UNIVERSITAT AUTÒNOMA DE BARCELONA
Facultat de Ciències, Departament de Geologia
TESI DOCTORAL

THE RODENT ASSEMBLAGES FROM THE LATE ARAGONIAN AND THE VALLESIAN (MIDDLE TO LATE MIOCENE) OF THE VALLÈS-PENEDÈS BASIN (CATALONIA, SPAIN)

Maig de 2007

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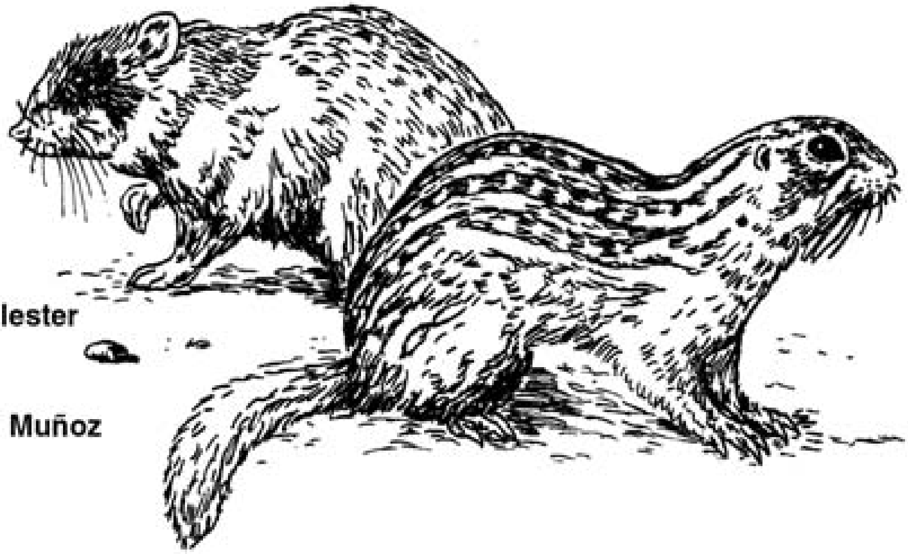

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A Roser

Contents

The cover picture shows recent relatives of some of the Miocene rodents described in the systematic part of this work: the southern flying squirrel (*Glaucomys volans*, top left); the hazel dormouse (*Muscardinus avellanarius*); the common hamster (*Cricetus cricetus*); and the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*). All drawings but *Glaucomys volans* modified after Grassé & Dekeyser (1955).

For almost every topic discussed in the following pages the data are insufficient. The student who attempts interpretations under these circumstances does so in the face of certainty that some of his conclusions will be rejected. It is, however, pusillanimous to avoid making our best efforts today because they may appear inadequate tomorrow. Indeed, there would be no tomorrow in science if this common attitude were universal.

From *Tempo and Mode in Evolution*
George Gaylord Simpson, 1944 (2nd ed., 1947: xviii)

"What shall it be this time?" he said, still with the faint suggestion of irony. "To the confusion of the Thought Police? To the death of Big Brother? To humanity? To the future?"

"To the past", said Winston.

"The past is more important" agreed O'Brien gravely.

From *1984*
George Orwell, 1949 (ed. 1950: 176-177)

Pròleg

El culpable de tot això és el Dr. Jordi Agustí, que em va convèncer de dedicar-me als rosegadors fòssils ja fa molt. Quan vam parlar per primer cop jo tenia 17 anys i el coneixia a través dels llibres de divulgació que havia escrit. Com la majoria d'adolescents interessats en la paleontologia a mi m'agradaven els dinosaures (és clar!), encara que l'èxit de la pel·lícula "Jurassic Park" havia fet que desenvolupés una mena de reacció al·lèrgica i em comencés a cansar d'ells al veure'ls com un objecte de "marketing". Sí, als 18 anys el meu interès per la paleontologia, que havia començat molt abans, seguia intacte, però els dinosaures cada cop m'agradaven menys. Mesos abans de parlar per primer cop amb el Dr. Agustí (jo sempre el tutejo, o sigui que a partir d'ara li direm Jordi) havia començat a deixar de banda els llibres sobre dinosaures per passar a altres camps de la paleontologia.

Vaig conèixer el Jordi arrel de la meva segona visita a l'Institut de Paleontologia M. Crusafont de Sabadell (IPS) (hi havia estat un cop abans quan tenia 8 anys). El motiu de la meva visita era la troballa d'unes dents de cavall fòssils a uns sediments quaternaris del meu poble, Canet de Mar. El Jordi no va prestar molta atenció a les dents sinó que es va interessar més en els dibuixos que jo n'havia fet i les mesures que n'havia pres. Immediatament em va proposar de col·laborar a la campanya de mostratge micropaleontològic que pensava dur a terme aquell estiu a la Conca de Guadix-Baza. No m'ho vaig pensar dos cops i al juny d'aquell any (quan faltaven poques setmanes pels exàmens de selectivitat) estava embotit a la "caixa" de darrera de l'antic "Land Rover" de l'Institut amb un munt de sacs, pales i pics. M'acompanyaven en Manel Llenas, un dels tècnics de camp de l'IPS, un recentment doctorat Oriol Oms i en Jordi. Vaig aprendre molt durant aquella breu campanya de camp, i realment vaig començar a desenvolupar un gran interès per la bioestratigrafia i la geologia de la zona. La geologia sempre m'havia agradat, però jo el que volia era ser paleontòleg. Podia triar dos camins per arribar al meu objectiu, el de la biologia o el de la geologia, i en aquells moments encara no estava segur de quin escollir. Crec que l'Oriol Oms va jugar un paper molt important en la meva decisió final. Quan parla, l'Oriol té la facultat de transmetre a l'oient la passió que ell sent pels temes que estudia. N'hi havia hagut prou amb sentir-lo parlar una setmana de paleomagnetisme i anàlisi de conques per decidir-me a triar la via geològica. Per què? Doncs perquè la geologia també m'interessava, i si per alguna raó no em dedicava a la paleontologia sabia que també m'ho passaria d'allò més bé treballant de geòleg.

Al 1998 vaig començar a cursar la llicenciatura de Geologia a la Universitat Autònoma de Barcelona (UAB). Vaig triar aquesta universitat per dos motius: hi havia més assignatures de paleontologia al pla d'estudis (incloent paleontologia de vertebrats!) i estava més a prop de Sabadell. Això em permetia anar al IPS dues o tres tardes a la setmana i continuar col·laborant amb el centre. Llavors el Jordi em va proposar fer feines de triatge i muntatge de col·leccions de micromamífers, una tasca que d'entrada em va semblar molt avorrida. No obstant al començar a trobar les primeres dents de rosegador vaig canviar d'opinió i vaig córrer a demanar informació al Jordi per poder identificar-les pel meu compte. El Jordi em va donar un plec de bibliografia bàsica que vaig llegir-me diverses vegades i em vaig posar a mirar-me detingudament les dents que trobava. Al cap de menys d'un mes em va oferir estudiar amb ell la fauna de rosegadors de la localitat de Can Missert per fer-ne un article. De nou, ho vaig acceptar sense pensar i ja no hi havia marxa enrere... m'havia "enganxat" a la paleontologia de rosegadors (no crec que hi hagi remei per a aquesta afecció). Per *fer aquest primer article em va caldre molt temps, ja que em faltava molta experiència, i no va estar llest fins al 2002, quan també s'hi va afegir el nou doctorant d'en Jordi, en Marc Furió, que s'ocupà de descriure els insectívors de Can Missert (en Marc també és addicte als insectívors, i crec que com jo no té remei).*

En acabar la carrera, al setembre de 2002, vaig demanar una beca predoctoral i mentre n'esperava la resolució vaig rebre una trucada del Jordi que canviaria el curs dels esdeveniments. Es necessitava un paleontòleg per a co-dirigir una intervenció paleontològica d'urgència a la Nova Fase del Dipòsit Controlat de Can Mata (Els Hostalets de Pierola, Anoia). Coneixia les localitats "clàssiques" dels Hostalets de Pierola, i sabia que era molt probable que sortís alguna cosa interessant, de manera que m'hi vaig apuntar. A més havia de ser co-director (co-director!) de la intervenció, cosa que m'omplia d'orgull ja que jo no feia ni un mes que tenia el títol de llicenciat. I és en aquest punt de la història quan apareixen tres personatges que seran molt importants en David M. Alba, en Jordi Galindo i el Dr. Salvador Moyà-Solà. En David i en Galindo (li acostumo a dir pel cognom) eren els altres co-directors de la intervenció. En David (ara ja doctorat), alumne del Dr. Moyà-Solà, havia exhaurit els seus anys de beca pre-doctoral sense haver acabat la tesi però amb un bon grapat de publicacions d'alt impacte sobre primats fòssils. En Galindo era un geòleg i paleontòleg de camp en el sentit pur i dur de la paraula, i de tots tres era de llarg el que havia vist més fòssils. En Salvador (també el tutejaré) era el nostre vincle amb l'IPS, i hauria d'haver fet un paper d'assessor, però en realitat era el nostre responsable científic, i, a efectes pràctics, el nostre cap.

