA: ORNITHISCHIA)
FROM THE UPPER CRETACEOUS BAJO BARREAL FORMATION OF LAGO COLHUÉ HUAPI,
SOUTHERN CHUBUT PROVINCE, ARGENTINA

LUCIO M. IBIRICU

Department of Biology, Drexel University, 32nd and Chestnut Streets, Philadelphia, Pennsylvania 19104
lmi23@drexel.edu

RUBÉN D. MARTÍNEZ

Laboratorio de Paleovertebrados, Universidad Nacional de la Patagonia “San Juan Bosco”,
C.C. 360, Comodoro Rivadavia (9000), Chubut, Argentina
rdfmartinez@yahoo.com

MATTHEW C. LAMANNA

Assistant Curator, Section of Vertebrate Paleontology,
Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213
lamannam@carnegiemnh.org

GABRIEL A. CASAL

Laboratorio de Paleovertebrados, Universidad Nacional de la Patagonia “San Juan Bosco”,
C.C. 360, Comodoro Rivadavia (9000), Chubut, Argentina
paleogac@yahoo.com.ar

MARCELO LUNA

Laboratorio de Paleovertebrados, Universidad Nacional de la Patagonia “San Juan Bosco”,
C.C. 360, Comodoro Rivadavia (9000), Chubut, Argentina
marceloxr400@yahoo.com

JERALD D. HARRIS

Dixie State College, Science Building, 225 South 700 East, St. George, Utah 84770
jharris@dixie.edu

KENNETH J. LACOVARA

Department of Biology, Drexel University, 32nd and Chestnut Streets, Philadelphia, Pennsylvania 19104
lacovara@drexel.edu

ABSTRACT

An associated partial postcranial skeleton is described as the third definitive ornithopod dinosaur record from the Upper Cretaceous Bajo Barreal Formation of central Patagonia, Argentina. Specifically, the specimen was recovered from the uppermost Cretaceous (Campanian–?Maastrichtian) Upper Member of the Bajo Barreal exposed on an ephemeral island in the southeastern portion of Lago Colhué Huapi in southern Chubut Province. Identifiable elements of the skeleton include four incomplete dorsal vertebrae, three partial anterior caudal vertebrae, a middle caudal neural arch, an incomplete posterior caudal vertebra, a dorsal rib fragment, the right calcaneum, and portions of the left metatarsal III and right metatarsal IV. Comparisons with corresponding elements in other ornithischians indicate that the material pertains to a medium-sized, non-hadrosaurid ornithopod. In particular, the morphology of the calcaneum is characteristic of ornithopods of this “grade”. The new discovery augments our understanding of the latest Cretaceous terrestrial vertebrate assemblage of central Patagonia and adds to the generally meager record of ornithischians in the Late Cretaceous of the Southern Hemisphere.

KEY WORDS: Campanian, Gondwana, Late Cretaceous, Maastrichtian, Ornithopoda, Patagonia, South America, Upper Member

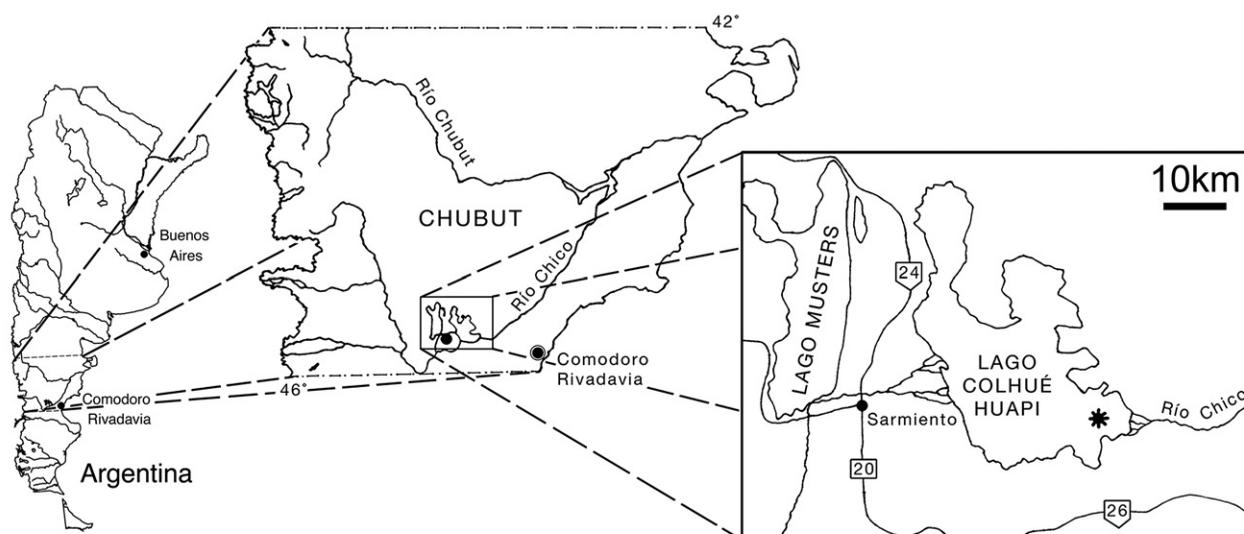


Fig. 1.—Location of Lago Colhué Huapi in southern Chubut Province, central Patagonia, Argentina (modified from Casal et al. 2007). Asterisk denotes ephemeral island where the new ornithopod specimen (UNPSJB-PV 960) was discovered.

INTRODUCTION

Continental deposits of the Bajo Barreal Formation exposed in central Patagonia, Argentina preserve a rich and important record of South American dinosaur evolution that spans much of the Upper Cretaceous (e.g., Lamanna et al. 2002; Martínez et al. 2004; Martínez and Novas 2006; Casal et al. 2007). At least two temporally distinct dinosaur faunas are known from these strata (Casal et al. 2007). The older and better known of these assemblages derives from the early Late Cretaceous (middle Cenomanian–Turonian)-aged Lower Member, which is well exposed in south-central Chubut Province at localities such as the estancias Ocho Hermanos and Laguna Palacios. This unit has produced fossils of turtles, crocodyliforms, pterosaurs, abelisauroid and tetanuran theropods, diplodocoid and titanosauriform sauropods, and the small-bodied ornithopod *Notohypsilophodon comodorensis* Martínez, 1998 (see Lamanna et al. 2002:table 1).

The second fauna, thought to date to the Campanian–Maastrichtian (Casal et al. 2007; Sciutto et al. in press), comes from the Upper Member of this formation as exposed in the southeastern region of Lago Colhué Huapi, on and around islands that periodically emerge when the water level of this lake is low (Fig. 1). Fossils thus far reported from these beds include the incomplete mandibles of a small crocodyliform (Lamanna et al. 2003), an articulated caudal series of the titanosaurian sauropod *Aeolosaurus colhuehuapensis* Casal et al., 2007, and an isolated left ilium of a medium-sized, probably iguanodontian ornithopod (Luna et al. 2003). The hadrosaurid *Secernosaurus koernerii* Brett-Surman, 1979, and the supposed ceratopsian *Notoceratops bonarellii* Tapia, 1919, also come from this area, and probably also from the Upper Member of the Bajo Barreal Formation (Casal et al. 2007).

