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Review and analysis of the radiation of the South American Hystricognathi (Mammalia, Rodentia)

Revue et analyse de la radiation des Hystricognathi (Mammalia, Rodentia) d'Amérique du Sud

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Abstract — The fossil record of the first genera of each family of South American Hystricognathi rodents is reviewed. On this basis the main events for the radiation of the infraorder on this continent are recognized. Two main events can be identified: the first occurs probably during the Eocene–Oligocene boundary, and the second at the Middle–Late Miocene boundary. (© 1999 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS.)

Rodentia / Hystricognathi / South America / evolution / Cenozoic

Résumé — On propose une revue de l'état actuel des connaissances sur les premiers genres représentatifs de chacune des familles des Rongeurs Hystricognathi d'Amérique du Sud. Sur la base de ces données, on déduit quelles sont les principales étapes de la radiation de cet infraordre sur ce continent. Deux tournants importants sont mis en évidence : l'un est probablement contemporain de la limite Éocène–Oligocène, l'autre de la transition Miocène moyen–supérieur. (© 1999 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS.)

Rodentia / Hystricognathi / Amérique du Sud / évolution / Cénozoïque

Résumen — Se revisa el estado del conocimiento de los primeros géneros de cada familia de roedores Hystricognathi sudamericanos y sobre esta base se analizan los momentos mas importantes de la radiaciòn del infraorden. Se detectan dos eventos de radiaciòn supragenèrica: uno ocurriría en el límite Eoceno–Oligoceno y el segundo en el límite Mioceno Medio–Tardio. (© 1999 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS.)

Version abrégée (voir p. 767)

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1. Introduction

Hystricognathi rodents were first recorded in South America in the Tinguiririca fauna (Chile), by a single jaw with three jugal teeth. Dates from immediately above the fossiliferous horizon indicate the fauna to be at least as young as 31.5 Ma, i.e. Early Oligocene (Wyss et al., 1993). However, it is not until the Late Oligocene Deseadan South American Land Mammal Age (SALMA), that the fossil record of this group becomes abundant and continuous. Anyway, an important degree of uncertainty still exists concerning the date of arrival of the earliest rodents on this continent, the early times of the radiation and the precise pre-Deseadan biogeographical context. During most of the Cenozoic, South America was isolated from other biogeographic areas, and this condition had great influence, not only on the tempo and mode of evolution of the early radiation of Hystricognathi, but also on its subsequent history. At least 160 fossil and extant genera of Hystricognathi have been described on this continent which are distributed in 16 families, 12 of which are extant. The state of the art concerning these animals is sufficient by now to allow us to propose a general scheme of the radiation emphasizing the main steps since Deseadan times. Nevertheless, some uncertainties still exist concerning: 1) the geographical setting of fossil localities which are far from being well distributed on the continent, 2) the biochronological framework for the fossil mammal record of South America which is not as accurate as that of other areas. Considering the first point one must bear in mind that most of the record comes from the austral part of the continent, i.e. Patagonia, for the Oligocene to Middle Miocene, but from central and northern Argentina for the Late Miocene to Pleistocene. This means that the Hystricognathi are scarcely known in the Brazilian Subregion. Concerning the biochronological framework, some recent results have been obtained in the calibration of the SALMAs, (Ortiz Jaureguizar et al., 1993; Flynn and Swisher 1995; Madden et al., 1997; Heizler et al., 1998; Kay et al., 1998) and allow to reinterpret the history of rodents on the continent and recognize its main evolutionary events.

Hartenberger (1998) proposed a general scheme of the radiation of the order Rodentia from the Early Eocene to Miocene with phylogenetic implications. This work is based on the occurrence of the first genera of all the known families, and their supposed phylogenetic relationships. He also discusses the main evolutionary events. Using the same method we analyze more precisely the dates of the first occurrences of the earliest genera of the families of the South American Hystricognathi, trying to recognize the outstanding features of their main evolutionary events.

