N. Jb. Geol. Paläont. Abh. **242** (1) 133–144 Stuttgart, November 2006

On the systematic position of a specimen previously assigned to Carnivora from the Pliocene of Argentina and its implications for the Great American Biotic Interchange

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With 3 figures

Prevosti, F. J., Gasparini, G. M. & Bond, M. (2006): On the systematic position of a specimen previously assigned to Carnivora from the Pliocene of Argentina and its implications for the Great American Biotic Interchange. – N. Jb. Geol. Paläont. Abh., **242**: 133–144; Stuttgart.

Abstract: A fragmentary right maxilla with the deciduous and permanent canines, recovered from the Chapadmalalan (late Pliocene) of Argentina, was originally described as a sabertooth marsupial (Thylacosmilidae). A latter reviewer suggested that it could be a placental carnivore (Carnivora). In this paper we review the status of this specimen and conclude that it is assignable to an artiodactyl Tayassuidae thus rejecting the occurrence of a non-procyonid carnivore in the Chapadmalalan (Pliocene) and providing the second oldest record of tayassuids in South America.

Key words: Pliocene, Argentina, Tayassuidae, Thylacosmilidae, GABI.

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1. Introduction

The Great American Biotic Interchange (GABI) (see Stehli & Webb 1985; Webb 1991; Woodburne 2004; Flynn et al. 2005; Cione & Tonni 2005) is recorded in South America as a stepwise event (see Cione & Tonni 1995, 1999, 2001, 2005). The first event corresponds to the presence of procyonids in the late Miocene (Huayquerian), followed by cricetid rodents in the latest

0077-7749/06/0242-0133 $ 3.00

Miocene-early Pliocene (Montehermosan), peccaries (Tayassuidae) in the middle Pliocene (late Chapadmalalan beds), camelids in Barrancalobian levels (late Pliocene), equids and canids in the Vorohuean (late Pliocene), and proboscideans in the Sanandresian (BERMAN 1994; CIONE & TONNI 1995, 1999, 2001, 2005; PARDIÑAS & TONNI 1998; LÓPEZ et al. 2001; SOIBELZON & PREVOSTI in press; Fig. 1). But the greatest diversity of North American taxa is first recorded during or after the Ensenadan (latest Pliocene-early/middle Pleistocene; see CIONE & TONNI 1995, 1999; 2001, 2005). These first pre-Pleistocene records come almost exclusively from Argentina, especially from the southern coast of Buenos Aires Province (CIONE & TONNI 2005). There are mentions of gomphotherids, camelids and tayassuids from the late Miocene of Peru (see CAMPBELL et al. 2000a, 2001); unfortunately only the description of the proboscidean has been published, while the other taxa have been mentioned in abstracts of scientific meetings (e.g. CAMPBELL et al. 2000b). Recently, PRADO et al. (2005) and ALBERDI et al. (2005) rejected the taxonomic and chronological assignation of the gomphotherids studied by CAMPBELL et al. (2000a). Another possible Tertiary tayassuid record comes from Colombia, but its age is doubtful ("Uquian?" = Marplatan?, see MENEGAZ & ORTIZ JAUREGUIZAR 1995).

Although recent reviews discard the pre-Pleistocene occurrence of some North American non procyonid carnivores (e.g. felids, see BERMAN, 1994; PREVOSTI in press), some relevant remains had not yet been re-studied. Among these, a specimen found in one of the lowest levels of the upper Chapadmalalan beds near Mar del Plata (Buenos Aires Province), was originally described as the hypodigm of a sabertoothed marsupial of the Thylacosmilidae family ("*Notosmilus pattersoni*" KRAGLIEVICH 1960). Later, MARSHALL (1976a, b) in a review of the Thylacosmilidae, noted that this specimen, which possesses a deciduous canine, is not a thylacosmilid or even a marsupial, and suggested that it could correspond to a placental carnivore (Order Carnivora). This reassignation was very important, because the morphology of this remain (a maxilla with the milk and permanent upper canine) clearly differs from that of the late Miocene-Pliocene South American recorded Carnivora (Procyonidae) and could had represented the oldest record of other carnivores (e.g. Felidae) in this continent. For this reason we decided to restudy this controversial specimen, comparing it with other mammals and test the mentioned hypothesis.