The new material was discovered and collected by one of us (Luna) in 1993, and pertains to a medium-sized, non-hadrosaurid ornithopod. This addition to the fauna of the Upper Member is significant for several reasons. First, it adds to the generally sparse record of Gondwanan Cretaceous ornithopods and expands the known paleobiogeographic range of non-hadrosaurid ornithopods in South America. Additionally, it augments understanding of the poorly-known fauna of the Upper Member, and therefore our knowledge of the latest Cretaceous continental vertebrate assemblages of central Patagonia.

Institutional abbreviation.—UNPSJB-PV, Universidad Nacional de la Patagonia “San Juan Bosco” Paleontología de Vertebrados, Comodoro Rivadavia, Chubut, Argentina.

SYSTEMATIC PALEONTOLOGY

Superorder Dinosauria Owen, 1842
 Order Ornithischia Seeley, 1887
 Suborder Ornithopoda Marsh, 1881

Genus and species indeterminate
 (Figs. 2–5)

Material.—UNPSJB-PV 960, an associated partial postcranial skeleton consisting of: UNPSJB-PV 960/11, incomplete ?anterior dorsal neural arch; UNPSJB-PV 960/5, incomplete ?anterior dorsal vertebra preserving posterior half of centrum and much of right side of neural arch; UNPSJB-PV 960/1, incomplete dorsal vertebra preserving centrum and ventral extreme of neural arch; UNPSJB-PV 960/6, incomplete dorsal vertebra consisting mainly of the ?anterior half of the centrum; UNPSJB-PV 960/2, 3, and 4, incomplete anterior caudal vertebrae preserving centrum

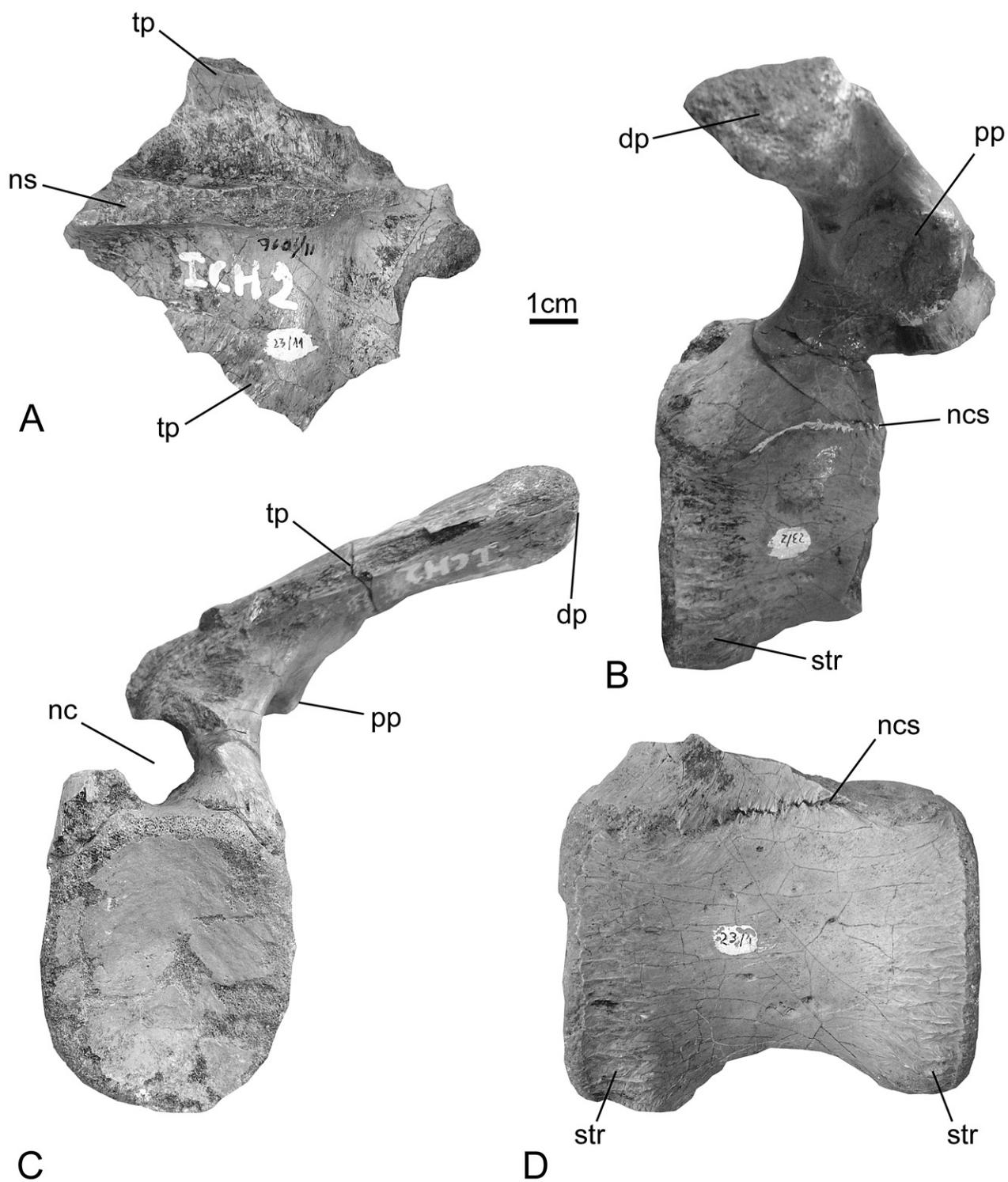


Fig. 2.—Incomplete dorsal vertebrae of the new ornithomimid specimen, UNPSJB-PV 960. **A**, ?anterior dorsal neural arch (UNPSJB-PV 960/11) in dorsal view. **B-C**, ?anterior dorsal vertebra (UNPSJB-PV 960/5) in right lateral and posterior views, respectively. **D**, dorsal vertebra (UNPSJB-PV 960/1) in lateral view. Abbreviations: **dp**, diapophysis; **nc**, neural canal; **ncs**, neurocentral suture; **ns**, base of neural spine; **pp**, parapophysis; **str**, striations; **tp**, transverse process.