2. Comments about the first genera

Following Hartenberger (1998) the oldest record so far known, i.e. 'Dasyproctidae indet.' *in* Wyss et al. (1993) could be referred to *Branisamys* from the Deseadean of Salla (Bolivia). This genus has been attributed either to the Dasyproctidae (Hoffstetter and Lavocat, 1970; Lavocat, 1976) or to the Dinomyidae (Patterson and Wood, 1982). *Branisamys* and the rodent from Chile share squared and tetralophodont molars, but these characters could be considered plesiomorphic and thus do not indicate close relationships. Moreover, they have significant differences: the rodent from Chile is smaller than *Branisamys luribayensis* (20 %), and its teeth are more derived in its greater degree of hypsodonty and its more persistent hypoflexid. Consequently, we prefer to maintain for the moment the assignation to Dasyproctidae indet.

Since the Deseadean SALMA, the rodent fossil record becomes largely more abundant and diversified and the following families are recognized: Eocardiidae, Chinchillidae, Neoepiblemidae, Erethizontidae, Cephalomyidae, Echimyidae and Acaremyidae.

The oldest genera of the Eocardiidae are *Asteromys* and *Chubutomys* from the Patagonian Deseadean beds; this family is known up to the Colloncuran SALMA (Early Middle Miocene). Eocardiidae is generally considered as the stem family for all Cavioidea s.s. (Caviidae, Hydrochoeridae) and it is difficult to separate its more derived species from the first Caviidae. We consider here that the oldest record for the Caviidae is *Prodolichotis* from the Laventan SALMA (Middle Miocene of Colombia; Fields, 1957; Walton, 1997). Anyway, the differentiation of modern Cavioidea s.s. (Patterson and Wood, 1982) occurs with the origination of Hydrochoeridae and two other subfamilies of Caviidae (Cardiomyinae and Caviinae) at the beginning of the Late Miocene (Vucetich, 1986).

The oldest Chinchillidae is *Eoviscaccia* (Vucetich, 1989), found in the Deseadan of both Lacayani (Bolivia) and, with doubts, Cabeza Blanca in Patagonia.

Protosteiromys from the Deseaden of Patagonia is the oldest representative of the Erethizontidae. The affinities of this family are controversial. Some authors include them in the Caviomorpha sensu Wood (1955), but recent interpretations propose that Erethizontidae could be the stem group for all Hystricognathi (*figure 1*; Bryant and McKenna, 1996; A. Candela, pers. com.).

The Abrocomidae are first recorded in the Huayquerian SALMA (Upper Late Miocene) with *Protabrocoma* and *Abrocoma*. These taxa could be synonymous, so we accept them provisionally. The relationships of this family are still controversial. It has been included in the Octodontoidea (Reig, 1986; Martin, 1992), but Glanz and Anderson (1990) relate it to the Chinchillidae. We follow Landry (1957) who relates them to the Cephalomyidae (*figure 1*).

The earliest Echimyidae (*Sallamys*, *Xylechimys* and *Deseadomys*) were found in the Deseadan. The relationships of the Echimyidae from the Deseadan to Colloncuran SALMAs with Recent forms are difficult to establish. Since the Huayquerian taxa that are closely related to modern representatives of the subfamily Eumysopinae are known.

