A new basal iguanodontian (Dinosauria, Ornithischia) from the Upper Cretaceous of Patagonia

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Abstract. We report the discovery of an almost complete skeleton of a new iguanodontian dinosaur, Talenkauen santacrucensis n. gen. et sp., from Maastrichtian rocks of southwestern Patagonia. Talenkauen is odd in the presence of plate-like structures on both sides of the thorax, which are better interpreted as uncinate processes than dermal armor. Talenkauen and the also Maastrichtian Thescelosaurus neglectus Gilmore from North America, represent the only two ornithischians in which this peculiar feature is currently known. Some derived features unite Talenkauen with other Gondwanan ornithopods, but all the evidence does not offer enough support for an iguanodontian clade endemic from the Southern Hemisphere. Small- to medium-sized ornithischians appear to have been the dominant plant-eating dinosaurs in Antarctica and Australia during the Cretaceous, in contrast with the outstanding abundance of medium sized to giant sauropods in central Gondwana (e.g., South America, Africa, India).

Resumen. Un nuevo iguanodontio basal (Dinosauria, Ornithischia) del Cretácico Superior de la Patagonia. Se reporta el descubrimiento de un esqueleto casi completo de un nuevo dinosaurio iguanodontio, Talenkauen santacrucensis n. gen. et sp., de rocas de edad Maastrichtiano del suroeste de Patagonia. Talenkauen posee placas en ambos lados del tórax, las cuales son interpretadas como procesos uncinados en lugar de armadura dérmica. Talenkauen y Thescelosaurus neglectus (Maastrichtiano, América del Norte), son los únicos dos ornitisquios en los que se conoce esta peculiar característica. Algunos caracteres derivados unen a Talenkauen con otros ornitópodos gondwánicos, pero el conjunto de la evidencia disponible no ofrece sustento suficiente para reconocer un clado de iguanodontes endémico del Hemisferio Sur. Los ornitisquios de pequeño y mediano tamaño parecen haber sido los dinosaurios herbívoros dominantes en Antártida y Australia durante el Cretácico, contrastando con la gran abundancia de saurópodos de mediano a gran tamaño registrada en Gondwana central (p. ej., América del Sur, África, India).


Introduction

The list of Cretaceous ornithischians from South America rapidly increased in the last few years thanks to discoveries of bone remains belonging to stegosaurs, ankylosaurs, basal ornithopods and hadrosaurs (e.g., Bonaparte, 1996; Salgado and Coria, 1996; Novas, 1997; Coria, 1999). Particularly, the Cretaceous record includes ornithopod dinosaurs referred as to hypsilophodontids (the Cenomanian Notho hypsilophodon comodensis from Bajo Barreal Fm.; Martínez, 1998) and basal iguanodontians (the Cenomanian Anabisetia saldiviai, from the Lisandro Fm., and the Campanian Gasparinisaura cincosaltensis from the Anacleto Fm.; Coria and Salgado, 1996; Coria, 1999; Garrido, 2000; Coria and Calvo, 2002). Such discoveries were interpreted by Coria (1999) as suggestive that a diverse evolutionary history of ornithopods took place in Gondwana prior to the faunal interchange proposed for the end of the Cretaceous (Bonaparte, 1986).

Here we report the discovery of an almost complete skeleton of a new iguanodontian dinosaur, Talenkauen santacrucensis n. gen. et sp. The specimen was recovered from Late Cretaceous beds exposed in the SW corner of Patagonia (figure 1.A), a region poorly explored for dinosaur remains (Novas et al., 2002a). The new basal ornithopod is odd in the presence of plate-like structures on both sides of the thorax, whose anatomical meaning will be discussed below. Also, this new dinosaur provides evidence for an iguanodontian clade endemic to the Southern Hemisphere, when considered with specimens from other regions of Gondwana (e.g., Africa, Australia, India).
New Zealand). The new material helps to understand better the adaptive radiation of basal ornithopods in Gondwana and the paleobiogeography of dinosaur faunas at the end of the Mesozoic.

**Abbreviations.** MPM, Museo Padre Molina, Río Gallegos, Santa Cruz.

**Systematic paleontology**

ORNITHISCHIA Seeley, 1888

ORNITHOPTERA Marsh, 1871

IGUANODONTIA Dollo, 1888

EUIGUANODONTIA Coria and Salgado, 1996

*Genus Talenkauen* Novas, Cambiaso and Ambrosio n. gen.

*Derivatio nominis.* "Talenk", small, "kaun", skull, in Aonikenk Indian language (Moreno, 1997), in reference to the proportionally small head of the animal.