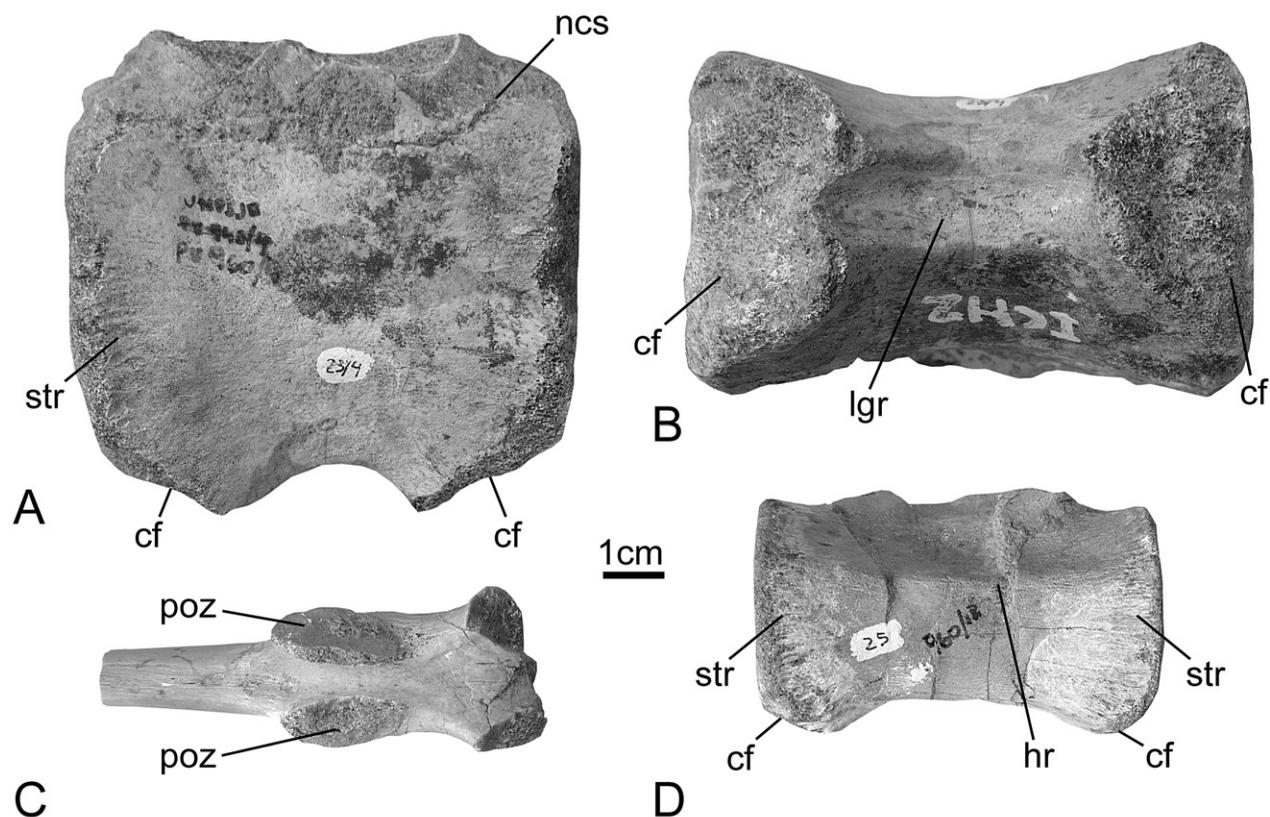


Fig. 3.—Incomplete caudal vertebrae of the new ornithopod specimen, UNPSJB-PV 960. **A–B**, anterior caudal vertebra (UNPSJB-PV 960/4) in lateral and ventral views, respectively. **C**, middle caudal neural arch (UNPSJB-PV 960/14) in ventral view; **D**, posterior caudal vertebra (UNPSJB-PV 960/12) in lateral view. Abbreviations: **cf**, chevron facet; **hr**, horizontal ridge; **lgr**, longitudinal groove; **poz**, postzygapophysis; **str**, striations.

and ventral extreme of neural arch; UNPSJB-PV 960/14, incomplete middle caudal neural arch; UNPSJB-PV 960/12, incomplete posterior caudal vertebra preserving centrum and ventral extreme of neural arch; UNPSJB-PV 960/10, dorsal rib fragment; UNPSJB-PV 960/7, right calcaneum; UNPSJB-PV 960/9, proximal end of left metatarsal III; UNPSJB-PV 960/8, distal end of right metatarsal IV; UNPSJB-PV 960/13, indeterminate fragment.

Locality.—Ephemeral island near the southeastern shore of Lago Colhué Huapi (45°35'52"S, 68°37'20"W), approximately 35 km east of the town of Sarmiento, southern Chubut Province, central Patagonia, Argentina (Fig. 1). Although UNPSJB-PV 960 was found disarticulated, all elements comprising the specimen likely pertain to a single ornithopod individual. The bones were recovered over a roughly circular area only ~3 m in diameter; moreover, no other vertebrate fossils were discovered within several hundred meters of this site.

Horizon and age.—Upper Member of the Bajo Barreal Formation (Upper Cretaceous). Geologic studies support a Campanian–?Maastrichtian age for the Upper Member of the Bajo Barreal Formation as exposed in the southeastern portion of Lago Colhué Huapi (Casal et al. 2007; Sciutto et

al. in press). The discovery of the titanosaurian sauropod *A. colhuehuapensis* in the Upper Member also supports a Campanian–?Maastrichtian age for this unit, because the genus *Aeolosaurus* Powell, 1987, is otherwise known only from Campanian–Maastrichtian deposits of northern Patagonia and Brazil (e.g., Salgado and Coria 1993; Santucci and Bertini 2001; Powell 2003; see Casal et al. 2007). In the Colhué Huapi area, the Upper Member of the Bajo Barreal Formation was deposited in a coastal environment adjacent to the Salamanca marine transgression (Sciutto et al. in press).

DESCRIPTION

Ontogenetic stage.—The lack of complete fusion between most vertebral centra and their respective neural arches suggests that the individual represented by UNPSJB-PV 960 was not fully skeletally mature at death (Galton 1981; Brochu 1996; Calvo et al. 2007b; Irmis 2007). However, although the neurocentral sutures of the Colhué Huapi ornithopod remain clearly visible, the firm attachment of the neural arches to the centra indicates that the specimen does correspond to a nearly adult individual.