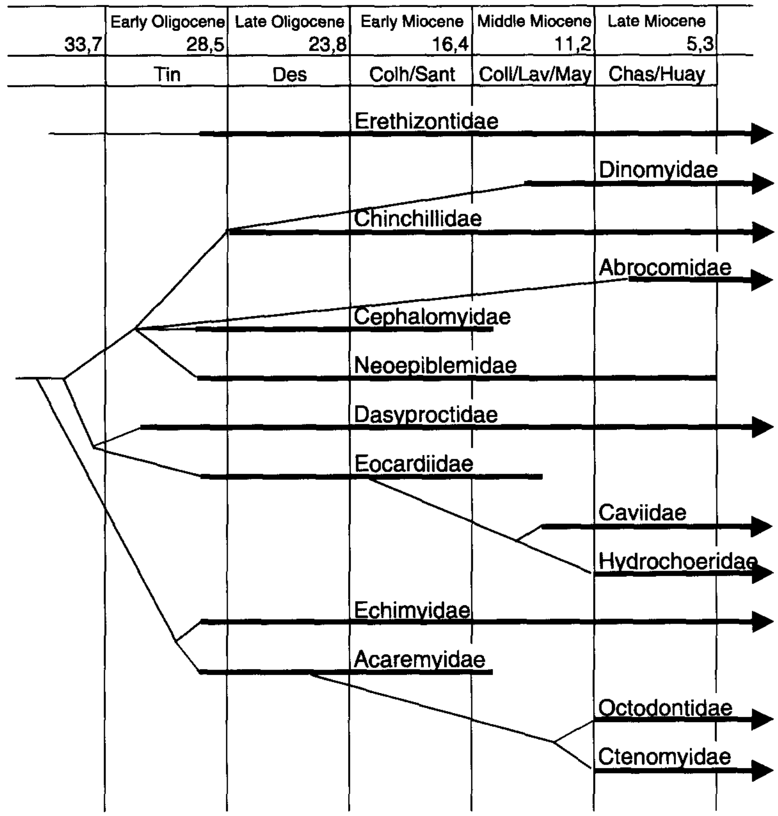

Figure 1. Phylogenetic relationships of the families of South American Hystricognathi. Chas: Chasicoan; Colh: Colhuehuapian; Coll: Colloncuran; Des: Deseadan; Lav: Laventan; Huay: Hyaquerian; May: Mayoan; Sant: Santacrucian; Tin: Tinguiririca.

Relations phylogénétiques des familles de Rongeurs d'Amérique du Sud. Chas : Chasiquien ; Colh : Colhuehuapien ; Coll : Colloncurien ; Des : Déséadien ; Lav : Laventanien ; Huay : Hyaquerien ; May : Mayoien ; Sant : Santacrucien ; Tin : Tinguiririca.

Ctenomys and related fossil genera are here considered as a family (Ctenomyidae) only for convenience, but some authors include them in the Octodontidae (Gallardo, 1997). Species linked to the origin of the Ctenomyidae are known from the Chasicoan SALMA (Verzi, in press). But representatives clearly related to Recent *Ctenomys* are known from the Huayquerian (*table*; Verzi et al., 1991), while *Ctenomys* itself is registered only since the Late Marplatan, i.e. Late Pliocene (Vucetich and Verzi, 1995; Verzi and Lezcano, 1996).

The earliest undoubted Octodontidae are recorded in the Chasicoan (*table*). Some older genera, like *Platypittamys*, have been referred to this family but their relationships are far from being established, and some of them have been referred to the Echimyidae (Reig, 1986). Here we follow Wood (1949) who established for them the family Acaremyidae.

Simplimus, the oldest undoubted Dinomyidae, comes from the Mayoan of Patagonia. Some older genera have been classified in the Dinomyidae but this is doubtful (Landry, 1957).

3. Main events of the radiation

Following Hartenberger (1998), the Caviida (sensu Bryant and McKenna, 1996) probably diversified before the end of the Oligocene taking into account that for the Deseadan 8 families and 20 genera (*table*; *figure 2*) are recognized. Moreover, the high degree of hypsodonty of many of these genera reinforces the hypothesis that the beginning of the radiation was much earlier. Likewise, the advanced tooth pattern of the rodent from Tinguiririca reinforces the idea that the early radiation occurred during the Early Oligocene or even in the Late Eocene (*figure 1*). If this is the case, the South American radiation could be not as diachronic from the African one as it is generally considered (cf. Hartenberger, 1998, p. 443, *figure 1*). The more recent radiometric results place the Deseadean between 29 to 25.65 Ma (Kay et al., 1998). For Patagonian outcrops, Flynn and Swisher (1995) give ages of 29–27 Ma. Anyway, correlations between Bolivian and Patagonian Deseadan localities are far from being elucidated. Vucetich (1991) demonstrated that the tooth pattern of some of the Patagonian genera looks more advanced than that of the Salla genera. This view is in agreement with previous suggestions made by Hartenberger (1975) who considered that Salla was older than the Patagonian localities of Cabeza Blanca and La Flecha; but Scarrit Pocket, where the supposed primitive *Platypittamys* was found, was considered older than Salla by this author. Nevertheless an alternative view would be to explain these discrepancies by the fact that in Patagonia the global climatic changes which occurred at the end of the Eocene had more influence there than in lower latitudes. In fact this hypothesis can be proposed after the recent radiometric data obtained by Heizler et al. (1998) for rocks containing Casamayoran mammals: these authors demonstrate that the Barrancan faunas (upper part of the Casamayoran) are much more younger than previously proposed, and new

Table. First genera per families of the South American Hystricognathi.

Premiers genres des familles de rongeurs Hystricognathi d'Amérique du Sud.