La intervenció era dura, ja que treballàvem moltes hores seguides i tan sols érem tres. Això sí, el fet de passar tantes hores junts havia fet que comencés a sorgir una relació d'amistat i camaraderia entre els membres de la reduïda tropa de paleontòlegs que encara dura i crec que durarà eternament. De tant en tant fèiem broma sobre les espectaculars troballes que trobaríem a Can Mata, sobretot en Galindo que, com si es tractés d'un oracle, pronosticava un descobriment espectacular. I llavors, quan feia més o menys un mes que les obres havien començat, en "Pau" ens va trobar. Referint-se als primats en Salvador sempre diu que els grans fòssils no els trobes, són ells que et troben a tu. Era això el que ens havia passat. Mentre seguia les obres als marges de l'abocador, al Barranc de Can Vila, la pala d'una excavadora havia deixat al descobert algunes restes fòssils, incloent una molar de dinoteri. Jo havia desviat la màquina cap a un altre indret, amb la intenció de revisar les restes amb els meus companys. L'endemà els tres ens posàrem a regirar els blocs de roca remoguts per l'excavadora, i quan en David va girar un bloc força gran el varem veure. Era una cara, no n'hi havia cap dubte però en David no contestava, s'havia quedat quiet amb la boca oberta i reia. Jo no parava de dir "És una cara! Mira, els dos ulls i el nas!" mentre en Galindo saltava amunt i avall per la muntanya. Varem trucar al Salvador i a en Jordi. El cotxe d'en Salvador apareixia a tota velocitat poc després i quan va mirar-se el fòssil va deixar anar un crit de sorpresa. Ja no me'n quedava cap dubte, es tractava de quelcom molt important. El que havia de venir després, la descripció del Pierolapithecus catalaunicus (popularment conegut com a "Pau"), la publicació a la revista "Science" de la troballa i l'increïble ressò mediàtic va sobrepassar de llarg tot el que m'havia imaginat en un principi.

Al 2003 vaig guanyar una beca pre-doctoral i vaig deixar l'excavació de Can Mata per dedicar-me en cos i ànima a la meva tesi; un projecte altament ambiciós en el que estudiaria la fauna de rosegadors de totes les localitats del Miocè Mitjà de la Conca del Vallès Penedès (incloent Can Vila i l'Abocador de Can Mata, és clar). Gràcies a la mediació del Jordi aquell mateix any em beneficiaria d'una beca del *programa EEDEN per fer una curta estada a Holanda on coneixeria alguns dels meus herois personals com Hans de Bruijn, Albert J. van der Meulen i Jan A. van Dam. La veritat és que gràcies als meus col·legues holandesos vaig aprendre molt i crec que mai els podré agrair tot el que em varen ensenyar. Al ser a Holanda també va començar a prendre forma la idea d'iniciar una línia de recerca en paleoecologia i paleobiogeografia basada en l'estudi dels rosegadors del Vallès-Penedès. Ja tenia un pla per la tesi: estudiaria totes les localitats i en una segona part del treball abordaria els aspectes paleoecològics i paleobiogeogràfics. Vaig començar a treballar al respecte, però poc després vaig interessar-me també per la tafonomia de petits mamífers (arrel de la lectura del llibre "Owls, caves and fossils" de P. Andrews). Així doncs... perquè no incloïa també un estudi tafonòmic de totes les localitats? La meva tesi començava a adquirir unes proporcions cada cop majors, i jo no m'adonava (o no em volia adonar) que no podria acabar-la en el temps previst.*

Finalment, aquest Febrer vaig tirar la tovallola. Era impossible, m'haurien calgut més anys (no sé ni tan sols quants). De manera que vaig decidir recopilar les publicacions que havia fet o que estaven en curs, modificar-les i escriure el volum que teniu a les mans. Inclou tots els temes que volia tractar segons el pla inicial: sistemàtica, bioestratigrafia, tafonomia, paleoecologia i paleobiogeografia. No obstant, no he pogut incloure totes les localitats. El lector s'ha de prendre aquesta tesi com una tarja de presentació on hi diu: "Això és el que vull fer i això és el que he fet de moment". Per descomptat que no he abandonat l'ambiciós projecte inicial, però crec que trigaré força temps a veure'l acabat. Ara bé, no escatimaré forces per assolir aquesta fita.

He tingut moments molt durs en la redacció d'aquesta tesi, moments en els que m'he replantejat força coses i en els que m'he desesperat quan no hi veia solució. No obstant tinc un remei infal·lible: simplement tanco els ulls i penso en la tarda del 5 de desembre de 2002 i en la cara d'en "Pau" tal i com la vaig veure per primer cop. Aquest record, gravat a foc dins meu, em dona forces i m'anima a seguir endavant, passi el que passi.

AGRAÏMENTS

Aquest treball s'ha pogut dur a terme gràcies al suport econòmic per part del DURSI (Departament d'Universitats Recerca i Societat de la Informació; actualment Departament d'Universitats i Recerca) de la Generalitat de Catalunya en la forma d'una Beca Predoctoral de Formació de Personal Investigador (FI) adscrita al Grup de Recerca de Paleobiologia del Neògen Mediterrani. També he d'agrair el suport de del programa EEDEN ("Environments and Ecosystem Dynamics of the Eurasian Neogene") de la "European Science Foundation" que em concedí una beca de viatge que em va permetre estudiar les col·leccions de la Universitat d'Utrecht i del Museu d'Història Natural de Leiden (Holanda). També agraeixo el suport i la confiança prestada pels projectes GL2006-4548/BTE del "Ministerio de Educación y Ciencia", Grup de Recerca de Qualitat SGR2001-00077 del DURSI (Generalitat de Catalunya) i SOMHI (Searching of Modern Hominoids Initiative), així com per part de l'Institut Català de Paleoecologia Humana i Evolució Social (Universitat Rovira i Virgili) i la Universitat Autònoma de Barcelona.

Voldria donar les gràcies a les següents institucions i empreses:

Al traspassat Institut de Paleontologia M. Crusafont de la Diputació de Barcelona per haver-me acceptat com a becari i haver-me proporcionat un espai i tot l'indispensable per treballar. Al recentment creat Institut Català de Paleontologia que s'ha fet càrrec de les despeses per l'ús del microscopi electrònic de rastreig de la Universitat Autònoma de Barcelona (UAB) i m'ha proporcionat un espai i material per poder seguir treballant. A CESPA GR pel fet que hagi finançat la intervenció paleontològica a la Nova Fase del Dipòsit Controlat de Can Mata. Molt especialment a l'empresa PALAEOTHERIA, S.C.P., que es fa càrrec de la intervenció, la confiança que han dipositat en mi posant sempre a la meva disposició tot el material recuperat i la informació registrada en el decurs de les excavacions. També els he d'agrair que m'hagin cedit algunes imatges de les memòries d'excavació i informes que han realitzat. Gran part d'aquesta tesi no s'hauria pogut escriure si no hagués estat per la dedicació i esforç dels paleontòlegs que treballen a diari a la Nova Fase del Dipòsit Controlat de Can Mata: gràcies a tots. A l'Ajuntament dels Hostalets de Pierola per prendre la iniciativa i proposar l'organització d'un camp de treball especialitzat en paleontologia durant l'estiu de 2005 i que va permetre que es processessin algunes mostres de microvertebrats. També agraeixo a aquesta institució que s'encarregués d'adquirir el material necessari per a aquesta activitat i que ens l'hagi deixat en préstec per a altres campanyes.

Per la seva implicació, responsabilitat, i per les contribucions que ha fet a aquest treball estic especialment agraït al meu director i mestre, el Dr. Jordi Agustí. Com ja he explicat al pròleg, ell és el culpable de que hagi decidit dedicar-me a l'estudi dels rosegadors fòssils, obrint així la porta a un món que no sembla tenir límits. Ara bé, si li torno a sentir a dir la frase "Això ja ho tens" li pego.

Al meu tutor i professor de paleontologia durant molts anys, el Dr. Josep Maria Pons, pels bons consells que m'ha donat i per haver actuat com a vincle necessari entre l'Institut de Paleontologia i la Universitat Autònoma.

Per les seves importants contribucions, per la quantitat d'hores que ha invertit en mi i per la confiança que ha dipositat en la meva feina dono les més sinceres gràcies al Dr. Salvador Moyà-Solà. A més li he d'agrair que hagi revisat bona part d'aquesta tesi, que m'hagi animat en els moments més difícils i que s'hagi convertit en la veu que sentia constantment dir "acaba, acaba, acaba". No sé com agrair-ho. Prometo que treballaré molt.

A tots els coautors dels articles que defineixen l'esquelet d'aquesta tesi: J. Agustí, S. Moyà-Solà, D.M. Alba, M. Köhler, S. Almécija, J. Galindo, J.M. Robles, M. Furió, L. Cabrera, M. Garcés, C. Angelone, C. Rotgers i P. Obradó. Sense ells aquest treball no existiria, o bé seria força més curt.

Als meus "germans de camp" David M. Alba i Jordi Galindo, per haver-me suportat a jornada completa durant gairebé 8 mesos al camp i per seguir suportant-me encara. Per tot el que hem fet plegats i el que hem de fer en un futur. També hem de treballar molt.

Al Dr. Ashraf M.T. Elewa per haver-me convidat a participar en el llibre "Migration of Organisms: climate, geography, ecology".

Als Drs. Hans de Bruijn, Albert J. van der Meulen, Wilma Wessels, Jan A van Dam, Jelle Reumer, Lars van den Hoek Ostende i a Kees Hordijk per haver estat els millors amfitrions durant la meva estada a Holanda. Als tres primers a més els he d'agrair tots els seus comentaris sobre la fauna de rosegadors del Barranc de Can Vila 1. Al Dr. De Bruijn li agraeixo que ens enviés els dissenys del sedàs de camp que utilitzem actualment i que m'ensenyés a netejar les fràgils dents de rosegador per mitjà d'ultrasons. També he d'agrair als meus col·legues holandesos, i especialment a Jan A. van Dam, que m'hagin servit de font de inspiració al llarg d'aquest treball.

A la Dra Marguerite Hugueney per la seva amabilitat durant la meva estada a Lyon i pels seus aguts (i extremadament útils) comentaris a una versió prèvia del capítol 3.

A la Dra Nieves López per trobar sempre un momentet per respondre als meus mails i per la seva ajuda amb la tafonomia al capítol 5.

Als Dr Miquel Garcés i especialment al Dr. Lluís Cabrera, pels seus comentaris i puntualitzacions al capítol 2 i 5.

Al Dr. Pierre Mein pels seus comentaris respecte al material d'*Hispanomys* de l'Abocador de Can Mata i per les interessantíssimes discussions referents a la classificació dels rosegadors.

Al Dr. Øyvind Hammer ("the man of the PAST") pels seus comentaris metodològics al capítol 6.