*Type species.* *Talenkauen santacrucensis* Novas, Cambiaso and Ambrosio n. sp.

*Diagnosis.* Same as species.

*Talenkauen santacrucensis* Novas, Cambiaso and Ambrosio n. sp.

*Figures 1B, C and 2A, B*

*Diagnosis.* Autapomorphies diagnosing *Talenkauen santacrucensis* include: well-developed epipophysis on cervical 3, and plate-like uncinate processes on the rib cage. The following reversals emerge from the cladistic analysis: lacrimal and premaxilla not in contact, and dentaries converge rostrally.

*Derivatio nominis.* Santacrucensis, referring to the southern Argentine province of Santa Cruz.

*Holotype.* MPM-10001, partially articulated specimen preserving rostrum, jaws, and teeth, precaudal vertebral column and ribs, pectoral and pelvic girdles, and fore- and hind limb bones (figures 1B.C). The specimen was found articulated in a cross-beded, fining-upward, medium-grained sandstone, interpreted as a fluvial channel body. The material was collected in February 2000.

*Locality and horizon.* Los Hornos Hill, southern coast of Viedma Lake, Santa Cruz Province, Argentina (Lat. 49°51'.62" S, Lon. 72°06'.263" W) (figure 1A). Pari Aike Fm., Upper Cretaceous, Locality and horizon.

*Figure 1 A, Map indicating fossil locality. B, C, Talenkauen santacrucensis* gen. et. n. sp. MPM 10001 (holotype). B, Partially articulated skeleton in right lateral aspect. C, Reconstructed skeleton. 

Abbreviations: ax, axis; cv 9, ninth cervical vertebra; d, dentary; d1, first dorsal vertebra; d16, sixteen dorsal vertebra; f, femur; fib, fibula; h, humerus; il, ilium; mtt, metatarsals II-IV; mx, maxilla; ot, ossified tendons; p, pubis; pd, predentary; ph, pedal phalanges; pmx, premaxilla; sc, scapula-coracoid; sk, skull; r, radius; t, tibia; up, uncinate processes. A, Mapa indicando la localidad del hallazgo. B, C, *Talenkauen santacrucensis* n. gen. et n. sp. MPM 10001 (holotipo).


Abreviaturas: ax, axis; cv 9 novena vértebra cervical; d, dentario; d1, primera vértebra dorsal; d16, dieciséis vértebra dorsal; f, fémur; fib, fibula; h, húmero; il, ilion; mtt, metatarsales II-IV; mx, maxilar; ot, tendones osificados; p, pubis; pd, predentario; ph, falanges del pie; pmx, premaxilar; sc, escápula-coracoides; sk, cráneo; r, radio; t, tibia; up, procesos uncinados.
Cretaceous ornithischian from Patagonia

A

B

C

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The humerus is slender, weakly expanded at its extremities, and the deltopectoral crest is extremely reduced, differing from the remaining ornithopods in which this crest is more developed (e.g., Thescelosaurus, Dryosaurus, Camptosaurus, Iguanodon). This peculiar morphology is shared with the hypsilophodontid Notoryctes (Martínez, 1998) and the iguanodontian Anabisetia (Coria and Calvo, 2002), both from the Cenomanian of Patagonia.

The ilium is slender, dorsoventrally low, and shorter than the femur. The dorsal margin is sigmoidal in outline, as is usual in iguanodontians (Coria and Salgado, 1996; Coria and Calvo, 2002). The prepubic process of the pubis is cranially elongate, ending at the level of the 13th dorsal. It is lateromedially flat and dorsoventrally deep, a condition shared with derived iguanodontians (Norman and Weishampel, 1990; Coria, 1999). The femur and tibia are massive, the latter being shorter than the femur (tibia/femur ratio: 0.94), as is usual for graviportal ornithopods. The anterior trochanter of the femur is (tibia/femur ratio: 0.94), as is usual for graviportal ornithopods. The anterior trochanter of the femur is appressed, but not fused, to the greater trochanter. Metatarsal III of Talenkauen is a robust bone (3.3 cm wide), whereas metatarsal II is notably narrow transversely (1.9 cm wide), thus departing from the more robust proportions of metatarsal II seen in most ornithopods (e.g., Tenontosaurus, Hypsilophodon, Dryosaurus, Camptosaurus, Iguanodon).