2. Material and methods

We compare the MMP 751-S with fossil and recent tayassuids, carnivores and thylacosmilids deposited in several institutions: American Museum of Natural History, New York (AMNH); Museo Argentino de Ciencias

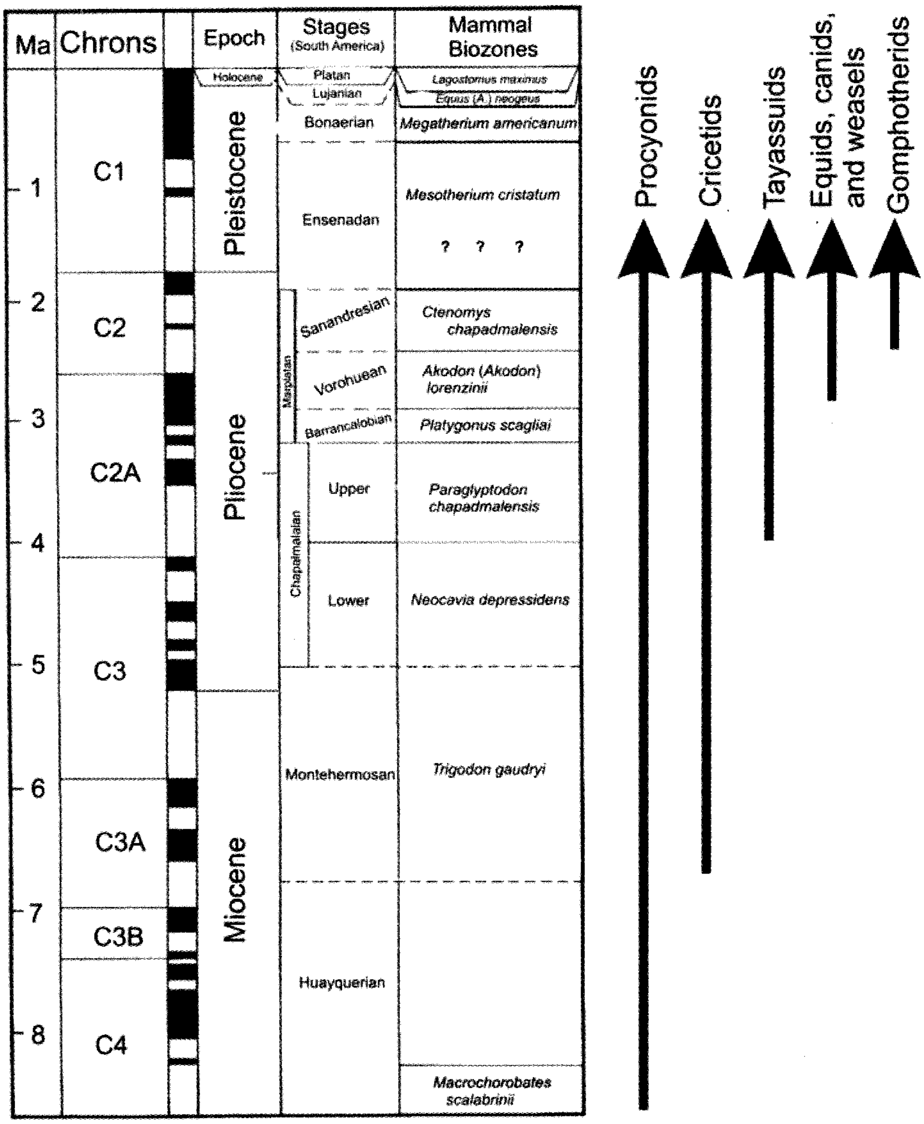

Fig. 1. Paleomagnetic, biostratigraphic and chronostratigraphic chart of South America, with the occurrence of North American mammals during Late Miocene and Pliocene. Modified from Cione & Tonni (2005).