Als Drs. Pablo Peláez-Campomanes i Lorenzo Rook, revisors de la versió publicada del capítol 7, pels seus comentaris i recomanacions. També estenc aquest agraïment a dos revisors anònims de la versió publicada del capítol 6.

A Jordi Blanchar i Ian Keleher per la revisió de l'anglès al capítol 7 i al pròleg, respectivament.

A en Marc Furió, un gran company de despatx, d'articles i de més d'una bona festa. Per cert, quan va ser l'última? Fa massa temps, segur. Haurem de fer-ne una de ben grossa quan ens doctorem els dos (si això surt bé, és clar).

Als meus nous companys de despatx a l'ICP: Sergio Almécija, Josep Fortuny, Bernat Vila i Andrés Santos. A en Sergio a més li he d'agrair (i crec que no sóc l'únic) que hagi posat música de fons a les nostres feines de recerca a base de punk, trash metal, hardcore i altres tipus de música per a la relaxació (bé, també posava jazz de tant en tant).

A Manel Llenas, tècnic de camp de l'IPS, per haver-me ensenyat gairebé tot el que sé sobre les tècniques de rentat.

Als soferts conserges de l'IPS Jordi Ferrer, Marisa i Santi als que he torturat amb maratonianes sessions de fotocòpies. A en Jordi Ferrer li he d'agrair també que no m'hagi deixat tancat a l'IPS.

A Isabel Pellejero per l'excel·lent feina de restauració de les restes de castor estudiades al capítol 3 i per no haver-me matat cada cop que li robava sense permís "Paraloid" per arreglar alguna dent que se m'havia trencat.

A Teresa Raquena i Teresa Esquirol, a les que he obligat a buscar les publicacions més rares a la biblioteca de l'IPS. Espero que em perdonin.

Al personal del servei de microscopia electrònica de la UAB, per haver-me ensenyat a utilitzar el microscopi electrònic de rastreig i per la seva amabilitat i atenció.

A tots els bons amics i col·legues que acabes fent si et dediques a la paleontologia: Josep Maria ("Vakilla") Robles, Sergio Almécija, Laura Celià, Pep Aurell, Àngel Galobart, Sandra Val, Cheyenn ("Pastelito") Rotgers, Andrés Santos, Bernat Vila, Josep Fortuny, Joan Madurell ("Madu"), Chiara Angelone, Raül Carmona, Bego Poza, Eli Blaya...i un llarg etcétera. Un treballa millor si hi ha bon ambient, gràcies macos!

Als meus amics de Canet i de tota la vida: Ginés, Marta, Marc, Maria Rosa, Xènia, Dani, Oriol i Beth. Per haver acceptat un "bitxo raro" com jo dins del seu cercle i per tot el seu suport. Prometo trucar més sovint.

A la meva avia adoptiva Emília Fayed Ariste, que sempre hi va creure però no ho va arribar a veure.

Al meu avi, Josep Vilar, que a base de comprar-me dinosaures de plàstic els dimecres quan hi havia mercat a Canet no feia més que alimentar la meva vocació.

Al meu nebodet suís, en Guim, que en el moment d'escriure aquestes línies té tres mesos justos. Per haver-me alegrat el dia regularment cada cop que rebia una foto seva per mail. Li he de comprar un dinosaure de peluix i idear un pla maligne per començar a atreure'l vers a la paleontologia ara que és petit i innocent.

Als meus pares, Josep Maria i Maria Rosa, a la meva germana Fani (bé, ella vol que li diguin Estefania) i al meu cunyat Víctor. Per haver cregut sempre en mi i per haver-me fet costat en tot, passés el que passés. Sense vosaltres no hauria pogut. Us estimo.

I finalment he de demanar perdó a la que ara és la persona més important de la meva vida. No sé com ho ha aguantat, o més ben dit, no sé com m'ha aguantat. Em sap molt greu haver-me quedat tancat a casa durant gairebé dos mesos seguits, sense sortir ni els caps de setmana. També et demano perdó per les meves enrabiades regulars cada cop que no me'n sortia. Ho sento Roser i et dono les gràcies per tot, per ajudar-me a tirar endavant i per estimar-me malgrat ser com sóc.

Foreword

Introduction. Aim and structure of this work

"Classical" thesis and compendia of publications

"Classical" thesis use to follow a strict plan: first an initial hypothesis or a number of objectives are exposed; then the researcher introduces the methodology that he is going to use throughout the work; the results of the application of these methods on the data are presented and discussed; and finally the text exposes the main conclusions of the work. I like this old way of working, and a significant number of my favorite texts on rodent paleontology are doctoral thesis of this kind. Nevertheless, at the present moment many working groups and universities do not encourage their pre-doctorate researchers to write a thesis of this kind. Why is that? The answer is simple: it delays publication. These long thesis require total dedication, so quite often the pre-doctorate researcher has insufficient time to write scientific papers. Furthermore, the final result is only rarely published as a special number of a journal or as a book.

Thesis as compendium of publications are gaining a high popularity, although many colleagues do not agree with this kind of works. This kind of thesis assures that a pre-doctorate researcher will be producing publications (which is very positive for any working group) while he is writing his own thesis. The question, as many colleagues would point out, is that the jury (or the readers) can never be sure of the authorship of the work; that is one cannot judge the contribution of our candidate to doctor to the final text.

The present thesis should be viewed as a compendium of publications, although an important part of the text within it is still unpublished and some parts have been written without the intention of submitting them to any journal. In the following lines I will try to explain to the reader which is the contribution of other workers to this thesis. Excerpts of the following papers (or the whole text in certain cases) are included in this volume:

- Alba, D.M., Moyà-Solà, S., **Casanovas-Vilar, I.**, Galindo, J., Robles, J. M., Rotgers, C., Furió, M., Angelone, C., Köhler, M., Garcés, M., Cabrera, L., Almécija, S., Obradó, P. 2007 in press. Los vertebrados fósiles del Abocador de Can Mata (els Hostalets de Pierola, l'Anoia, Cataluña), una sucesión de localidades del Aragoniense superior (MN6 y MN7+8) de la cuenca del Vallès-Penedès. Campañas 2002-2003, 2004 y 2005. *Estudios Geológicos*. ***Chapter 2.***

- **Casanovas-Vilar, I.**, Alba, D.M., Moyà-Solà, S., Galindo, J., Cabrera, L., Garcés, M., Furió, M. Robles, J.M., Köhler, M. & Angelone, C. Biochronological, taphonomical and paleoenvironmental background of the fossil great ape Pierolapithecus catalaunicus (Primates, Hominidae). Submitted to *Journal of Human Evolution*. ***Chapters 2, 4 and 5.***

- **Casanovas-Vilar, I.,** Alba, D.M., Almécija, S., Robles, J.M., Galindo, J. & Moyà-Solà, S. Taxonomy and paleobiology of the genus Chalicomys Kaup, 1832 (Rodentia, Castoridae) with the description of a new species from Abocador de Can Mata (Vallès-Penedès Basin, Catalonia, Spain). Submitted to *Journal of Vertebrate Paleontology*. ***Corresponds almost entirely to chapter 3.***

- **Casanovas-Vilar, I.,** & Agustí, J. 2007. Ecogeographical stability and climate forcing in the Late Miocene (Vallesian) rodent record of Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 248, 169-189. ***Corresponds to chapter 6 (with minor changes).***

- **Casanovas-Vilar, I.**, Moyà-Solà, S., Agustí, J. & Köhler, M. 2005. The geography of a faunal turnover: tracking the Vallesian Crisis. In: Elewa, A. T. (Ed.), *Migration of Organisms: Climate, Geography, Ecology*. Springer-Verlag Publishers, Heidelberg, Germany. pp. 247-301. ***Corresponds to chapter 7 (with major changes affecting the methodology used and the results).***

The rest of this thesis has not been published, although a modified version of chapter 4 is in progress with the intention of publishing it as a separate paper. I have been the main contributor to some of these papers, particularly to those devoted to taphonomy, paleoecology and palebiogeography. However, I have also taken important parts from these papers which I have not written, such as general information on the geology and macrofauna recovered at Abocador de Can Mata (Els Hostalets de Pierola, Vallès-Penedès Basin) (in chapter 2) or the historic perspective of the study of great apes in the Vallès-Penedès Basin (in chapter 4). Concerning the description of the beaver femur from Abocador de Can Mata (chapter 3) and its paleobiological implications it is entirely a work by D.M. Alba, S. Almécija and S. Moyà-Solà. Furthermore, the co-authors of this paper also provided major contributions to other sections of chapter 3, including the description of the dentognathic material and the subsequent discussion. The co-authors of the papers on which chapters 6 and 7 are based provided important contributions to the discussion and interpretation of the statistical results.

Aim and structure of this work

Before I started writing this thesis I devised a number of objectives. While these objectives remain the same, on reflection they were perhaps too ambitious. The initial version of this thesis was intended to be a “classical” thesis. The main objectives included the description of the rodent fauna of Abocador de Can Mata and all the Middle Miocene sites from the Vallès-Penedès area; the proposal of a local biozonation; the taphonomic study of all these sites; and finally the paleoecological and paleobiogeographical implications of the results. I abandoned the above project in February of 2007 since I realized that it may take several more years to complete. I had been working for four years and more than half of the work was still pending! I therefore reconsidered my options and decided to compile my publications (completed with the unpublished data) to include the results that these two years of study had produced, and the output is the present volume. The objectives are still the same and although I have not compleated them yet I would like this thesis as a prelude of what I want the finished work to look like.

The thesis is structured into seven chapters that follow this foreword:

Chapter 1. This chapter provides an introduction to the study of fossil rodents focusing in the Vallès-Penedès area. It also introduces the terminology and methods that are used in the systematic part of this work (chapters 3 and 4). I could not resist to write a few pages on the origin of rodents and the Glires concept as well as a short review on the anatomy, origin and classification of the groups that are treated in the systematic part. Some new interpretations regarding the classification and content of certain groups are provided, and although they are not discussed in detail their inclusion obeys the justification of the classification of rodents used. A detailed discussion of these issues is beyond the scope of this work.