Family	First genera	Provenance	Age	Reference
Erethizontidae	*Protosteiromys*	Patagonia	Deseadan, Late Oligocene	Wood and Patterson, 1959
Dinomyidae	*Simplimus*	Patagonia	'Mayoan' Middle Miocene	Ameghino, 1904
Chinchillidae	*Eoviscaccia*	Bolivia	Deseadan	Vucetich, 1989
Abrocomidae	*Protabrocoma*	central Argentina	Huayquerian, Late Miocene	Kraglievich, 1927
	Abrocoma	central Argentina	Huayquerian	Rovereto, 1914
Cephalomyidae	*Cephalomys*	Patagonia and Bolivia	Deseadan	Ameghino, 1897
	Litodontomys	Patagonia	Deseadan	Loomis, 1914
Neoepiblemidae	*Scottamys*	Patagonia	Deseadan	Wood and Patterson, 1959
Dasyproctidae	*Incamys*	Bolivia and Patagonia	Deseadan	Hoffstetter and Lavocat, 1970
	Branisamys	Bolivia	Deseadan	Hoffstetter and Lavocat, 1970
	Gen. et sp. indet.	central Chile	"Tinguiririca" Late Eocene	Wyss et al., 1993
Eocardiidae	*Chubutomys*	Patagonia	Deseadan	Wood and Patterson, 1959
	Asteromys	Patagonia	Deseadan	Ameghino, 1897
Caviidae	*Prodolichotis*	Colombia	Laventan, Middle Miocene	Kraglievich, 1932
Hydrochoeridae	*Procardiatherium*	central Argentina	Chasicoan, Late Miocene	Ameghino, 1885
Echimyidae	*Sallamys*	Bolivia	Deseadan	Hoffstetter and Lavocat, 1970
	Deseadomys	Patagonia	Deseadan	Wood and Patterson, 1959
	Xylechimys	Patagonia	Deseadan	Patterson and Pascual, 1968
Octodontidae	*Chasicomys*	central Argentina	Chasicoan	Pascual, 1967
Ctenomyidae	*Xenodontomys*	central Argentina	Chasicoan	Kraglievich, 1927
	Palaeoctodon	central Argentina	Chasicoan	Rovereto, 1914
Acaremyidae	*Platypittamys*	Patagonia	Deseadan	Wood, 1949
	Migraveramus	Bolivia	Deseadan	Patterson and Wood, 1982

dating bracket the boundary stratotype of the Barrancan sub-age between 32.74 to 36.01 Ma. These new data indicate a Priabonian (Late Eocene) for the Barrancan faunas and imply that the Mustersan SALMA represent the Early Oligocene. Thus the climatic events which occurred near the Eocene/Oligocene boundary (34.7 Ma) would have had some influence on the evolutionary events as is the case in northern continents (Meng and McKenna, 1998): between the Barrancan and the Deseadean most of the South American ungulates become much more hypsodont. It can be speculated that this phenomenon also occurred in the rodent fauna, and so although the Patagonian rodents are more hypsodont than the Bolivian ones, this does not mean that they are necessarily younger.

From the Latest Oligocene to the early Middle Miocene almost no new Hystricognath family or subfamily is recorded in South America: as illustrated in *figure 3*, first and last occurrences of subfamilies (FSf, LSf in *figure 3*) and families are only 11.11 % for the Colhuehuapian and Santacrucian, but as high as 20 % for FSf and 50 % for LSf in the Colloncuran. For the same period there is an important turnover in genera (*figure 2*; Vucetich, 1986).

A second radiation occurs at the end of the Middle Miocene and the beginning of the Late Miocene (*figure 2*; Vucetich, 1986; Vucetich and Verzi, in press) which implies the extinction of most of the earlier taxa (82.6 % of genera and 50 % of subfamilies, *figures 2* and *3*), and the

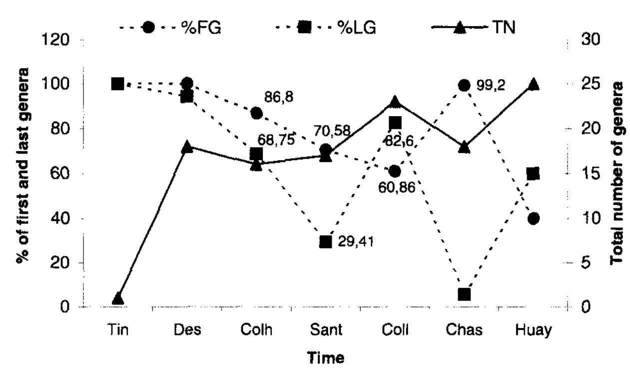

Figure 2. Total number and percentages of first and last records of genera per age. FG: first genera; LG: last genera; TN: total number. Other abbreviations as in *figure 1*.