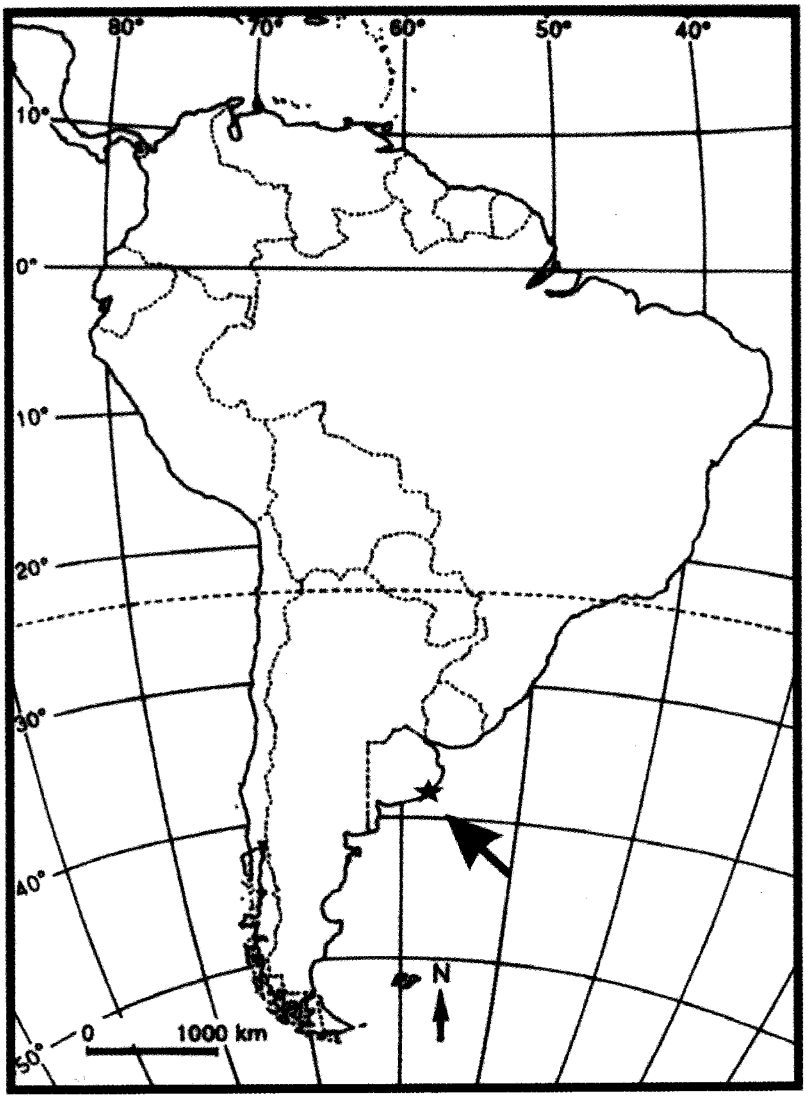

Fig. 2. Map of South America showing the geographic position of the fossil locality where MMP S 751 was collected (black asterisk).

Naturales “Bernardino Rivadavia” (MACN); Museo de La Plata (MLP); Museo Municipal de Ciencias Naturales de Mar del Plata “Lorenzo Scaglia” (MMP); Florida Museum of Natural History, Gainesville (UF). Other abbreviations used are: DI3: upper deciduous third incisor; DC1: upper deciduous canine; dc1: lower deciduous canine; I3: upper permanent third incisor; C1: upper permanent canine; c1: lower permanent canine.

Measurements were taken with digital calipers, with 0.01 mm accuracy. We followed the biostratigraphic, chronostratigraphic, and geochronologic schemes of Cione & Tonni (2005).

3. Systematic Paleontology

Order	Artiodactyla Owen, 1848
Suborder	Suiformes Jaeckel, 1911
Superfamily	Suoidea Gray, 1821
Family	Tayassuidae Palmer, 1897
Subfamily	Tayassuinae Palmer, 1897 indet.

Studied material: MMP S-751 (Fig. 3), right maxillary fragment with the deciduous canine (DC1) and the tip of the definitive (C1). It corresponds to a juvenile specimen.

Geographical and stratigraphical provenance: at first salient northeast from Baliza Caniú (Partido de General Pueyrredón, Provincia de Buenos Aires, Argentina; ≈ 38° 07’ S, 57° 34’ W, see Kraglievich 1952; Fig. 2). The fossil bearing bed is the third level of the Chapadmalal “Formation” which is one of the lowest in the unit (Kraglievich 1952). Later, this level was included in the Playa San Carlos Alloformation (see Vizcaíno et al. 2004). The Chapadmalal “Formation” beds are included in the *Paraglyptodon chapadmalensis* Biozone, which is the stratigraphic basis of the Upper Chapadmalalan (see Cione & Tonni 2005). A bed with putative impact glasses near the top of the Chapadmalal “Formation” yielded an age of 3.3 Ma (Schultz et al. 1998). The base of the Chapadmalal “Formation” was magnetostratigraphically considered of Gilbert age (ca. 4 Ma; Orgeira & Valencio, 1984). Thus the age of this specimen could be bracketed between 3.3 and ca. 4 Ma.