Chapter 2. After a short introduction to the geology of our study area, the Vallès-Penedès Basin, I have focused on the sites of Abocador de Can Mata (Els Hostalets de Pierola). The works for the extension of a rubbish dump (the so-called Abocador de Can Mata) have resulted in the discovery of tens of new micro- and macromammal sites in the Vallès-Penedès covering the Late Aragonian (MN 7+8 and probably MN 6). The local biozonation of the Vallès-Penedès is reviewed and updated according to the preliminary results from the field campaigns at Abocador de Can Mata.

Chapter 3. A new species of the castorine *Chalicomys* from Abocador de Can Mata is described. This species is represented by dentognathic material as well as by a partial femur. The taxonomic validity of the nomen *Chalicomys* Kaup, 1832 (instead of *Palaeomys* Kaup, 1832 and *Chelodus* Kaup, 1832) is discussed. The morphology of the femora of several castorine species is compared in order to infer their commitment to aquatic locomotion.

Chapter 4. In 2002 a new great ape genus and species, *Pierolapithecus catalaunicus*, was discovered thanks to the works at the Abocador de Can Mata. The type-locality, Barranc de Can Vila 1, which is situated next to the works, was excavated during the following year, resulting in the recovery of an abundant small mammal sample. The rodents of Barranc de Can Vila 1 are described in this chapter and the relative age of the site is inferred according to the composition of the rodent fauna and the size and morphology of the cricetid *Democricetodon larteti*.

Chapter 5. In this chapter we carry out a taphonomic study of the micro- and macromammal remains recovered at Barranc de Can Vila 1 in order to determine the origin of the accumulation and particularly the predator contribution to it. Concerning the small mammals, the accumulation does not seem to be predator-derived so the small mammal sample is considered suitable for paleoecological inferences which are carried out using multivariate techniques.

Chapter 6. The composition and structure of rodent taxocenosis from three Iberian basins with a reasonably complete record (Calatayud-Teruel, Duero and Vallès-Penedès) for the latest Aragonian and Vallesian is explored by the means of Correspondence Analysis (CA). CA classifies the rodent assemblages into four great groups that are interpreted as rodent paleocomunity types (RPTs). On the basis of paleobotanical and paleomastological data available for some of the sites considered (or time-equivalent localities) each RPT is considered to be characteristic of certain environmental conditions. The reasons for the stability of the recognized RPTs during long time intervals are discussed.

Chapter 7. The Vallesian Crisis, which involved the disappearance of a number of forest-adapted taxa of Middle Miocene origin, appears to be a well-established event in the Vallès-Penedès Basin and in other Iberian Basins as well. Nevertheless, the occurrence of this event in other areas of Europe is still debated. In order to refine the chronologic and geographic extension of the Vallesian Crisis we analyze the changes in diversity, origination and extinction rates in the Middle and Late Miocene (13.8 – 4.9 Ma) mammal record of Europe.

The work finishes with a final summary and conclusions. Appendices with data tables and additional information are provided at the end of certain chapters.

Chapter 1

Introduction to fossil rodents

1.1. The study of fossil rodents

1.1.1. The study of fossil rodents in the Vallès-Penedès Basin, a historical perspective

The early students

The first notice of the finding of a fossil rodent in Catalonia is attributed to Almera (1896) who reported *Sciurus feignouxi* from the Fontsanta site, in Subirats del Vallès (Vallès-Penedès Basin). This cite was substituted by *Cricetodon gerandium* in an “errata” accompanying the offprints of this work. In later publications Almera reports the presence of rodents in another site from the Vallès-Penedès Basin: Rubí (*Sciurus feignouxi* and *Cricetodon gerandium* in Almera, 1900). During the first half of the 20th century J. R. Bataller surveyed the area and discovered many new sites (see for example Bataller, 1918; 1924; 1928), such as Trinxera del Ferrocarril de Sant Quirze, which delivered some rodent remains. In 1938 this author published a monograph on the fossil rodents (including the lagomorphs) from Catalonia: “Els Ratadors (sic) Fòssils de Catalunya” (Bataller Calatayud, 1938). In this work Bataller describes the rodent material of many sites and suggests a chronological arrangement of the studied localities based on their stratigraphic position and in the comparison with the rodent fauna of other European sites. The sites from the Els Hostalets de Pierola (Penedès) are here reported for the first time. Bataller (1938) mentioned three localities (Can Mata de la Garriga, Font d’Ocata and Riera Claret), although he situated five fossiliferous sites in a map (Bataller Calatayud, 1938: plate V). The faunal list for the Els Hostalets de Pierola sites includes the following rodents (Bataller Calatayud, 1938): *Sciurus spermophilinus* (= *Spermophilinus bredai*)[1]; *Cricetodon sansaniense* (= *Hispanomys lavocati*); *Cricetodon affine* (including mandibles and maxillary fragments of *Megacricetodon ibericus* and also some mandibles of *Hispanomys lavocati*); and *Miospalax monacensis* (very worn molars of *Hispanomys lavocati*). The same species (except *Sciurus spermophilus*) besides two beavers (*Steneofiber minutus* and *Steneofiber minutus* raça *catalaunica*; see chapter 3) are cited from Trinxera del Ferrocarril de Sant Quirze (Bataller Caltayud, 1938). This monograph was planned for publication as a chapter of the book “Geologie de la Mediterranée occidentale” by Marcet (1926) although it was finally not included. The original text was written in 1926, and the 1938 published version corresponds to an extended and corrected version. Unfortunately part of the material studied in 1926 was destroyed during Spanish Civil War.

From the 1940s onwards the paleontologists M. Crusafont, J. F. de Villalta and (somewhat later) J. Truyols extensively studied the Neogene successions of the Vallès-Penedès area. As a direct result of their intensive field work an important number of new sites and taxa were discovered which were situated in a stratigraphic frame (for a synthesis see for example Crusafont & Truyols, 1954a or Crusafont *et al.*, 1955). Nevertheless, these authors did not pay much attention to fossil rodents, except for the monography “Los Castores Fósiles de España” (Crusafont Pairó *et al.*, 1948) devoted to

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[1] Throughout this section we indicate the current ascription of the material recovered by the different workers in brackets.

fossil beavers and written by Crusafont and Villalta with the collaboration of J. R. Bataller. This work is structured into two parts a general and descriptive one written by the three authors and a second morphometric one entirely written by Crusafont (Crusafont Pairó, 1948). These workers invited the Swiss paleontologist Samuel Schaub to study the fossil cricetids from the sites of the Vallès-Penedès (which then included the sites near Sant Quirze, Els Hostalets de Pierola and Terrassa). Schaub published the description of the material first in German (Schaub, 1944). Later Crusafont translated this work into Spanish and included Schaub's figures of the described specimens (Schaub, 1947a). In these works Schaub defines a new species of cricetid, *Cricetodon ibericus* (= *Megacricetodon ibericus*), from Els Hostalets de Pierola. From the same set of sites he also describes *Cricetodon decedens* (recognizing two different forms according to their absolute size which would be later recognized as different species: *Hispanomys lavocati* Freudenthal, 1967 and *Hispanomys dispectus* Agustí, 1980); *Cricetodon* cf. *brevis* (= *Cricetulodon hartenbergeri* according to Agustí, 1981a; 1981b); *Cricetodon helveticus* (= *Eumyarion leemani* according to Agustí, 1981a; 1981b); and *Cricetodon larteti* (= *Democricetodon crusafonti*). In a short communication Scaub (1947b) also descrived the murine *Progonomys cathalai* from Viladecavalls (Late Vallesian).

From the 1950s to the late 1970s

The discovery of the very rich site of Can Llobateres between Sabadell and Barberà del Vallès (Crusafont Pairó, 1930; Villalta & Crusafont, 1943a) provided an abundant rodent fauna that was preliminarily studied by Crusafont and co-workers (see Crusafont Pairó & Truyols Santoja, 1960 for a review of these first results). Nevertheless, these remains were not described until the 1960s by Hartenberber & Thaler (1963) and Hartenberger (1965; 1966). The first of these works (Hartenberger & Thaler, 1963) presents an overview of the fossil rodents (mainly murines) discovered at Can Llobateres while the ones exclusively written by Hartenberger are devoted to the description of the cricetids (1965) and the eomyids and glirids (1966). In these two works Hartenberger defined several new species (and also genera and subgenera) of cricetids such as *Cricetulodon sabadellensis*, *Ruscinomys thaleri* (= *Hispanomys thaleri*) and *Cotimus leemani* (= *Eumyarion leemani*); glirids *Muscardinus* (*Muscardinus*) *crusafonti* (= *Muscardinus hispanicus* De Bruijn, 1966) and *Muscardinus* (= *Eomuscardinus*) *vallesiensis* (= *Muscardinus vallesiensis*); and the minute eomyids *Pseudotheridomys* (*Keramidomys*) *pertesunatoi* (= *Keramidomys pertesunatoi*) and *Eomys catalaunicus* (= *Eomyops catalunicus*). The same year Freudenthal (1966) re-described the *Cricetodon decedens* material from Els Hostalets de Pierola already studied by Schaub (1944, 1947a) and defined a new species, *Cricetodon lavocati* (= *Hispanomys lavocati*), for the large-sized specimens recovered at the pre-Vallesian sites of the series. In 1967 Hartenberger described a remarkably complete skull of this species (*Ruscinomys lavocati* in Hartenberger's work) from the "bloc de marne", a Vallesian site of Els Hostalets de Pierola which had delivered abundant micromammal remains. Hartenberger (1967) also described a partial cranium of *Megacricetodon ibericus* (*Megacricetodon* aff. *gregarium* in the original work) from the same site.