An outstanding feature of Talenkauen is the presence of plate-like, polygonal structures on both sides of the thorax (figure 2B). The plates are thin (no more than 3 mm thick) and dorsoventrally elongate (the major diameter is 180 mm). The external surface of the plates is smooth, lacking foramina or grooves, and no muscle scars are apparent. The plates are located mid-length on dorsal ribs 1 through 8, but are not fused to the ribs.

**Discussion**

Among the anatomical features of Talenkauen, the presence of polygonal plates on both sides of the thorax is outstanding. This character is shared with the Maasrichtian hypsilophodontid Thescelosaurus neglectus from North America (Fischer et al., 2000), and these are the only two ornithopods in which such plates are documented. At first glance, the shared presence of plate-like structures on the chest raised the possibility that Talenkauen and Thescelosaurus were closely related. However, no other derived characters uniting these ornithopods were recognized. Moreover, several iguanodontian features present in Talenkauen are absent in Thescelosaurus. As well, many features distinctive of the latter taxon are lacking in the Patagonian genus. The presence of plate-like structures in the hypsilophodontid Thescelosaurus and the iguanodontian Talenkauen implies that such plates may have been independently acquired. However, because ossification depends on maturity, size, and sex, their presence among ornithopods may be more widespread than thought.

The plate-like structures of Talenkauen are dismissed as defensive devices because of their fragility and their arrangement in a restricted portion of the thorax. This contrasts with the thick and profusely ornamented dermal ossifications of armored dinosaurs (e.g., ankylosaurs, stegosaurs, titanosaurs). The absence of vascular grooves on their surfaces, their proximity to the caudal margin of ribs, as well as their serial arrangement on the thorax, support their homology with the uncinate processes present in living and extinct diapsids (e.g., Sphenodon, crocodiles, basal maniraptorans, and most birds; Heilmann, 1926; Paul, 2002). It is remarkable, however, that the supposed uncinate processes of Talenkauen and Thescelosaurus are considerably expanded and widely overlap each other, representing a condition not yet recorded in other extinct diapsids, in which such processes are modest, strip-like projections. The presence and development of uncinate processes is far from being functionally understood (Paul, 2002). As far as birds are concerned, uncinate processes participate in thoracic movements for lung ventilation (Fedde, 1987). Because the length of the uncinate processes in birds is proportional to the effectiveness of the external intercostal muscles to set the ribs into motion, a particularly well-developed
musculature would be expected in Talenkauen. This suggests an important participation in rib cage dynamics through well-developed intercostal muscles.

The available fossil record clearly shows that during the Cretaceous, ornithopod dinosaurs were diverse on southern landmasses (Taquet, 1976; Bartholomai and Molnar, 1981; Rich and V.-Rich, 1989; Hooker et al., 1991; Coria, 1999; Novas et al., 2002b), including a wide array of Mid- to Late Cretaceous hypsilophodontids (e.g., Fulgurotherium, Notohypsilophodon, Antarctic hypsilophodontid; Rich and V.-Rich, 1989; Hooker et al., 1991; Martinez, 1998) and basal iguanodontians (e.g., Gasparinisaura, Anabisetia, Talenkauen, M. uttaburrasaurus, Ouranosaurus, Kangnasaurus, Lurdusaurus, Antarctic iguanodontian; Taquet, 1976; Bartholomai and Molnar, 1981; Cooper, 1985; Coria and Salgado, 1996; Salgado et al., 1997; Coria, 1999; Taquet and Russell, 1999; Coria and Calvo, 2002; Novas et al., 2002b).

Although documentation of ornithopod diversity in the southern continents has considerably increased in the last years, the recognition of an iguanodontid clade endemic to Gondwana has not been possible. Some features emerged in the present study as potential synapomorphies uniting Talenkauen with some of these Gondwanan iguanodontians. For example, the greatly reduced deltopectoral crest on the humerus is shared with Anabisetia (Coria and Calvo, 2002) and Notohypsilophodon (Martínez, 1998), and a transversally compressed second metatarsal is shared with the Patagonian Anabisetia and Gasparinisaura (Salgado et al., 1997), the South African Kangnasaur (Cooper, 1985), and an unnamed Late Cretaceous iguanodontian from the Antarctic Peninsula (Novas et al., 2002b). However, in the context of all anatomical data no support currently exists for the identification of a clade of southern iguanodontians (figure 2C). Moreover, the South American Anabisetia, Talenkauen, and Gasparinisaura constitute successively more remote outgroups of the globally distributed Dryomorpha.