Description: The material is a small fragment of the right maxilla with the deciduous and definitive canines. The fragment of maxilla shows a rough surface such as observed in juvenile mammals, and internally has part of a concavity (part of the choana). The C 1 emerges in front of and mesolingually to the DC1.

The deciduous canine is very curved, convex anteriorly and concave posteriorly; it is slightly inclined labially. Enamel is present on the tip covering its entire surface up to nearly half of the tooth height. The anterior surface of the tip has a slightly developed subplane bezel due to the wear produced through contact with the posterior face of the lower canine. The posterior edge of the tip is slightly sharpened.

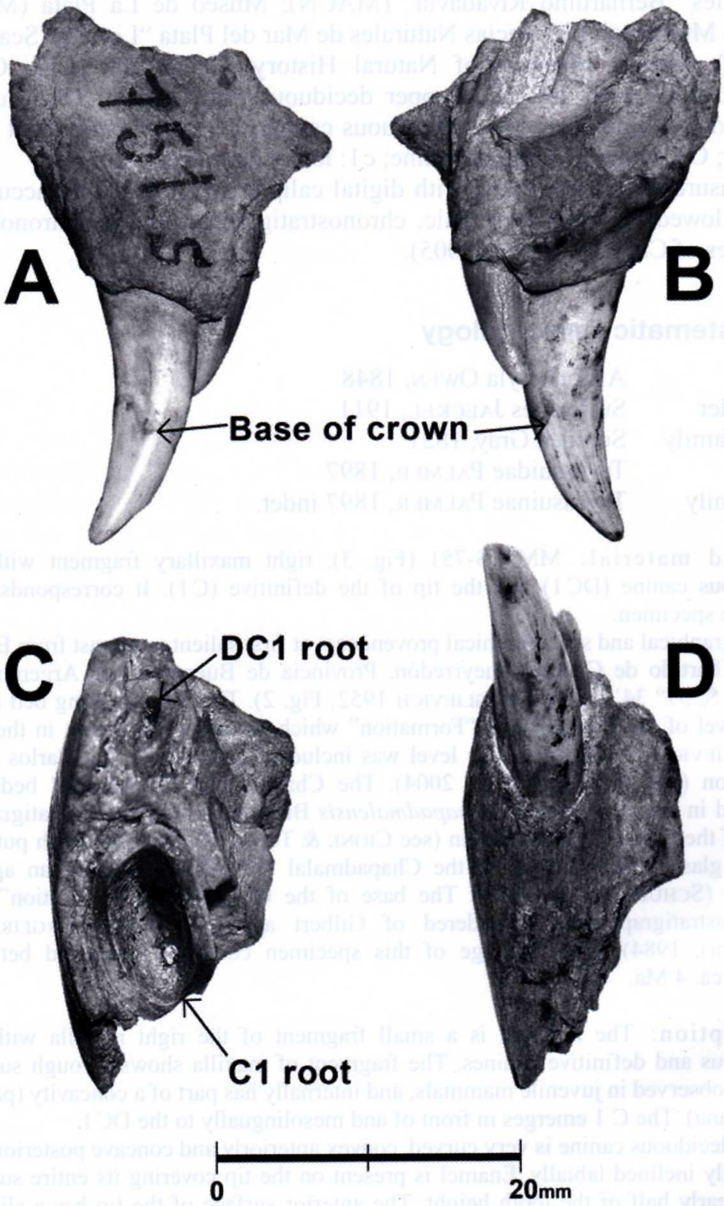

Fig. 3. Tayassuidae indet. (MMP S 751) in labial (A), lingual (B), dorsal (C), and occlusal (D) views.

Naturales "Bernardino Rivadavia" (MACN); Museo de La Plata (MLP); Museo Municipal de Ciencias Naturales de Mar del Plata "Lorenzo Scaglia" (MMP); Florida Museum of Natural History, Gainesville (UF). Other abbreviations used are: DI3: upper deciduous third incisor; DC1: upper deciduous canine; dc1: lower deciduous canine; I3: upper permanent third incisor; C1: upper permanent canine; c1: lower permanent canine.