During the 1970s further rodent remains were found at the newly discovered sites from the basin. Particularly the site of Castell de Barberà (near Barberà del Vallès) provided an abundant rodent fauna apparently very similar to that of Can Llobateres. Nevertheless, the absence of *Hipparion* s. l. indicated a Late Aragonian age for this site (Vindobonian in Crusafont-Pairó & Golpe, 1972).

From the late 1970s to the present

By the late 1970s J. Agustí, who was finishing his degree on biology, started to review the fossil rodents recovered at many sites under the supervision of M. Crusafont. First he reviewed the material attributed to the cricetids *Cricetodon*, *Hispanomys* and *Ruscinomys* in his degree thesis (the main results would be published in two short publications: Agustí, 1977a; 1977b). The scientific activity carried out by this author would be frenetic during the following years. Agustí (1978a) defined a new species of cricetid, *Fahlbuschia crusafonti* (= *Democricetodon larteti*)[2]; compared the Early Vallesian rodent faunas of the Vallès-Penedès to other sites of the Iberian Peninsula (1978b); contributed to the description of the rodents of Castell de Barberà (Aguilar *et al*., 1979)[3]; re-described the material of *Megacricetodon ibericus* from Els Hostalets de Pierola (Agustí, 1980a); revised once more the genus *Hispanomys* in the Vallès-Penedès Basin with the description of new species (Agustí, 1980b); and studied the rodent fauna of several sites of the Ampurdà Basin (Gibert *et al*., 1980). These works were compiled (together with unpublished data from several localities) in his doctoral thesis (Agustí, 1981a; 1981b). During the following years most of the systematic part of this thesis would be published as separate papers, many of them including the contributions of J. Gibert on insectivores (see for example Agustí, 1983; Agustí & Gibert, 1982a; 1982b). This author also proposed a first biozonation of the Catalan Neogene in his thesis that was also published as a separate paper (Agustí, 1982a).

During the late 1980s this intensive activity in the study of rodents continued, but focused in other Spanish basins, such as the Guadix-Baza Basin (Granada). Nevertheless, the recovery of more material using screen-washing techniques continued at new and old sites from the Vallès-Penedès Basin (see section 1.1.2.). At the same time the study of the rodent assemblages from the basin progressively shifted towards works oriented to the biostratigraphic and paleoecologic applications of fossil rodents and other mammals (Agustí *et al*., 1984; Agustí *et al*., 1985; Agustí & Moyà-Solà, 1990; 1991 are probably the most outstanding contributions). Aldana-Carrasco (1991) studied the sciuromorphous rodents (squirrels and beavers amongst others) of the Vallès-Penedès Basin[4], which had not been considered by Agustí (1981a) since his thesis is entirely devoted to myomorphous rodents.

By the late 1990s an important number of new rodent sites were discovered as a result of the magnetostratigraphic survey of the Western Vallès area by M. Garcés as part of his doctoral thesis (Garcés, 1995; see also chapter 2). Although provisional faunal lists appeared in several papers (Garcés *et al*., 1996; Agustí *et al*., 1997) for the moment being only the rodents of two of these sites (Creu Conill 20 and Creu Conill 22, Early Vallesian) have been described (Casanovas-Vilar *et al*., 2006). Great part of the fossil material has not been prepared yet. Even more recently, thanks to the extension works of a rubbish dump situated at the area of Els Hostalets de Pierola tens of new micro- and macromammal sites have been discovered (see chapter 2). Field campaigns

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[2] On the basis of the material from Sant Quirze (Trinxera) and the lower levels of Els Hostalets de Pierola already described by Schaub (1944, 1947) and assigned to *Cricetodon larteti*

[3] This paper was published in a volume of the French journal "Palaeovertebrata" entitled "Rongeurs Miocènes dans le Vallès-Penedès". This volume was divided into two parts: a first one written by Hartenberger & Crusafont (1979) and devoted to the rodents of Can Ponsic I and a second one by Aguilar and co-workers devoted to the rodents of Castell de Barberà. The study of the rodents of Can Ponsic I was the last contribution of M. Crusafont to the study of the Miocene rodents of the area.

[4] In his review of the flying squirrels of Europe Mein (1970) had studied most of the material of this family recovered at the Vallès-Penedès Basin. This author defined a new species, *Cryptopterus crusafonti* (=*Miopetaurista crusafonti)* on the basis of the material from Can Ponsic.

are still on course, and for most of the micromammal sites only test samples are available for the moment.

1.1.2. Collecting methods

Fossil microvertebrates are rarely found during systematic excavations. Accordingly, the remains of small animals such as rodents or insectivores were very rare in ancient collections (except in those corresponding to karstic sites). During the 1950s specific methods were devised in order to recover these minute fossils. In this first epoch of fossil microvertebrate sampling the sediment removed during the excavation of fossil vertebrates was sieved in nearby water streams. These methods yielded rich samples, specially in the karstic sites, where microvertebrate remains use to be derived from the pellets of owls and other birds of prey. In sites situated in different sedimentary contexts these methods did not always provide rich samples.

A new method that allowed the processing of large amounts of sediment was developed by the late 1960s. The Dutch paleontologists working at the Calatayud-Teruel Basin were the first to introduce these techniques into Spain (see Daams & Freudenthal, 1988a for a summary), while in the Vallès-Penedès Basin these methods were used somewhat later, by the late 1970s. This method consists in several phases:

1) The area to be sampled is prospected in the search of suitable facies for the preservation of microvertebrate remains. The most favourable sediments for fossil accumulation appear to be lutites and marls, while sands and rudites are nearly always void of concentrations of microvertebrate remains. Appropriate environments for microvertebrate preservation appear to be lacustrine or palustrine ones, although other continental environments (such as alluvial flood plain or the distal areas of alluvial fans) have also provided abundant microvertebrate samples. Small fossils may be found after a close inspection of these lithologies. However, microvertebrates may also be found in favourable layers even if they are not detected at naked eye. Other criteria, such as the presence of lignites, macrovertebrate bones or fragments and shells of terrestrial or freshwater mollusks appear to be good signs of the presence of microvertebrate fossils.
2) A test sample of 100 – 150 kg of sediment is picked up. Usually the sediment is dried using an oven. Afterwards the sediment is immersed in water. If the sediment was completely dehydrated it will quickly collapse. The sediment is screen-washed using small sieves with mesh sizes of 10 mm, 2.5 mm, 0.7 mm and 0.5 mm. The fraction under 0.5 mm is discarded since practice has shown that it contains hardly any small mammal teeth, and the few remains found in it seem to be of little diagnostic value. Hosepipes with moderate water pressure are used in screen-washing. Screen-washing removes all the mud and leaves a residue that is inspected under a stereomicroscope in order to recover the small mammal remains. The residue is discarded. The result is positive if a single small mammal cheek teeth is found. However, localities are not intensively sampled unless they provide rich test samples consisting in at least 5-10 cheek teeth.
3) A final sample is collected. The amount of sediment collected at this phase may be very important, usually exceeding a thousand of kg. The size of the final samples is calculated on the basis of the number of cheek teeth recovered in the test samples. A total number of 100 recovered cheek teeth is considered adequate for a final sample. For example, if three cheek teeth have been recovered in a test sample of 150 kg a final sample of 5000 kg is required in

order to recover 100 cheek teeth. This procedure assumes that the small mammal remains are uniformly distributed in the rock volume. Sequential sampling (see Etter, 1999 for a description and an example applied to invertebrate paleontology), involving the recovery of progressively greater samples from the same site may be a better approach for the calculation of the final sample. However, this method is very time-consuming, so it has not been applied to microvertebrate sampling. In the case of the sites from the Abocador de Can Mata (see chapter 2) the final samples never are smaller than 1300 kg of sediment.

4) The final sample is screen-washed. The methods used are similar to those used in the case of test samples, although the amount of sediment to be processed is at least ten times greater and requires a somewhat different equipment. Screen-washing of the final samples is usually carried out at the field, near a water stream or a lake, which will save a lot of water. The sediment is extended over plastics and dried at the air. In summer, the sediment is completely dehydrated in about 24 hours. Afterwards, it is immersed in water using several washing-bowls where it quickly collapses. For screen-washing a special sieve equipment, that allows the processing of large amounts of sediment by two or more persons, is used. The sieves used at the 2002-2004 field campaigns at Abocador de Can Mata and Can Vila were based in the original designs by Daams and Freudenthal (see Daams & Freudenthal, 1988a). A sieve based on a design by Dr. H. de Bruijn[5] has been used since the 2005 campaign (fig. 1.1.). These sieves are very similar, although the one designed by H. de Bruijn is larger, so four persons can work simultaneously (in the other one only two persons can work at the same time). These structures are foldable and can be mounted easily in a few minutes. They consist in three to four washing trays that are situated at different levels according to their mesh size. Mesh size decreases as we move from the highest tray (10 mm) to the lowest one (0.5 mm). The sediment is dropped in the 10 mm mesh and washed using hosepipes with moderate water pressure. The coarser sediment is trapped in this tray while water and the finer one passes trough a ramp to the 2.5 mm mesh, and afterwards to the 0.7 mm and 0.5 mm meshes where it is further washed. The process results in the removal of mud and the fraction under 0.5 mm and the separation of the residue into different fractions according to their granulometry. The trays must be emptied regularly since an excess of sediment may completely obtrude the mesh holes. Once a final sample is processed the sieves are thoroughly cleaned before proceed with another one.

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[5] To whom we whish to express once more our most sincere thanks.

Figure 1.1. The sieve equipment used since the 2005 field campaign at Abocador de Can Mata (ACM). Top left: Detail of the 0.7 mm sieve.

In the case of sediments including a certain proportion of highly carbonatic cement, the immersion in a solution of CH_3-COOH at 10 % will surely reduce the amount of residue. The immersion of compact sediment blocks in diesel oil for a few minutes is also helpful for breaking up well-cemented sediments. After screen-washing the final sample is usually reduced to 1 – 10 % of the original volume.