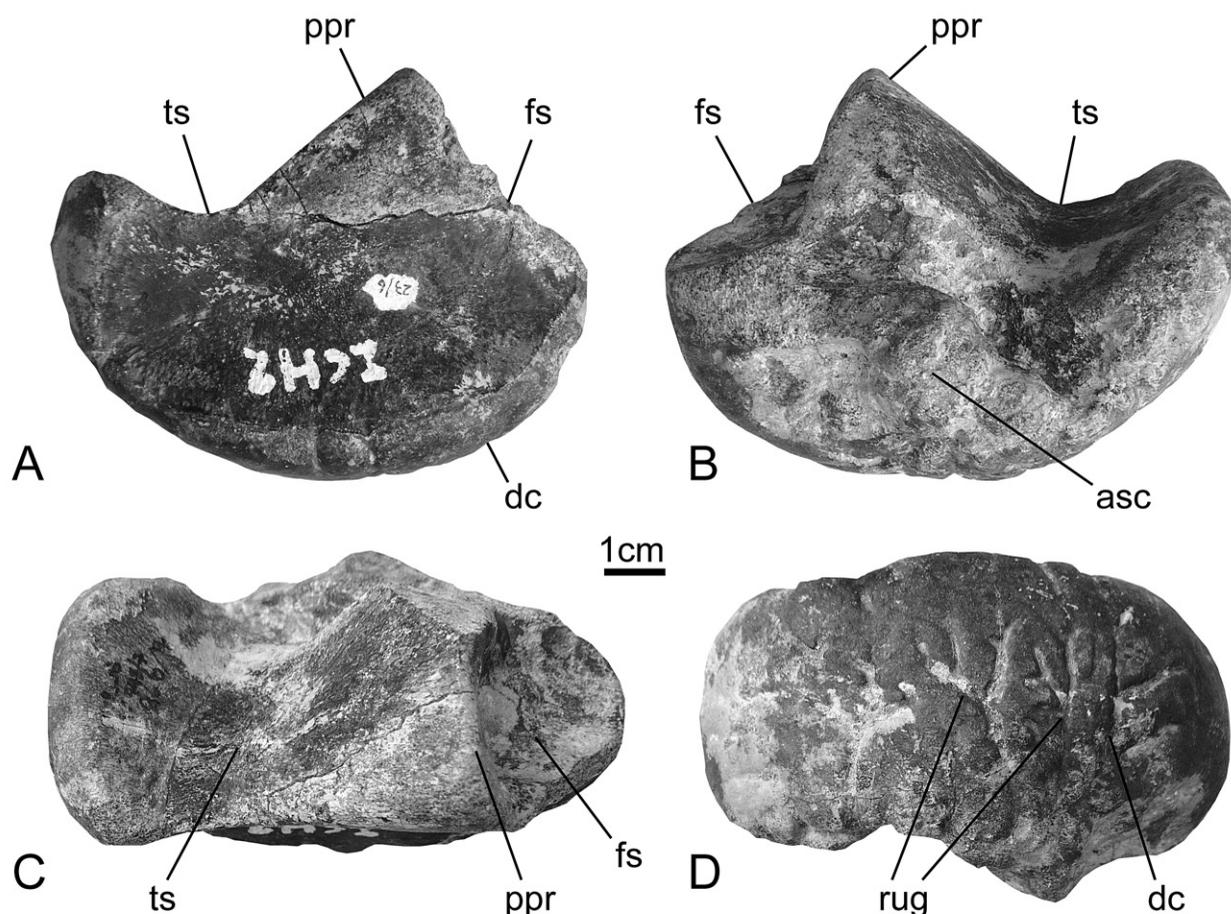


Fig. 4.—Right calcaneum of the new ornithomimid specimen (UNPSJB-PV 960/7) in **A**, lateral; **B**, medial; **C**, proximal; and **D**, distal views. Abbreviations: **asc**, astragalar contact; **dc**, distal condyle; **fs**, fibular surface; **ppr**, proximal process; **rug**, rugosities; **ts**, tibial surface.

Axial skeleton.—An incomplete dorsal neural arch (UNPSJB-PV 960/11; Fig. 2A) preserves much of its ventral portion, from the dorsal margin of the neural canal to the base of the neural spine. Although only the medial bases of the transverse processes are preserved, these processes were clearly inclined steeply dorsolaterally, slightly more so than in the more complete dorsal vertebra, UNPSJB-PV 960/5. The right parapophysis is well preserved and situated far ventrally, near the base of the transverse process. It is oval in lateral profile with its long axis oriented approximately dorsoventrally, and is slightly smaller than the parapophysis of UNPSJB-PV 960/5. For these reasons, we believe UNPSJB-PV 960/11 to be the most anteriorly situated of the vertebrae of the Colhué Huapi ornithomimid for which serial position can be reliably assessed. A thin lamina connected to the ventral margin of the parapophysis extends anteroventrally and may have continued onto the centrum. Posteriorly, the neural arch exhibits two deep fossae that are separated medially by the neural canal. In dorsal view the neural arch is rhomboid in shape.

Another incomplete dorsal vertebra (UNPSJB-PV

960/5; Figs. 2B, 2C) preserves the posterior half of the centrum and much of the right side of the neural arch, including the ventral end and the complete transverse process. The posterior articular surface of the centrum is gently concave and suboval in contour, slightly taller dorsoventrally than wide transversely. Circumscribing this articular surface are well-developed, mostly longitudinally-oriented lateral striations (Fig. 2B). These striations continue onto the ventral surface of the centrum, where they become much deeper and more pronounced, giving the posterior end of the centrum a “corrugated” appearance in ventrolateral and ventral views. The robust transverse process is directed dorsolaterally at an angle of approximately 45° to the horizontal (Fig. 2C). In dorsal view, this process is rectangular. The parapophysis is proportionally large, oval in outline, and located anteroventral to the base of the diapophysis. An anteroventrally-oriented lamina arises from the ventral end of the parapophysis, as in UNPSJB-PV 960/11. The diapophysis occupies the lateral extreme of the transverse process. As with UNPSJB-PV 960/11, the inclination of the transverse process and the size and