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The tip of the root is observed in the upper portion of the specimen. This part of the canine is transversally compressed.

The apex of the definitive canine is well preserved. This tooth is sharp and longitudinally curved just as the deciduous one. Its anterior border is defined by a sharp edge. The portion of the tooth that emerges from the alveolus is covered by enamel. Its cavity is markedly enlarged compared to the one for the deciduous tooth. Thus, this tooth is hypertrophied. In addition, it has an oval section and the dentine is thin. Nevertheless, it is thicker than that observed in the deciduous canine.

Measurements: DC1 length: 6. 10; DC1 width: 3.98; C1 length: 12.7; C1 width: 6.20 mm. The last two measurements were taken on the broken dorsal surface of the maxillary, but are not the full adult dimensions.

4. Discussion

The original assignation of MMP S 751 was made by KRAGLIEVICH (1960). This author considered that it belonged to a thylacosmilid, and considered it as the hypodigm of his new genus "*Notosmilus pattersoni*" (now a synonym for *Achlysictis lelongi*, see GOIN 1995) but he did not give any good justification for this. In fact, he recognised that this specimen lacked some features typical of "*Thylacosmilus*" (= *Achlysictis*), such as the labial longitudinal median crest. It is possible that the presence of a large and transversally compressed upper definitive canine plus the presence of thylacosmilid remains in the Chapadmalal "Formation" induced this author to propose the original determination.

Later, MARSHALL (1976a, b) suggested that MMP S 751 was not a thylacosmilid or even a marsupial, firstly because the upper permanent canine lacks both the extreme lateral constriction and the labial keel typical of *Thylacosmilus*, and, secondly because deciduous canines are unknown in marsupials, a fact that definitively excludes this specimen as pertaining to this group. Apart from that, he commented that the oval section of the upper canines showed some affinities with Order Carnivora, also he suggested that the preserved teeth could be not DC1-C1 but DI3-I3 or even, although more improbably, dc1-c1.

The description used by MARSHALL (1976a, b) to relate this specimen to Carnivora is very broad and is not a particular link to the order. The general morphology of MMP S 751 (i.e. the presence of a large and laterally compressed C1) allows to exclude most of the carnivores (e.g. Procyonidae) in which the canines are more conical and resemble those of sabertooth cats (Machairodontinae). The procyonid *Nasua* possesses laterally compressed C1, but the canine is more laminar, and has a different pattern of crests. Besides, the DC1 is not hypertrophied and transversally compressed as in *Smilodon* and *Homotherium* (RUSCONI 1931; MERRIAM & STOCK 1932;

VIRET 1954; RAWN SCHWATZINGER 1983; TEJADA FLORES & SHAW 1984), and the apex of the crown is more acute and slender than in Machairodontinae. In *Megantereon cultridens* the DC1 has a similar transverse section at its base, but the crown is more robust, straight, and the labial border is more convex (KURTÉN & CRUSAFONT PAIRO 1977). The C1 of *Smilodon* emerges lingually to the DC1 and not mesiolingually as in MMP S 751 (see MERRIAM & STOCK 1932; TEJADA FLORES & SHAW 1984). The same pattern could be seen in *Machairodus giganteus* (see ZDANSKY 1924). Furthermore, the tip of the C1 is more slender and orientated more distally with respect to the rest of the crown than in the machairodontines. Also the shape of the preserved bone indicates that it is a maxilla and not part of a lower jaw, thus excluding the possibility mentioned by MARSHALL (1976a) that these teeth could represent dc1 and c1.

The following characters allow us to determine this maxilla as an indeterminate Tayassuinae: the location and orientation of the definitive and deciduous canine (C1 located in front and mesolingually of DC1); the shape and size of the crown of both teeth (DC1 greatly curved, convex anteriorly and concave posteriorly, slightly inclined labially; C1 sharp and curved longitudinally just as the DC1); the wear surface of the deciduous tooth (slight development of a sub-plane bezel in the anterior face of the tip and its posterior border slightly sharp-edged); the development of the enamel (DC1 on the tip covering practically half of the tooth, and their entire surfaces; C1 with enamel covering the portion emerged from the alveolus); the shape and size of the root cavity (DC1 transversally flattened and dentine slender than C1; C1 with oval section).