5) The different fractions of the residue are inspected under a stereomicroscope in the search for small fossils. In order to facilitate this process it may be useful to further separate the residue according to granulometry using hand sieves. A residue of constant granulometry takes less time to be inspected. However, this process is very time-consuming. The recovered remains are usually classified in five small boxes: mollusk shells and shell fragments (including other remains such as mineralized seeds); small macrovertebrate bones; complete microvertebrate postcranial bones; microvertebrate teeth; and undetermined microvertebrate bone fragments. Certain kinds of remains, such as mandibles, skull fragments or anguid osteoderms may be separated in different boxes if they are abundant.

Once the small fossil remains are separated from the residue they are assigned a collection number preceded by the acronym IPS (Institut de Paleontologia de Sabadell). A single IPS number is given to each box containing mollusk remains and undetermined microvertebrate bone fragments. Usually the same is applied to microvetebrate postcranial bones, although certain bones (such as humerous of talpids) are separated and given an IPS number. The rodent and lagomorph incisors are only given discrete IPS numbers in a few cases. The cheek teeth are carefully ordered and a single IPS number is given to each one. Each cheek teeth is mounted on a assembleable piece (from a construction game for kids) using a non-greasy gum. The corresponding IPS number is written on each piece (the field number[6] is also written in some cases) and the pieces are stored in small plastic boxes. Sometimes the cheek teeth still present sediment filling small cavities that has to be removed before the teeth are mounted on the piece. Small needles and/or ultrasound cleaning may be used to remove this sediment. Ultrasounds can only be used for a few seconds on teeth, since they may result in the total break up of the material.

All the material studied in the systematic part of this work (chapters 3 and 4) is housed within the collections of the Institut Català de Paleontologia in Sabadell and has been assigned a collection number (IPS). The material recovered at the test samples from the Abocador de Can Mata is also housed at this institution and has been assigned a field number.

1.2. What is a rodent? Origin and classification of rodents

1.2.1. Main anatomical traits of rodents

Today, rodents are the most diverse and abundant terrestrial mammals. Rodents are commonly described as small and diversified terrestrial mammals, specialized for gnawing and with a high rate of reproduction. The size of rodents is usually small, most being between 80 to 350 mm in length (Hartenberger, 1985), with the large-bodied *Hydrochoerus* and *Castor* being exceptions (there are even larger fossil rodents, such as the Pliocene caviomorph *Telicomys*, which reached the size of a rhinoceros!). Rodents comprise close to over 40 % of all mammal species, and they are not only highly diversified at the species level but also at the family level. The number of species and families of rodents differs according to the opinion of the authors, although a number close to 2000 rodent species is widely accepted (see for example MacDonald, 2001). There are about 30 extant families besides a similar number of fossil ones (Hartenberger, 1998), however only a few of them comprise more than 10 genera (Hartenberger, 1985). These include the Muridae and the Sciuridae for example. The Muridae are distributed worldwide, including Australia and New Guinea, where it is the only terrestrial placental mammal family found (excluding dingoes, introduced in Holocene times). The squirrels (Sciuridae), with nearly 300 species distributed throughout the Eurasia, Africa, North and South America. The data on reproduction and gestation for recent families indicate that only some of them, such as the Muridae and the Arvicolidae, are characterized by high reproduction rates, while rates are much moderate in other families (French *et al.*, 1975). High reproduction rates are associated to short longevities, while in the case of the families presenting lower reproduction rates longevities are longer (French *et al.*, 1975).

Anatomically, rodents are characterized by a number of autapomorphic traits (Hartenberger, 1985):

1) One upper and one lower enlarged, evergrowing incisor.
2) Long diastema between incisors and premolars on both jaws, due to the loss of canines and anterior premolars.
3) Incisor enamel restricted to the buccal (= anterior) face
4) Paraconid lost on lower cheek teeth
5) Orbital cavity lying just dorsal to cheek teeth
6) Ramus of zygoma lies anterior to first cheek teeth
7) Glenoid fossa appears as antero-posterior trough.

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[6] This field number is assigned when picking up the cheek teeth.

Nevertheless, popular culture and many unspecialized books tend to stress the chisel-shaped (called gliriform) incisors as the most distinctive feature of rodents. The fossil record indicates that such modified incisors appeared several times independently in different orders or even subclasses of vertebrates (such as in certain multituberculates, Paleogene primates, the marsupial *Vombatus*, the insular bovid *Myotragus* from the Balearic Islands or the Triassic mammal-like reptile *Bienotherium*). Therefore, gliriform incisors are not synonymous with Rodentia. Embryological data have demonstrated that the enlarged and evergrowing incisors of rodents and the closely related lagomorphs (see section 1.2.2) are in fact the second incisors in both upper and lower jaws (Adloff, 1898, Luckett, 1985). These authors observed the development of small, abnormal deciduous first incisors in the prenatal jaws of both groups. Luckett (1985) reported the presence of abnormal deciduous third incisors in both groups (its proximity to the second deciduous incisors suggest that these teeth are not deciduous canines), although in the case of lagomorphs the third upper deciduous incisor follows a normal development, resulting in the small second incisors (the so called peg teeth) on the lagomorph premaxillary. In the abnormal teeth the dentin forms a spherical clump or knot, and both enamel and ameloblasts are lacking. The abnormal deciduous teeth do not erupt. The rodent lower incisors are firmly inserted in the lower jaws and they extend internally beneath the last molar in many forms. The upper incisors extend internally until the roots of the first cheek teeth, although in certain genera they end somewhat more distally. The morphology and degree of curvature of the incisors is highly variable. Fossorial rodents have relatively large incisors, probably because they use them as a pick for digging. According to their orientation there are three kinds of upper incisors: proodont (pointing forwards), ophistodont (pointing backwards) and orthodont (vertically oriented).

The cheek teeth are separated from the incisors by a large diastema. All rodents have lost the two first upper premolars and all the lower ones except the fourth. Many rodents have further reduced the number of cheek teeth (such as the Muroidea) resulting in the presence of just three upper and three lower molars (the third molars are very reduced in many muroids and they have even disappeared in some of them such as the Australian water rat *Hydromys chrysogaster*; family Muridae). The cheek teeth are rooted in most rodents; however, a considerable number of genera and families have developed unrooted evergrowing hypsodont cheek teeth. The cheek teeth morphology is very diverse, and is an extremely useful tool for taxonomic studies.

Rodents are generally viewed as small herbivores (feeding on seeds, fruits, leaves or grasses), although this is only true for some of them. Many rodents are omnivores and include insects and small animals in their diet. There are also fully carnivorous rodents (which feed on small animals and eggs), such as several tropical squirrels that only feed on insects (for example the long-nosed squirrel, *Rhinosciurus laticaudatus*, from Sumatra and Borneo).

Overall, the skull of rodents is low and flattened, with a conspicuously developed splachnocranium in relation to the neurocranium. The zygomatic arch is complete with the midportion spanned by the jugal. The paraoccipital processes are often large. The premaxillary bones are long and reach the frontal. The pterigoyd fossa is well developed for the insertion of these strong masticatory muscles. The temporal muscle is reduced, while the masseters are very developed. The glenoid fossa is longitudinally elongated and lacks the postglenoid process. This character, coupled with the lack of a postglenoid process, allows a high propalinal mobility of the mandible (Turnbull, 1970). The jaws are protruded for gnawing. Since the span from condylus to incisive occlusal surface is horter for the lower jaw than is the corresponding span above (from the glenoid fossa to the incisive occlusal surface), the only way for the incisors to occlude is by a forward shifting of the lower jaws. The mandible can also be rotated through its longitudinal axis thanks to the transversus mandibulae muscle, which is situated just behind the mandible symphysis. The contraction of this muscle aligns the tips of the lower incisors. The mandible presents an angular process were masseter muscles are inserted. Most of rodents present also a coronoid process (it is lacking in recent Ctenodactylidae). The anatomy of the mandible, the arrangement of the masseter muscles and the structure of the zygoma have been used for the classification of rodents above the family level (see section 1.2.3.).

The skeleton of rodents is rather unspecialized in many of them which have retained the plesiomorphic condition for mammals. Many rodents present five digits with long nails on both fore and hind limbs, although the thumb is very reduced or has completely disappeared in an important number of forms. The digits II to V present claws, while the pollex and the hallux may present nails. The clavicles are usually present. A long tail is also usually present. The number of caudal vertebrae is highly variable, being maximum in jumping forms and minimum in fossorial forms and the Caviidae. A few rodents (such as the harvest mouse, *Micromys minutus* or the North American porcupines of the genus *Coendou*) present prehensile tails that are used as a fifth member for climbing. The limbs show different morphologies according to their functions: digging, swimming, jumping, climbing, running, etc. Most rodents are plantigrade, however certain rodents adapted for running in open spaces (such as the capybara or the agouti) are digitigrade and their nails resemble small hoofs. Rodents that use their fore limbs for digging present robust bones on the arms and very long nails. The semiaquatic forms usually present webbed feet, and certain ones present a dorsoventrally (e.g. beaver) or laterally (e.g. muskrat) flattened tail that is also used to aid in the aquatic locomotion. Many bipedal jumping forms present reduced arms and elongated hind limbs. The metatarsal bones are elongated and even fused into a single bone in certain genera (such as in the jerboa *Dipus*). The digits I and V are reduced or even lacking in these forms. Certain arboreal rodents present a patagium (such as the flying squirrels or the scaly-tailed squirrels) which is used for gliding.

1.2.2. The origin of rodents and the Glires concept

The relationships of rodents to lagomorphs and of both groups to other eutherian orders have long been disputed. Linnaeus included rodents and lagomorphs in a single order, Glires, in the second edition of his “Systema Naturae” (Linnaeus, 1740). In its original definition Glires included the following genera: *Histryx*, *Lepus*, *Sciurus*, *Castor* and *Mus*. In subsequent editions of the “Systema Naturae” *Rhinoceros* (sic) (10th edition; Linnaeus, 1758) and the bat *Noctilio* (12th edition; Linnaeus, 1766) were also included into this order (*Rhinoceros* was quickly resituated by Linnaeus in the 12th edition of “Systema Naturae” within the order Belluae, including *Eqvs* (sic!), *Hippopotamus*, *Rhinoceros* and *Sus*).