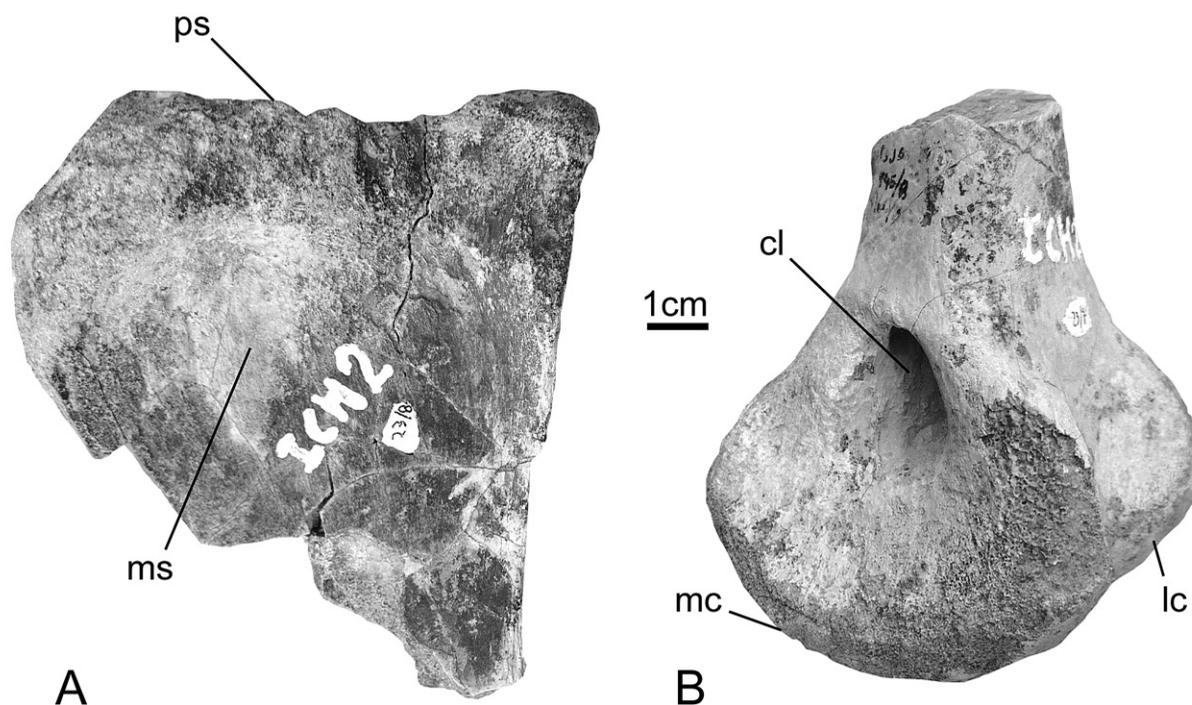


Fig. 5.—Metatarsals of the new ornithopod specimen, UNPSJB-PV 960. **A**, proximal end of left metatarsal III (UNPSJB-PV 960/9) in medial view; **B**, distal end of right metatarsal IV (UNPSJB-PV 960/8) in medial view. Abbreviations: **cl**, collateral ligament cavity; **lc**, lateral condyle; **mc**, medial condyle; **ms**, medial surface; **ps**, proximal surface.

position of the parapophysis indicate that UNPSJB-PV 960/5 probably occupied an anterior position in the dorsal series of this ornithopod.

The centrum of a third incomplete dorsal vertebra (UNPSJB-PV 960/1; Fig. 2D) possesses a flat anterior articular surface and a slightly concave posterior articular surface, is ventrally concave in lateral view, and is hourglass-shaped in ventral view. Its articular surfaces are suboval, slightly taller than wide, and exhibit a prominent “lip” or rim. On each of the lateral surfaces, ventral to the well-defined neurocentral contact, are two pairs of nutrient foramina. The striations observed adjacent to the posterior central margin of UNPSJB-PV 960/5 are also well developed in this vertebra and occur near the anterior end of the centrum.

The centra of three incomplete caudal vertebrae (UNPSJB-PV 960/2, 3, and 4; Figs. 3A, 3B) are amphiplatyan to slightly amphicoelous and significantly longer anteroposteriorly than wide transversely. Comparison with well-represented caudal sequences of other ornithopods (e.g., *Hypsilophodon* Huxley, 1869 [Galton 1974a], *Tenontosaurus* Ostrom, 1970 [Forster 1990; Winkler et al. 1997], *Iguanodon* Mantell, 1825 [Norman 1980]) demonstrates that these vertebrae were situated in the anterior portion of the tail. As observed in lateral view (Fig. 3A), there are modest striations toward each of the subrectangular intercentral articular surfaces, but they are much less

pronounced than on the dorsal vertebrae. Ventrally (Fig. 3B), each centrum exhibits a marked longitudinal groove that is perforated by two nutrient foramina. All three of these anterior caudal centra present prominent anterior and posterior facets for chevron attachment.

The single middle caudal neural arch (UNPSJB-PV 960/14; Fig. 3C) preserves only the postzygapophyseal region and the ventral portion of the neural spine. The postzygapophyses are oval in contour and anteroposteriorly elongate, and the neural spine is transversely compressed and oriented posterodorsally.

The centrum of the only preserved posterior caudal vertebra (UNPSJB-PV 960/12; Fig. 3D) is amphiplatyan and much longer anteroposteriorly than tall dorsoventrally and wide transversely. As observed in the anterior caudals UNPSJB-PV 960/2, 3, and 4, there are modest striations on its lateral and ventral sides, approaching the articular surfaces. Nevertheless, a marked difference between the centrum of UNPSJB-PV 960/12 and those of UNPSJB-PV 960/2, 3, and 4 is the presence of a prominent horizontal ridge extending across each lateral surface of the first. Situated slightly dorsal to the dorsoventral midline of the centrum, this ridge divides both of its lateral surfaces into dorsal and ventral portions, lending the centrum a hexagonal contour in anterior and posterior views. In ventral view, the centrum of UNPSJB-PV 960/12 exhibits a shallow longitudinal groove that extends between the anterior

and posterior facets for chevron attachment, of which the posterior is more prominent than the anterior. Only the ventralmost portion of the neural arch is preserved, which is transversely widest anteriorly.

Appendicular skeleton.—The complete right calcaneum (UNPSJB-PV 960/7; Figs. 4A-D) is semicircular in medial and lateral views, slightly concave laterally, and mediolaterally compressed. There is a strong, oblique proximal projection that divides the articular cotyle into an anterior portion that articulated with the distal end of the fibula and a posterior portion that received part of the distolateral condyle of the tibia. The fibular articular surface is slightly concave and subrectangular in proximal view, whereas the tibial surface is wide and strongly concave. The medial surface of the element exhibits a pronounced astragalar contact as well as a deep, marked groove. The tibial articular surface is open medially; conversely, the anteromedial edge of its fibular counterpart is delimited by a thin lip. The distal surface of the calcaneum is convex and displays marked rugosities.

The proximal end of the left metatarsal III (UNPSJB-PV 960/9; Fig. 5A) is expanded in anterior view and has a slightly concave articular surface. In proximal view, the metatarsal exhibits an irregular triangular outline. The medial surface is wide and flat where it articulated with metatarsal II; conversely, the lateral surface of metatarsal III has a longitudinally-oriented crest associated with a slight depression at the contact with metatarsal IV.

Only the distal end of the right metatarsal IV (UNPSJB-PV 960/8; Fig. 5B) is preserved. Its articular surface is convex with two asymmetrical condyles, of which the medial is the more robust and rounded and the lateral is sharper and more dorsoplantarily extended. The condyles are plantarily separated by an intercondylar groove. Marked, generally mediolaterally-oriented rugosities and striations cover the entire distal articular surface. On its medial surface, the medial condyle possesses a deep, oval cavity that indicates the origin of collateral ligaments.