Nombre total (TN) et pourcentages des premières (FG) et dernières (LG) occurrences des genres dans chaque âge mammalien. Les autres abréviations sont les mêmes que sur la *figure 1*.

origin of new families and subfamilies. During this time interval which spans about 5 My, an important climatic event takes place (Janis, 1993) and in South America this event is contemporaneous with the Quechua Phase of the Andean orogeny (Pascual and Ortiz Jaureguizar, 1990 and bibliography therein). So the conjunction of the climatic and tectonic events generated important modifications in austral environments which became more and more arid.

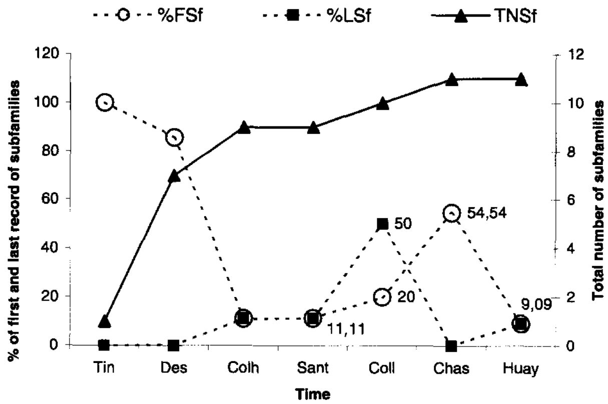

Figure 3. Total number and percentages of first and last records of subfamilies per age. FSf: first Subfamilies; LSf: last Subfamilies; TN: total number. Other abbreviations as in *figure 1*.

Nombre total (TN) et pourcentages des premières (FSf) et dernières (LSf) occurrences des sous-familles dans chaque âge mammalien. Les autres abréviations sont les mêmes que dans la *figure 1*.

This change is clearly registered in the Hystricognathi rodent faunas of the Chasicoan. Nevertheless, up to now we cannot tell if this occurs gradually or abruptly, because the rodents of the final Middle Miocene of southern South America are poorly known. But we note the occurrence of new families in this period, during Laventan and Mayoan SALMAs (*table*).

This second radiation marks the renewal of the southern South American Hystricognathi faunas. They reach their modern aspect through the first occurrences of the most typical families and subfamilies of the Patagonian Subregion: Ctenomyidae; Octodontidae; Abrocomidae; Cardiomyinae (Caviidae), Eumegamyinae (Dinomyidae), and also the Hydrochoeridae, Caviinae (Caviidae) and Eumysopinae (Echimyidae) (Pascual and Odreman Rivas, 1971; Vucetich, 1986; Verzi et al., 1991; Verzi et al., 1995; Vucetich and Verzi, 1995).

The conclusion of this analysis confirms that the first radiation of the South American Hystricognathi is contemporaneous with the global Eocene/Oligocene origination/extinction event named *Grande Coupure* in northern continents, as proposed by Hartenberger (1998). In other respects, we demonstrate that South American Hystriconathi are not affected by the events of the Oligocene–Miocene boundary. The most recent evolutionary event which has important consequences at the supra-generic level occurs between the Middle Miocene to Latest Miocene. Up to now this last diversification event is the best documented by the fossil record.

Version abrégée

C'est une mandibule unique portant M/1–M/3, provenant du gisement de Tinguiririca (Chili), qui constitue la plus ancienne découverte relative à l'infraordre Hystricognathi (Rodentia) en Amérique du Sud. Des couches immédiatement au toit de l'horizon fossilifère ont donné un âge radiométrique de –31,5 Ma (Wyss et al., 1993). Cependant, ce n'est qu'à partir des niveaux Oligocène supérieur du Déséadien Salma (*South American Land Mammal Age*) que les rongeurs deviennent abondants et diversifiés dans les gisements. La diversité atteinte chez les Hystricognathi de ce continent a permis de décrire à ce jour 160 genres fossiles et actuels, répartis dans 16 familles, dont 12 ont des représentants dans la faune actuelle. Par ailleurs, il ne faut pas oublier que, pendant la plus grande partie du Cénozoïque, l'Amérique du Sud est un continent isolé et que cette situation a pesé sur l'évolution du groupe.