In a broad sense, Glires designate small gnawing mammals. Although Linnaeus proposed this order with clear taxonomic value, gradually authors of the 19th and the early 20th century expressed serious doubts concerning its taxonomic value. Indeed, the result of their studies was to divide Glires into two major groups: rodents and lagomorphs (see Brandt, 1855; Tullberg, 1899; and Gidley, 1912). However, the term “Glires” was maintained as a supraordinal taxon including rodents an lagomorphs in both paleontological and neontological literature of the 20th century. Ignorance of any paleontological ancestors for both groups was the reason invoked by Simpson (1945) for retaining Glires in his very influential mammalian classification. This supraordinal grouping is supported by important similarities between rodents and lagomorphs in their cranial anatomy (Novacek, 1985; Luckett & Hartenberger, 1993) and embryologic development (Luckett, 1985).

On the 1990s, molecular data re-opened the debate on rodent relationships by the claim that "the guinea pig is not a rodent" (Graur *et al.*, 1991; D'Erchia *et al.*, 1996). This proposal not only contradicted the conventional view of a monophyletic origin of the rodents but also conflicted with the Glires concept. However, these molecular results have been criticized because only a few rodent and lagomorph species were included in the analyses, i.e., mouse, rat, guinea pig. It has been suggested that the proposed parphyly of rodents is an artifact that might be corrected by the analysis of a larger taxonomic sampling (Luckett & Hartenberger, 1993). Recent molecular analyses, which rely on the combination of numerous independent nuclear markers, now led to a robust support for rodent monophyly (Murphy *et al.*, 2001). These studies have also revealed a close relationship between rodents and lagomorphs, further supporting the Glires clade (Murphy *et al.*, 2001). Murphy and co-workers (2001) also suggest that the Glires form a higher clade together with their close relatives: the primates, the tree shrews (Scandentia) and the flying lemurs (Dermoptera). This clade was called Euarchontoglires and also includes the shrews, moles and hedgehogs (Eulipotyphla). The divergence of Euarchontoglires from the remaining eutherian major clades (namely the Afrotheria, the Xenarthra and the Laurasitheria) is traced back to the Late Cretaceous (ca. 100 Ma) by Murphy and co-workers (2001).

On paleontological grounds, the origin of Glires is hypothesized to have taken place close to the Cretaceous-Tertiary boundary (Luckett & Hartenberger, 1985; Hartenberger, 1998, Meng, 2004; Asher *et al.*, 2005) a result compatible with some recent estimates from molecular studies (Huchon *et al.*, 2002). Older dates, extending back to the Cretaceous (80-100 Ma) for the divergence of Glires have been proposed by certain molecular studies (Kumar & Hedges, 1998). Paleontological support for an older date for Glires divergence has also been proposed by studies supporting a close relationship between fossil Zalambdalestids and Glires (McKenna, 1994; Archibald *et al.*, 2001). Zalambdalestids are an extinct central Asian group of eutherain mammals that first appeared 85 to 90 Ma. This hypothesis, which would imply the presence of a Glires stem lineage more than 20 million years before the first appearance of any undisputed placental mammal, has been strongly refuted by some authors (Meng, 2004; Asher *et al.*, 2005).

The study of Central Asian (Mongolian and Chinese) Paleocene mammal faunas has revealed the existence of a high diversity of small herbivore mammals that are recognized as basal Glires. The phylogeny and distribution of basal Glires show that their early divergence area, if not center of origin was in Asia (Dawson, 2003; Meng, 2004). These early Glires include the genera *Heomys* and *Mimotoma*, which appear very close to rodents and lagomorphs respectively (Li, 1977; Li & Ting, 1985; Li *et al.*, 1987; Meng, 2004; Asher *et al.*, 2005). These ones and closely related genera are informally known as "eurymylids" or "eurymyloids". Their taxonomic arrangement is far from clear. Certain recent classifications (see for example McKenna & Bell, 1997) have considered *Heomys* as a true rodent, while others have placed it in a separate family, the Eurymylidae, that includes other basal Glires (such as *Eurymylus* and *Rhombomylus*): (Li & Ting, 1985; Meng, 2004; Asher *et al.*, 2005). Li *et al.* (1987) subdivide the Asiatic "eurymyloids" in different families: the order Mimotonida, which would include *Mimotoma*, may be ancestral to lagomorphs and would be included with them into the superorder Duplicidentata; the Eurymylidae (including *Eurymylus* and

Heomys) and the Rhombomylidae (including *Heomys*) would define the order Mixodontia, which would be included with the Rodentia in the superorder Simplicidentata. The main lines of this supraordinal arrangement are also followed by McKenna & Bell, 1997).

Heomys concurs with all the diagnostic characters of rodents defined by Hartenberger (1985; see also section 1.2.1.) except for some details on the structure of the cheek teeth: the occurrence of two lower premolars (third and fourth); the presence of a relatively large third upper premolar; the transversely elongated upper molars; and the presence of a broad hypocone shelf (Li & Ting, 1985; Li & Chow, 1994).Nevertheless, all character analyses of eurymylids lead us to think that a reasonable ancestor of rodents should arise from a primitive eurymylid, even if *Heomys* seems to be somewhat too specialized to be a direct ancestor of rodents (Li & Chow, 1994).

The Late Paleocene (Gashatan) Bayan Ulan fauna of Inner Mongolia provides the first record of a rodent, or a very close rodent relative. This is *Tribosphenomys*, a relatively well-represented genus that has been regarded as a sister group of the Rodentia, or as a rodent of the family Alagomyidae (Meng & Wyss, 1994; Meng *et al.*, 1994; Hartenberger, 1998; Meng, 2004). Slightly younger mammal faunas that represent the latest Paleocene or earliest Eocene from China and Mongolia record the earliest unquestionable rodents of Asia (Dashzeveg, 1990a, 1990b; Dashzeveg *et al.*, 1998). The first Asian rodents include species belonging to four different families: Alagomyidae, Ischyromyidae, Yuomyidae and Cocomyidae (Dawson, 2003). This fact suggests a rapid diversification of rodents after their Paleocene origin.

As early as by the Late Paleocene the rodents extended their range out of Asia. Ischyromyids and alagomyids have been recorded from the Early Clarforkian (latest Paleocene) from Montana and Wyoming in North America (Dawson & Beard, 1996). These early rodents from Asia and North America appear to have inhabited warm and moist environments (Dawson, 2003). Rodents appear in Europe somewhat later, by the Early Eocene (MP7), being represented by ailuravine, pseudoparamyine, microparamyine and ?paramyine ischyromyids (Escarguel, 1999), suggesting an interval of earlier rodent presence in Europe (Dawson, 2003). Although the marine Turgai Strait created an important faunal barrier in the Eocene, especially between the northern parts of Asia and Europe the question still arises of the origin of European rodents, whether they stem directly from Asia or indirectly via North America (Escarguel, 1999; Dawson, 2003).

1.2.3. Major groups of rodents

From the beginning of their history rodents are diversified at the family level, and in the Early Eocene no less than 11 families can be recognized (Hartenberger, 1998). From this period rodents are present in Europe, Asia, North America and Africa. The spectacular diversification and expansion of rodents took place in a surprisingly brief time interval: a few million years. This rapid diversification and both fossil and recent diversity of rodents have always been a challenge for those students interested in their origins, intraordinal structuring and ways and time of diversification. Despite the noticeable progress achieved from the late 1990s onwards the intraordinal structuring of the order and the phylogenetic relationships between most groups are far from resolved.

Early attempts for the division of the order Rodentia above the family level were based on the anatomy of the zygomasseteric area and the mandible. Brandt (1855)[7] proposed a division of the order into three great groups[8] on the basis of the morphology of the masseter muscles and the zygomatic:

1) Sciuromorpha. The superficial masseter, which is rather piriform, originates from a bump anterior to the toothrow, the masseteric tubercle. The insertion area for the superficial masseter is situated on the angular process, at the posterior border of the mandible. The lateral masseter originates from the ventral and messial border of the zygomatic arch and from the area of the rostrum immediately anterior to it. The front of the zygomatic arch is developed into a large and distinctive groove on the mesial wall of the zygomatic process, the zygomatic plate. The lateral masseter is inserted on the lateral surface of the mandible. The medial masseter originates only from the ventral margin of the zygomatic arch and also inserts on the lateral side of the mandible. The sciuromorphous condition is found on squirrels, beavers and pocket gophers amongst others.
2) Hystricomorpha. The medial masseter is very developed. It originates from the rostrum, as far forward as the middle of the lateral surface of the premaxilla, and runs through an hypertrophied infraorbital foramen. The medial masseter inserts on the lateral surface of the mandible. The superficial and lateral masseters originate from the ventrolateral border of the zygomatic arch and insert on the lateral surface of the mandible. The origin area of the superficial masseter is situated mesially respect to the origin area of the lateral masseter. The hystricomorphous condition is characteristic of guinea pigs, agouties, capybaras and many other South American rodents. It is also found in porcupines (both Erethizontidae and Hystricidae) and certain Old World families such as the Bathyergidae (mole rats) or the Thryonomyidae (cane rats).
3) Myomorpha. The medial and the superficial portions of the masseter are mesially directed. The medial masseter passes through a moderately enlarged, keyhole-shaped infraorbital foramen until it finally inserts on the lateral surface of the mandible. This medial masseter originates from the side of the rostrum, although it does not extend far forward as in hystricomorphous rodents. The superficial masseter originates from the masseteri tubercle and inserts on the angular process as in sciuromorphous rodents. The morphology and insertion areas of the lateral masseter are also analogous to the sciuromorphous condition. The Muroidea and the Gliridae are myomorphous.