COMPARISONS

To ascertain the evolutionary affinities of UNPSJB-PV 960 within Ornithischia, we compared the specimen to the following genera within this clade: the basal neornithischians *Hexinlusaurus* Barrett et al., 2005, and *Yandusaurus* He, 1979 (He and Cai 1984); the basal (i.e., non-iguanodontian) ornithopods *Hypsilophodon* (Galton 1974a; Torres and Viera 1994), *Orodromeus* Horner and Weishampel, 1988 (Scheetz 1999), *Parksosaurus* Sternberg, 1937 (Parks 1926; Galton 1973), and *Thescelosaurus* Gilmore, 1913 (Gilmore 1915; Galton 1974b, 1995; Boyd et al. 2009); the basal ornithopods or basal iguanodontians *Gasparinisaura* Coria and Salgado, 1996 (Coria and Salgado 1996a; Salgado et al. 1997) and *Notohypsilophodon* Martínez, 1998 (Martínez 1998); the non-hadrosaurid iguanodontians *Camptosaurus* Marsh, 1885 (Gilmore 1909; Galton and Powell 1980; Carpenter and Wilson 2008), *Dollodon* Paul, 2008 (Norman

1986), *Dryosaurus* Marsh, 1894 (Janensch 1955; Galton 1981), *Iguanodon* (Norman 1980), *Kangnasaurus* Houghton, 1915 (Cooper 1985), *Macrogyphosaurus* Calvo et al., 2007 (Calvo et al. 2007b), *Mantellisaurus* Paul, 2006 (Hooley 1925; Norman 1986), *Ouranosaurus* Taquet, 1976 (Taquet 1976), *Tenontosaurus* (Forster 1990; Winkler et al. 1997), and *Zalmoxes* Weishampel et al., 2003 (Weishampel et al. 2003); and representative hadrosaurids (see Weishampel and Horner 1990; Horner et al. 2004; Suzuki et al. 2004; Brett-Surman and Wagner 2007; Prieto-Marquez 2007). Regrettably, the Patagonian Late Cretaceous ornithopods *Anabisetia* Coria and Calvo, 2002, *Secernosaurus* Brett-Surman, 1979, and *Talenkauen* Novas et al., 2004, could not be extensively compared to UNPSJB-PV 960 because the portions of their respective skeletons that overlap with material preserved in the Colhué Huapi ornithopod have not yet received detailed descriptions. Moreover, although the ceratopsian (Tapia 1919) or ornithopod (Molnar 1980; Coria and Cambiaso 2007) *Notoceratops* Tapia, 1918, was recovered from the same general area as was UNPSJB-PV 960, and thus might be relevant to resolving the relationships of the latter, it is based only on a partial mandible and is thus not directly comparable to the new specimen.

The axial skeleton of UNPSJB-PV 960 exhibits many similarities with those of non-hadrosaurid ornithopods while simultaneously lacking characters of Hadrosauridae. For example, the strongly-developed longitudinal striations on the lateral and ventral articular margins of the dorsal centra are comparable to those observed in many non-hadrosaurid ornithopods, such as *Camptosaurus*, *Dryosaurus*, *Kangnasaurus*, *Macrogyphosaurus*, *Notohypsilophodon*, *Orodromeus*, *Tenontosaurus*, and *Thescelosaurus*. The ventral surfaces of the dorsal centra are concave as in the non-hadrosaurid iguanodontians *Camptosaurus*, *Dollodon*, *Iguanodon*, *Mantellisaurus*, *Tenontosaurus*, and *Zalmoxes*. The suboval outline of the posterior articular surface of the centrum of the probable anterior dorsal UNPSJB-PV 960/5 is similar to the condition in a variety of basal neornithischians and non-hadrosaurid ornithopods, such as *Camptosaurus*, *Hexinlusaurus*, *Iguanodon*, *Kangnasaurus*, *Mantellisaurus*, *Notohypsilophodon*, *Ouranosaurus*, and *Yandusaurus*. In hadrosaurids, on the other hand, anterior dorsal centra display “heart-shaped” posterior articular surfaces (Lambe 1920; Lull and Wright 1942; Horner et al. 2004; Prieto-Marquez 2007). The rectangular dorsal contour of the transverse process of UNPSJB-PV 960/5 is a feature documented in the non-hadrosaurid iguanodontians used in the present comparison.

The anterior caudal centra of UNPSJB-PV 960 possess subrectangular articular surfaces, a feature shared with non-hadrosaurid ornithopods including *Kangnasaurus*, *Notohypsilophodon*, and *Tenontosaurus*, whereas in hadrosaurids these articular surfaces are usually hexagonal in outline (Horner et al. 2004). Marked longitudinal grooves on the ventral surfaces, which may be sexually dimorphic features (Nopcsa 1929), are also seen in at least some

specimens of basal ornithopods and basal iguanodontians like *Gasparinisaura*, *Hypsilophodon*, *Macrogyphosaurus*, *Notohypsilophodon*, and *Zalmoxes*, and are slightly developed in *Kangnasaurus*. Moreover, hadrosaurid caudal centra are strongly concave laterally (Prieto-Marquez 2007); however, in the Colhué Huapi ornithopod, this concavity is slight. Finally, the strongly developed chevron facets of the anterior caudal centra of UNPSJB-PV 960 are comparable to those of many ornithopods, including *Camptosaurus*, *Dollodon*, *Dryosaurus*, *Hypsilophodon*, *Iguanodon*, *Ouranosaurus*, *Tenontosaurus*, *Thescelosaurus*, *Zalmoxes*, and hadrosaurids.