Bien que le registre fossile pour les Rongeurs soit loin d'être uniforme à l'échelle du continent (par exemple aucun fossile significatif n'a été trouvé au Brésil), de nouveaux étalonnages radiométriques, qui précisent la position dans l'échelle stratigraphique de plusieurs âges mammaliens Salma (Ortiz Jaureguizar et al., 1993 ; Flynn and Swisher, 1995 ; Madden et al., 1997 ; Heizler et al., 1998 ; Kay et al., 1998), permettent de réinterpréter dans ce cadre général l'histoire du groupe sur ce continent, et de situer ses principales étapes.

Afin de proposer un schéma phylogénétique des Hystricognathi d'Amérique du Sud, nous avons suivi la méthode préconisée par Hartenberger (1998), qui consiste à identifier les premiers genres représentants des différentes familles et d'évaluer leurs relations phylogénétiques. On note que, dès le Déséadien, 20 genres appartenant à 8 familles (Dasyproctidae, Eocardiidae, Chinchillidae, Neoepiblemidae, Erethizontidae, Cephalomyidae, Echimyidae et Acaremyidae) sont identifiés (*tableau*). Il existe des différences notables dans les compositions fauniques entre les gisements du Déséadien de Patagonie et de Bolivie.

Deux étapes remarquables pour cette radiation peuvent être mises en évidence : l'une précède le Déséadien, l'autre, mieux documentée, se situe à la transition Miocène moyen – Miocène supérieur. Alors que, manifestement, le Déséadien marque l'apparition, dans les faunes d'Amérique du Sud, de plusieurs taxons d'Hystricognathi, de nouvelles datations des âges mammaliens immédiatement sous-jacents permettent de préciser la date d'arrivée probable, sur le continent, des premiers rongeurs et le début de leur radiation. En effet, Heizler et al. (1998), pour des couches qui contiennent des faunes du Barrancien (partie supérieure du Casamayorien), ont mis en évidence des âges radiométriques compris entre 32,74 à 36,01 Ma. Ces nouvelles données conduisent à accorder un âge Priabonien (Éocène supérieur) aux faunes du Barrancien, et le Mustersien doit donc être rapporté à l'Oligocène basal. Aussi est-il probable que les événements climatiques globaux qui se produisent à la limite Éocène–Oligocène aient eu une influence sur l'évolution des faunes, sur ce continent aussi : on note d'ailleurs qu'entre le Barrancien et le Déséadien, la plupart des Ongulés sud-américains acquièrent des dents hypsodontes. On peut supposer que ce même type d'évolution a affecté aussi les Hystricognathi. Par ailleurs, le constat que les rongeurs de Patagonie du Déséadien présentent des molaires plus hypsodontes que ceux de Bolivie, n'implique pas forcément le diachronisme des faunes : cette différence pourrait être la résultante de leurs situations latitudinales distantes, les variations climatiques étant plus sensibles dans les régions les plus australes ; l'adaptation à l'hypsodontie pourrait y être plus accentuée. Durant la période Oligocène terminal – début du Miocène moyen, aucune nouvelle famille ou sous-famille n'apparaît (*figure 3*). Une seconde radiation se produit à la transition Miocène moyen–supérieur, et l'on constate alors l'extinction de la plupart des taxons anciens (82,6 % des genres et 50 % des sous-familles et familles ; *figures 2* et *3*), tandis que de nouvelles familles et sous-familles apparaissent. Durant cette période qui s'étend sur environ 5 Ma, il se produit une importante fluctuation climatique à l'échelle globale (Janis, 1993), alors que, simultanément, dans le continent sud-américain, on enregistre la phase Quechua de surrection des Andes. La conjonction de ces deux événements induit des conséquences notables dans les transformations évolutives des Hystricognathes sud-américains du Chasicien. Néammoins, pour le moment, il est impossible de dire si ces transformations sont lentes et graduelles, ou au contraire brutales (*tableau* et *figures 2* et *3*).

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