Paleobiogeographical isolation between Gondwana and Laurasia has been postulated for most of the Cretaceous (Bonaparte, 1986). Some dinosaur clades with outstanding autapomorphies (e.g., abelisaurid theropods) have been considered as the result of this prolonged endemism (Bonaparte, 1986; Novas, 1997). Notably, the effects of such physical isolation are weakly manifested in the morphology of the southern ornithopods. With the exception of some bizarre features such as the developed cranial bulla of the Australian M. uttaburrasaurus (Bartholomai and Molnar, 1981), the elongate neural spines of the African Ouranosaurus (Taquet, 1976), and possibly the expanded uncinate processes of Talenkauen, the anatomy of basal iguanodontians from Gondwana resembles that of their Jurassic and Cretaceous relatives from Laurasia.

Available evidence suggests that Cretaceous dinosaur faunas of South America were dominated by the herbivorous Sauropoda, represented by abundant skeletal remains belonging to diplodocimorphs and titanosauriforms (Novas, 1997). Even in southern Patagonia, including the fossil locality where Talenkauen was found, remains of titanosauriforms are quite abundant. Contrary to expectations, the Cretaceous record of Antarctic dinosaurs does not include at the moment any sauropod remains, but it does ornithischians. A remarkable disparity in the relative abundance and taxonomic diversity of sauropods and ornithischians is apparent in the Gondwanan realm: whereas in South America, Madagascar and India the Cretaceous record of sauropods overwhelms that of ornithischians, in southern Gondwana (e.g., Antarctica, Australia, and New Zealand; Bartholomai and Molnar, 1981; Gasparini et al., 1987; Rich and V.-Rich, 1989; Hooker et al., 1991; Wiffen, 1996; Rich et al., 1999; Case et al., 2000; Novas et al., 2002b) the sauropod record is sparse. Instead, ornithischians of different affiliation (e.g., iguanodontians, hypsilophodontids, nodosaurids) have been frequently found in the higher paleolatitudes of Gondwana. It is concluded that herbivorous dinosaurs were not evenly distributed on the Gondwanan landmasses, but a certain degree of provincialism is apparent.

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References


Cooper, M. 1985. A revision of the ornithischian dinosaur.


Appendix

List of characters and data matrix used to analyze the phylogenetic relationships of Talenkauen santacruceanus n. gen. et n. sp.
The list of characters is modified from the following sources: Winkler et al. (1997), Coria and Salgado (1996), and Sereno (1999).
The data matrix was analyzed cladistically using the NONA (ver. 1.8) software package (Goloboff, 1993), available from http://www.cladistics.org. Lesothosaurus, Scutellosaurus, and Marginocephalia were employed as outgroups, and the tree was rooted on Lesothosaurus. One tree was obtained, which has the following values: L = 82, Ci = 63, Ri = 74. Lista de caracteres y matriz de datos utilizados para analizar las relaciones filogenéticas de Talenkauen santacruceanus. La lista de caracteres ha sido modificada de las siguientes fuentes: Winkler et al. (1997), Coria y Salgado (1996) y Sereno (1999). La matriz de datos fue analizada cladísticamente utilizando el software de NONA (ver. 1.8) (Goloboff, 1993), disponible desde http://www.cladistics.org. Lesothosaurus, Scutellosaurus y Marginocephalia fueron empleados como grupos externos, y el árbol fue enraizado en Lesothosaurus. Se ha obtenido un solo árbol, el cual presenta los siguientes valores: L = 82, Ci = 63, Ri = 74.

List of characters / Lista de caracteres
1. Contact of lacrimal / premaxilla: (0) absent; (1) present.
2. Premaxillary teeth: (0) present; (1) absent.