With regard to the calcaneum, the semicircular shape, the wide anteromedially-posterolaterally-oriented proximal ridge that separates the fibular and tibial cotyles, the strong astragalar contact, and the deep medial groove are features that the Colhué Huapi ornithopod shares with basal ornithopods and non-hadrosaurid iguanodontians such as *Camptosaurus*, *Gasparinisaura*, *Hypsilophodon*, *Iguanodon*, *Kangnasaurus*, *Notohypsilophodon*, *Ouranosaurus*, and *Zalmoxes*. In contrast, the calcanei of hadrosaurids are typically W-shaped in proximal view (Weishampel and Horner 1990; Horner et al. 2004). The proximal surface of the calcaneal fibular cotyle of the central Patagonian form is only slightly concave in lateral view, as in most basal neornithischians and non-hadrosaurid ornithopods including *Dryosaurus*, *Gasparinisaura*, *Hexinlusaurus*, *Hypsilophodon*, *Iguanodon*, *Kangnasaurus*, *Mantellisaurus*, *Notohypsilophodon*, *Ouranosaurus*, and *Zalmoxes*. In *Camptosaurus* and hadrosaurids, on the other hand, this cotyle is more deeply concave (Brett-Surman and Wagner 2007). Likewise, the tibial cotyle of UNPSJB-PV 960 is strongly concave in lateral view and, when naturally articulated, would have distally enveloped at least the anterior portion of the distolateral tibial condyle. A comparable condition occurs in non-hadrosaurid ornithopods such as *Gasparinisaura*, *Hypsilophodon*, *Iguanodon*, *Kangnasaurus*, *Notohypsilophodon*, *Ouranosaurus*, and at least some specimens of *Camptosaurus*. Conversely, the hadrosaurid calcaneum has a flat tibial articular surface that does not distally overlap the tibia; as such, in these derived ornithopods both the calcaneum and the distal terminus of the tibia articulate with the lateral distal tarsals (Brett-Surman and Wagner 2007). Lastly, when the calcaneum of UNPSJB-PV 960 is viewed laterally, the length of its fibular cotyle is noticeably less than that of the tibial cotyle. This character state is shared with selected non-hadrosaurid ornithopods such as *Gasparinisaura*, *Kangnasaurus*, *Notohypsilophodon*, and *Ouranosaurus*. In *Camptosaurus*, *Hexinlusaurus*, *Hypsilophodon*, and *Zalmoxes*, these cotyles are subequal in length in lateral view, whereas in Hadrosauridae, *Iguanodon*, and *Mantellisaurus* the fibular cotyle is clearly longer than the tibial. Intriguingly, in overall appearance, the calcaneum of UNPSJB-PV 960 most closely resembles those of the Late Cretaceous Gondwanan ornithopods *Gasparinisaura* (Salgado et al. 1997: figs. 4.10-4.13) and *Kangnasaurus* (Cooper 1985: figs. 20, 21).

In the Colhué Huapi specimen, the proximal end of metatarsal III has a flat medial surface that contacted metatarsal II, as in *Camptosaurus*, *Gasparinisaura*, *Hexinlusaurus*, *Iguanodon*, and *Ouranosaurus*. In contrast, the proximal end of the hadrosaurid third metatarsal exhibits a “notch” on the medial side for the reception of metatarsal II (Weishampel and Horner 1990; Horner et al. 2004). Similarly, the subtriangular proximal outline of metatarsal III of UNPSJB-PV 960 is also observed in basal neornithischians and non-hadrosaurid ornithopods such as *Camptosaurus*, *Dryosaurus*, *Gasparinisaura*, *Hexinlusaurus*, and *Iguanodon*. In hadrosaurids, on the other hand, the proximal contour of metatarsal III is ovoid (Horner et al. 2004); indeed, in some taxa (e.g., *Nipponosaurus* Nagao, 1936) it is described as “raindrop-shaped” (Suzuki et al. 2004). Regrettably, the shafts of metatarsals III and IV of the Colhué Huapi ornithopod are not completely preserved. Nevertheless, from the portions that are present, it may be inferred that both were long and slender, as in gracile taxa such as *Anabisetia*, *Dryosaurus*, *Gasparinisaura*, *Hexinlusaurus*, and *Hypsilophodon*, and in contrast to the more robust metatarsal shafts present in *Camptosaurus*, *Iguanodon*, *Ouranosaurus*, and hadrosaurids. The distal end of metatarsal IV of UNPSJB-PV 960 has two asymmetrical condyles that are plantarily separated by an intercondylar groove, features that occur in non-hadrosaurid iguanodontians including *Thescelosaurus*, *Iguanodon*, and *Ouranosaurus*. An intercondylar groove is also present in some hadrosaurids, but appears to be less pronounced than in more basal ornithopods. The deep, ovoid collateral ligament fossa on the distomedial end of metatarsal IV is comparable to that observed in at least one specimen of *Camptosaurus* (Carpenter and Wilson 2008: fig. 33D). Conversely, collateral ligament pits are described on both the lateral and medial sides of the distal end of metatarsal IV in other *Camptosaurus* individuals (Gilmore 1909) and the hadrosaurid *Nipponosaurus* (Suzuki et al. 2004).

As is evident from the comparisons above, UNPSJB-PV 960 exhibits similarities with a variety of non-hadrosaurid ornithopodan taxa, and several differences with hadrosaurids. Accordingly, we regard the specimen as pertaining to a non-hadrosaurid ornithopod. Unfortunately, however, because of its fragmentary condition, it is not possible to definitively determine whether the Colhué Huapi form is a basal (i.e., non-iguanodontian) ornithopod or a plesiomorphic representative of Iguanodontia.

DISCUSSION

A Gondwanan ornithopod clade?—Fossils of ornithischian dinosaurs are relatively rare in Patagonia, and where present, are predominantly those of ornithopods (Coria and Cambiaso 2007). Non-hadrosaurid ornithopods comparable to UNPSJB-PV 960 have been previously recovered from Upper Cretaceous rocks in several Patagonian regions, including *Anabisetia* from the Cenomanian–

TABLE 1. Measurements (maxima, in mm) of the calcanei of UNPSJB-PV 960 and *Notohypsilophodon comodorensis* (UNPSJB-PV 942).

	UNPSJB-PV 960/7	<i>Notohypsilophodon</i>
Mediolateral width	87.1	24.1
Proximodistal height (lateral)	63.7	16.2
Anteroposterior length	86.6	23.2

Turonian Cerro Lisandro Formation of east-central Neuquén Province (Coria and Calvo 2002), *Gasparinisaura* from the Santonian–Campanian Anacleto Formation of northwestern Río Negro Province (Coria and Salgado 1996a; Salgado et al. 1997; Cerda 2008), *Macrogyphosaurus* (Calvo et al. 2007b) and unnamed material (Coria 1999; Calvo et al. 2007a; Coria and Cambiaso 2007) from the Turonian–Coniacian Portezuelo Formation of Neuquén, *Notohypsilophodon* from the middle Cenomanian–Turonian Lower Member of the Bajo Barreal Formation of south-central Chubut Province (Martínez 1998), *Talenkauen* from the ?Maastrichtian Pari Aike Formation of southwestern Santa Cruz Province (Novas et al. 2004), and generically indeterminate material from the Cenomanian Candeleros Formation of Neuquén (Coria et al. 2007), the Coniacian Mata Amarilla Formation of Santa Cruz (“*Loncosaurus argentinus*” Ameghino, 1899 [Coria and Salgado 1996b]), and the Campanian–Maastrichtian Allen Formation of Río Negro (Coria et al. 2007). Thus, the Patagonian record of non-hadrosaurid ornithopods encompasses multiple taxa and spans most of the geographic extent of the region as well as practically all of the Late Cretaceous.