Comparing this material with those deposited in the institutions aforementioned, we found it difficult to assign it to a specific genus. However, according to the shape of the apex of DC1 and C1, the size of the C1 considering the cavity of its root and the slenderness of the C1, it is probable that the maxillary fragment with DC1 and C1 could belong to any species of *Platygonus* or *Catagonus*. The canines of both *Platygonus* and *Catagonus* are similar in being longer from alveolus to tip, and in proportion to that length, more slender than the shorter, broader canines of *Tayassu* (see WETZEL 1977).

The family Tayassuidae range in age from late Eocene (Chadronian) to Recent in North America, from late Miocene to Recent in Central America, and from middle Pliocene (late Chapadmalalan) to Recent in South America (MCKENNA & BELL 1997; WRIGHT 1998).

Some hypotheses have been advanced about the way peccaries arrived in South America coming form North America. WETZEL (1977) suggested that a species of *Platygonus* colonized South America and produced the other South American tayassuid lineages via adaptive radiation. However, WRIGHT

(1998) indicates that all tayassuid genera known from South America were distinct in North America by the late Hemphillian. Therefore according to this author, a minimum of three colonization events is required to account for tayassuid diversity in South America. According to MENEGAZ & ORTIZ JAUREGUIZAR (1995) three groups of genera (*Tayassu, Catagonus* and *Platygonus* groups) can be recognized in South America, plus another one including two genera with uncertain validity (?*Mylohyus* and ?*Prosthennops*). The genus *Platygonus* is represented by diagnostic specimens in the Pliocene and Pleistocene of South America. Fossils remains of *Catagonus* and *Tayassu* are recorded in Pleistocene and Holocene sediments of this continent. Most of the fossils belonging to tayassuids are found in Argentina, Brazil and Uruguay. The presence of genera such as *Prosthennops* and *Mylohyus* in South America is controversial because those taxa are based on fragmentary remains (see MENEGAZ & ORTIZ JAUREGUIZAR 1995).

In South America, and more precisely in Buenos Aires Province, six tayassuid remains come undoubtedly from Chapadmalalan sediments (see REIG 1952; KRAGLIEVICH 1959), and there is one another with uncertain stratigraphic provenance. The last one of the above mentioned records is considered doubtful, because the only available information indicates that comes from sediments deposited in "Chapadmalal region" without any specific data (AMEGHINO 1908). AMEGHINO (1908) recognized the Chapadmalalan and Ensenadan beds in that region. Later, KRAGLIEVICH (1959) considered that AMEGHINO's (1908) Chapadmalalan could includes "Uquian" (= Marplatan) and Chapadmalalan sediments, depending on the geographic area where the outcropping occurs (see CIONE & TONNI 1995). One specimen, the holotype of *Platygonus marplatensis*, comes from the same level as MMP S 751 (third level of the Chapadmalal "Formation"). Both represent the oldest record of tayassuids in South America. The other remains mentioned were found in upper levels (e.g. level nine). All these records correspond to the *Platygonus* group (*Platygonus marplatensis* and *Argyrohyus chapadmalensis* species; GASPARINI, pers. obs.).

The identification of MMP S 751 as a tayassuid, allow the following conclusions: 1) discards its assignation to Carnivora, and thus refutes the hypothesis of the Chapadmalalan presence of a non procyonid Carnivora; and 2) provides the second oldest fossil record of tayassuids in South America.

Acknowledgements

A travel grants from the American Museum Natural History, Field Museum of Natural History (Department of Geology), and Florida Museum of Natural History (Vertebrate Paleontology Collection) allowed visiting the USA collections. The following curators assisted us in the collection revision: Alejandro Dondas, John Flynn, Judy Galkin, Richard Hulbert, Alejandro Kramarz, Bruce MacFadden, Mariano Merino, Marcelo Reguero, Bruce Patterson, Min.-Tho Schulenberg, Bill Simpson, William Stanley, Richard Tedford. We thank Eduardo Tonni for reading and commenting an early version of the manuscript and Richard Tedford and Ascanio Rincón for their help with some bibliographical cites, Cecilia Morgan for improving the English version, and Andres Giacosa for his help with the figures. This is a contribution to the projects UNLP N-336 and PICT 8395. To Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) for financial support.

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Manuscript received: June 1st, 2006.
Revised version accepted by the Stuttgart editor: September 1st, 2006.

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