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3. Eversion of premaxilla: (0) absent; (1) present.
4. Anterior processes on maxilla: (0) 1 process; (1) 2 processes.
5. Tooth ridges connect to denticles: (0) absent; (1) present.
6. Strong central ridge on maxillary tooth: (0) absent; (1) present.
7. Denticles on premaxilla: (0) absent; (1) present.
8. Ventral processes on premaxilla: (0) single; (1) double; (2) wedge-shaped premaxilla.
9. Size of antorbital fenestra or fossa: (0) large; (1) small.
10. Quadratojugal size: (0) large; (1) reduced.
11. Ossified sternal ribs: (0) absent; (1) present.
12. Ossified hypaxial tendons: (0) present; (1) absent.
13. Humerus’ scapula length ratio: (0) < 1; (1) = 1.
14. Number of phalanges on manus digit III: (0) 4; (1) 3.
15. Number of vertebrae in sacrum (ordered): (0) 5; (1) 6; (2) > 6.
16. Prepubic process (ordered): (0) absent; (1) short; (2) long rod; (3) long shallow blade; (4) deep anteriorly.
17. Femur–distal anterior intercondylar groove (ordered): (0) none; (1) shallow <$10% of anterior–posterior width; (1) deep = >10% anterior–posterior width.
18. Metatarsal III length ratio: (0) < 0.3; (1) < 0.3; (2) MT V absent.
19. Relative size of the palpebral: (0) 80% or more of the maximal anteroposterior width of the orbit; (1) 70% or less of the maximal anteroposterior width of the orbit.
20. Antorbital fossa shape: (0) triangular; (1) circular or ovate.
21. Dorsal and ventral margins of the dentary: (0) rostrally convergent; (1) parallel.
22. Dorsal margin of iliac blade: (0) convex; (1) sinusus.
23. Size of the external nares relative to the basal skull length: (0) less than 15%; (1) 20% or more.
24. Enamel of the medio-dorsal side of maxillary tooth: (0) present; (1) absent.
25. Participation of the jugal in the antorbital fenestra: (0) included; (1) excluded.
26. Jugal–postorbital articulation: (0) medially-faced; (1) laterally-faced.
27. Brevis shelf: (0) reduced; (1) well developed.
28. Metatarsal I: (0) present; (1) reduced or absent.
29. Maxillary tooth crowns: (0) low; (1) high.
30. Foot on the distal ischial shaft: (0) absent; (1) present.
31. Ischial shaft: (0) laterally flattened; (1) rounded in cross section.
32. Ischial process on the distal ischial shaft: (0) absent; (1) present.
33. Caudal process of jugal: (0) well developed; (1) reduced.
34. Position of the obturator process on the ischial shaft: (0) ventrolateral; (1) lateral.
35. Premaxilla, orientation of lower rim: (0) ventrolateral; (1) lateral.
36. Quadratojugal size: (0) 10% or less; (1) 30% or more of quadratojugal height.
37. Premaxilla, orientation of lower rim: (0) ventrolateral; (1) lateral.
38. Maxillary crown, anteroposterior width: (0) equal; (1) narrower than dentary crowns.
39. Maxillary crown shape: (0) subtriangular; (1) diamond-shaped; (2) lanceolate.
40. Maxillary primary ridge strength: (0) less; (1) more prominent than dentary primary ridge.
41. Postaxial cervical neural spine height: (0) prominent; (1) rudimentary.
42. Cervicals 4–9, form of central surfaces: (0) slightly amphicoelous; (1) slightly opisthocoelous; or (2) strongly opisthocoelous.
43. Manual digit II ungual length: (0) shorter; (1) longer than manual digit I ungual.
44. Premaxilla–maxilla diastema: (0) absent; (1) present.
45. Ischial obturator process: (0) absent; (1) present.
46. MT II transverse compression: (0) absent; (1) present.
47. Deltopectoral crest: (0) well developed; (1) less developed.

Diagnostic characters / Caracteres diagnósticos

Unambiguous character support for clades found in the analysis of the data set is presented below. The first number refers to the character on the list above, and the derived state is given in brackets. See presentation en continua o los caracteres no ambiguos diagnósticos de cada nodo resultantes del análisis de datos. El primer número se refiere al carácter mientras que los estados derivados se expresan entre paréntesis.

Omnithopoda 1(1), 44(1)
Euornithopoda 25(1), 45(1)
Hypsilophodontia 37(1), 41(1), 46(1), 34(1)
Euiguanodontia 6(1), 10(1)
Dryomorpha 5(0), 39(1), 40(1)
Anabisetia saldiviai 1(0), 21(0)
Hypsilophodon 33(1)
Iguanodontia 3(1), 7(1), 9(1), 14(1), 17(1), 20(1), 21(1), 23(1), 36(1)
Tenontosaurus 24(1), 33(1), 42(1)
M usturaburrasaurus + Euiigu 37(1), 41(1), 46(1)
Gasparinisa 16(2), 17(0), 28(1), 32(1)
Tal enkau nant sau trancusi on + Anabi sietia saldiviai + Dryomorpha 38(1)
Tal en kau n ant sau trancusi on 4(0), 21(0)
Anabisetia saldiviai + Dryomorpha 5(0), 39(1), 40(1)
Dryomorpha 28(1), 29(1), 46(0)
D ry saurus 41(0)
Ankylopollexia 18(2), 43(1)

Data matrix / Matriz de caracteres