Several workers (e.g., Coria and Calvo 2002; Novas et al. 2004; Calvo et al. 2007b; Coria and Cambiaso 2007) have raised the hypothesis that some or all of these ornithopods may pertain to a clade that was endemic either to South America in particular, or to the Southern Hemisphere more generally. Although this hypothesis is appealing from a paleobiogeographic standpoint, character evidence in support of it is presently limited to only a few features, such as well-developed epiphyses on the third cervical vertebra (shared by *Macrogyphosaurus* and *Talenkauen*; Calvo et al. 2007b), strong posteroventral expansions of the middle and posterior chevrons (shared by *Gasparinisaura* and *Macrogyphosaurus* [Calvo et al. 2007b] as well as an unidentified Australian Cretaceous ornithopod [Vickers-Rich and Rich 1999: fig. 150; Lamanna pers. obs.] and the North American *Parksosaurus* [Parks 1926]), a rudimentary humeral deltopectoral crest (shared by *Anabisetia*, *Notohypsilophodon*, and *Talenkauen*; Novas et al. 2004), and a proximally mediolaterally compressed metatarsal II (shared by *Anabisetia*, *Gasparinisaura*, and *Talenkauen*, as well as the South African *Kangnasaurus* and an unnamed form from the Antarctic Peninsula; Novas et al. 2004) (mineralized intercostal plates, until recently believed exclusive to *Macrogyphosaurus*, *Talenkauen*,

and *Thescelosaurus* [Calvo et al. 2007b]), are now known to have had a broader distribution within basal Ornithopoda [Butler and Galton 2008]). Although our study of the Colhué Huapi ornithopod failed to yield evidence to conclusively support or reject the hypothesis of an endemic Gondwanan ornithopod clade, we did identify an additional osteological character state that may be relevant to resolving this question: an anteroproximally–posterodistally elongate tibial cotyle of the calcaneum (presently known only in the Gondwanan Cretaceous ornithopods *Gasparinisaura*, *Kangnasaurus*, *Notohypsilophodon*, *Ouranosaurus*, and UNPSJB-PV 960). Future analyses should evaluate the potential utility of this character for ornithopod systematics.

Body size of the Colhué Huapi ornithopod.—The fragmentary nature of UNPSJB-PV 960 precludes a precise determination of the body size of the ornithopod individual to which it pertained. Nevertheless, a comparison of the dimensions of its calcaneum with that of the single known specimen of the only ornithopod taxon recorded from the Lower Member of the Bajo Barreal Formation, *Notohypsilophodon* (UNPSJB-PV 942; Martínez 1998; Casal and Luna 2002) (Table 1), indicates that the new specimen represents a much larger-bodied form, probably similar in size to *Macrogyphosaurus* (Calvo et al. 2007b). Moreover, given that UNPSJB-PV 960 was likely not skeletally mature at death, fully adult exemplars of the taxon it represents probably attained slightly larger dimensions.

Cretaceous ornithischians of central Patagonia.—The Bajo Barreal Formation preserves at least two distinct dinosaur assemblages thought to be of different Late Cretaceous ages, and therefore may represent successive stages of faunal evolution in central Patagonia. Recovered from strata of the Lower Member of the Bajo Barreal exposed in the vicinity of Lago Musters, the ornithischian component of the older (middle Cenomanian–Turonian) fauna is limited thus far to the small-bodied basal ornithopod or basal iguanodontian *Notohypsilophodon* (Martínez 1998). In contrast, the younger (Campanian–?Maastrichtian) assemblage is preserved in sediments assigned to the Upper Member of the Bajo Barreal Formation that crop out further to the east, in the southeastern sector of Lago Colhué Huapi and neighboring areas. Definite ornithischians from this assemblage include only the isolated left ilium of a medium-sized probable iguanodontian (Luna et al. 2003)

and UNPSJB-PV 960 (the specimen described here). The discovery of the latter therefore constitutes a significant addition to the poorly known Late Cretaceous ornithischian fauna of central Patagonia. UNPSJB-PV 960 is only the third definitive ornithopod specimen recorded from the entire Bajo Barreal Formation, and the second from the more recent (Campanian–?Maastrichtian) dinosaur assemblage it preserves.

Regrettably, due to the lack of overlapping material, UNPSJB-PV 960 cannot be directly compared with the ilium reported by Luna et al. (2003). Therefore, it is presently unclear whether or not these two fossils pertain to the same ornithopod taxon. However, the Colhué Huapi form is clearly distinct from the more ancient *Notohypsilophodon*. In addition to their disparate body sizes (Table 1), the two forms differ in the morphology of the tibial cotyle of the calcaneum, which, when viewed laterally, is more strongly concave in UNPSJB-PV 960. The evidence available at present therefore tentatively suggests that the more recent (Campanian–?Maastrichtian) ornithischian assemblage of the Bajo Barreal Formation may have been distinct from its geologically older (middle Cenomanian–Turonian) counterpart.

Two other ornithischians from the Cretaceous of central Patagonia have become controversial in recent years: the purported ceratopsian *Notoceratops* and the fragmentary hadrosaurid *Secernosaurus*. The controversies surrounding these taxa concern the lack of a clear stratigraphic provenance for the holotypes and only known specimens of both, as well as the contentious interpretation of *Notoceratops* as a ceratopsian, a situation complicated by the apparent loss of its holotype (Coria and Cambiaso 2007). Nevertheless, both specimens are known to have come from the area of the Río Chico in southeastern Chubut Province (Tapia 1919; Brett-Surman 1979); more specifically, the holotypic partial dentary of *Notoceratops* is described as coming from “Lago Colhué-Huapi (sic), near the source of the Río Chico” (Tapia 1919, translated from Spanish). As pointed out by Casal et al. (2007:60), the only continental Cretaceous geologic unit that crops out in the vicinity of the Río Chico is the Upper Member of the Bajo Barreal Formation; consequently, it is likely that the only known specimens of both *Notoceratops* and *Secernosaurus* were recovered from this unit.

Although *Notoceratops* was initially regarded as a ceratopsian (Tapia 1919; Huene 1929), several recent workers have questioned this identification, with some suggesting that the taxon may instead pertain to Ornithopoda, either as a hadrosaurid (Molnar 1980) or a more basal iguanodontian (Coria and Cambiaso 2007). Because it is an ornithopod from the same general geographic region, and probably an equivalent stratigraphic unit, the taxon represented by UNPSJB-PV 960 may have relevance for resolving the controversial systematic position of *Notoceratops*. Unfortunately, however, the Colhué Huapi specimen does not preserve the dentary, and is thus not directly comparable to known material of this alleged ceratopsian.

Similarly, comparisons of UNPSJB-PV 960 and the ilium reported by Luna et al. (2003) to corresponding skeletal elements of the holotype of *Secernosaurus* could prove productive; nevertheless, to date, the latter taxon has received only a preliminary description (Brett-Surman 1979) and thus such comparisons are not presently possible. In summary, additional comparative research and increased paleontological exploration of exposures of the Bajo Barreal Formation in the area of Lago Colhué Huapi and the Río Chico are needed to improve our understanding of the latest Cretaceous ornithischian assemblage of central Patagonia.

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