Ellerman (1940) added a fourth group, the Protrogomorpha, which would include a sole member: the mountain beaver (*Aplodontia rufa*). In the Protrogomorpha the medial and lateral masseters originate from the ventrolateral border of the zygomatic arch. The medial masseter is situated quite vertically and inserts on the lateral surface of the mandible. The superficial masseter originates from the anteroventral border of the zygomatic and is piriform and rather oblique. The protrogomorphous condition is also

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[7] Earlier, in 1839, Waterhouse published a classification of rodents and pointed ourt that the animals he included in the order could be divided into two major groups, the rabbits and all others. The latter, in turn, were divisible into three groups according to their zygomasseteric structure. The groups of Waterhouse (1839) are approximately equivalent to those of Brandt (1855); however, Waterhouse did not assign any name to the three recognized subdivisions.

[8] In fact, Brandt (1855) proposed a fourth group according to the structure of the masticatory muzzles and the skull: the Lagomorpha. Lagomorphs would be part of the order Rodentia until they were recognized as a different order by Gidley (1912).

found in many early rodents such as the Ishcyromyideae and the first representatives of the Gliridae (*Eogliravus* and *Gliravus*, see section 1.3.5.).

Tullberg (1899) proposed another subdivision of the order Rodentia encompassing the three groups already defined by Brandt (1855)[9]. Tullberg (1899) brought a second structural condition into this classification, namely the orientation of the angular process of the mandible. The angular process is the area which receives much of the masseter muscle. Tullberg (1899) distinguished two groups of rodents according to this trait:

1) Sciurognatha. The angular process is situated in the same plane than the mandibular corpus. The sciurognathous condition may appear associated to all the zigomasseteric configurations described above.
2) Hystricognatha. The origin of the angular process is distinctly lateral to the plane defined by the mandibular corpus, and the angular process often appears to be flared laterally. The coronoid process is usually reduced in hystricognathous forms. Most hystricognathous rodents are also hystricomorphous.

The subdivisions of the order proposed by Brandt (1855) and Tullberg (1899) left their footprint in many of the classifications of rodents proposed during the 20th century. Ellerman (1940) classified the rodents into two tribes (sic): Sciurognathi and Hystricognathi. These tribes were further subdivided into four subribes (sic) mainly based on the zigomasseteric structure of their members: Bathyergomorphi and Hystricomorphi within the Hystricognathi; and Sciuromorphi (including aplodontids) and Myomorphi within the Sciurognathi. Simpson (1945) defined three different suborders according to the zigomasseteric structure (Sciuromorpha, Myomorpha and Hystricomorpha). This classification was uncritically followed by many paleontologists. Later on, Chaline and Mein (1979) proposed two suborders according to the morphology of the mandible (Sciurognatha and Hystricognatha) and several infraorders. The suborder Sciurognatha would include the following infraorders: Protrogomorpha, Theridomorpha, Sciuromorpha, Ctenodactylomorpha, Myomorpha. The suborder Hystricognatha would include two infraorders the Phiomorpha and the Caviomorpha. Chaline & Mein (1979) emphasized a question previously pointed by several authors (Ellerman, 1940; Simpson, 1945; Grassé & Dekeyser, 1955): the parallel development of the same zigomasseteric configuration in apparently unrelated groups of rodents. Myomorphy and Hystricomorphy provide increased strength to the jaw muscles and evidence an increase of the propalinal moving during food processing. Accordingly, the arrangement of rodents according to this character results in polyphyletic groups. On the contrary, Chaline & Mein (1979) consider valid the subdivision of rodents into two suborders according to the morphology of the mandible. Certain authors (such as Wood, 1985) have claimed for a parallel development of hystricognathy in both New and Old World hystricognaths.

The past decades have witnessed a great progress in the intraordinal structuring of the order Rodentia which has resulted from the study of Asian fossils of the early rodents and of molecular analysis of large taxonomic samples including members of most of the rodent families. Nevertheless, the phylogentic relationships remain unclear particularly in the case of the non-hystricognathous families (Hartenberger, 1998). These advances were expressed in the monumental “Classification of Mammals Above the Species Level” by McKenna & Bell (1997) which was not particularly well received by rodent paleontologists (Freudenthal & Martín-Suárez, 1999; De Bruijn, 2001;

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[9] According to this author the Sciurognathi would include the Sciuromorphi and the Myomorphi, while the Hystricognathi would include the Hystricomorphi and the Bathyergomorphi.

Dawson, 2003; and personal communications by J. Agustí, P. Mein & H. de Bruijn). In the opinion of De Bruijn (2001) the classification of rodents by McKenna & Bell (1997) presents oversplitting in certain parts and overlumping in others (such in the case of the superfamily Muroidea, see section 1.3.6.). In this work we will take the work by McKenna & Bell (1997) as starting poinf for the classification of rodents. This classification is not fully satisfactory and particular problems are discussed in the following sections (see tables 1.1-1.4. for a classification of the rodent genera described in chapters 3 and 4).

After the publication of the "Classification of Mammals…" (McKenna & Bell, 1997) recent studies, both molecular and morphological, have shed new light on the intraordinal structuring of rodents. Huchon *et al.* (2002) analyzed and compared the performance of three nuclear genes for a large sample covering most rodent families and also including representatives of the remaining orders of mammals. Their results recognize three well resolved clades: a squirrel- and dormouse related clade (including *Marmota*, *Aplodontia*, *Dryomys* and *Glis*); a mouse-related clade (including *Anomalurus*, *Castor*, *Dipodomys*, *Thomomys*, *Dipus*, *Tachyroyctes*, *Mus* and *Rattus*); and a third clade called Ctenohystrica (including *Massoutiera*, *Trichys*, *Bathyergus*, *Thryonomys*, *Petromus*, *Echymys*, *Cavia*, *Erethizon* and *Chinchilla*). In the first clade squirrels appear more closely related to the mountain beaver than to dormice. This clade had been suggested previously on the basis of morphological data (Lavocat & Parent, 1985; Hartenberger, 1998). Three subclades can be recognize within the mouse-related clade: *Anomalurus*; a clade including murines and jerboas (already recognized by many authors); and an unexpected clade grouping beavers with pocket mice an pocket gophers (which is strongly supported). The Ctenohystrica are divided into three clades with the ctenodactylid *Massouteria* as an outgroup: Hystricidae, Phimorpha s.s. (i.e. Bathyergidae, Trhryonomyidae and Petromuridae) and Caviomorpha (i.e. Octodontoidea, Cavioidea, Erethizontoidea and Chinchilloidea). The results of Huchon *et al.* (2002) confirm the monophyly of Hystricognathi, but the monophyly of Sciurognathi is statistically rejected. These workers also intended to reconcile molecular and morphological-paleontological insights and placed the rodent radiation between the Paleocene and the Eocene.

A few years earlier Hartenberger (1998) had proposed a subdivision of rodents into six suborders. The molecular results of Huchon *et al.* (2002) agree with the phylogeny proposed by Hartenberger (1998) in many aspects. This author proposed a first suborder which would include the exclusively fossil (Eocene) Alagomyidae. The second suborder includes several fossil families besides the dormice and the squirrels, fitting well with the squirrel- and dormouse related clade of Huchon *et al.* (2002). The beavers, the pocket mice, the pocket gophers and the jerboas are included by Hartenberger (1998) within this clade. The third suborder (Parasciurognatha Lavocat, 1951) includes three families: the recent Anomaluridae and the extinct Zegdumyidae and Theridomyidae. Huchon *et al.* (2002) include *Anomalurus* in the mouse-related clade, however it clearly appears as an outgroup to the rest of the members of this clade. The fourth suborder (Murida) includes the Muridae and their relatives. The fifth and sixth suborder agree with the Ctenohystrica of Huchon *et al.* (2002). The Ctenodactylidae is the only recent family of the fifth suborder, while the sixth suborder includes three infraorders: Phiomorpha, Caviida, and an unnamed infraorder including the New World porcupines.

These recent studies have improved our knowledge of rodent relationships. Nevertheless, the use of the taxonomic hierarchies proposed in these works does not seem advisable until more studies (both morphological and molecular) confirm or clarify their results.

1.3. General remarks on the anatomy, biometry and classification of the families of rodents that appear on the systematic part of this work

1.3.1. Methods and abbreviations

In the tables and descriptions of the systematic part of this work the following abbreviations are used for dental elements: I (incisor), P (premolar), M (molar). "d" indicates that this is a deciduous element (example: dP for a deciduous premolar). Upper teeth are indicated by a superindex (example: M^1), while lower teeth are indicated by a subindex (example: M_2).

The measurements taken in the case of cheek teeth usually involve mesio-distal length (L) and bucco-lingual width (W); however the methodology for taking these measurements varies in each rodent family (see sections 1.3.3 – 1.3.6). In all cases the measurements are expressed in millimeters. Estimates (due to minor damage or distortion) are in brackets and the symbol ">" indicates that the measurement could not be reliably taken, but exceeded the measurement reported. The measurements were taken using a "Nikon Measuroscope 10" optic caliper connected to a digital monitor "Nikon SC-112" except in the case of the castorid remains described in chapter 3, which were measured using a "Mitutoyo" digital hand caliper. The measurements taken are given in the tables that accompany the description of the different taxa (the wear stage is also provided in such tables in the case of castorid cheek teeth). In the case of cheek teeth, when the number of measured specimens of a certain dental element is less than five all the measurements are given. On the contrary, when this number is greater than five we give the mean values for all the measurements taken. The number of measured specimens and the minimum and maximum values for each measurement and dental element are also provided. In many cases, the measurements taken are compared graphically to other samples by the means of multiple scatterplots using different symbols for each sample. Cumulative bar charts, where each bar represents the total length of the toothrow, are used to illustrate the relative proportions of the cheek teeth in a few cases.

Light camera drawings were performed using a "Wild PYP 308700" light camera attached to a "Wild M3X" or "Wild M3Z" stereomicroscope. Scanning electromicroscope (SEM) micrographs were taken using a "Hitachi S-570" SEM at the Servei de Microscopia of the Universitat Autònoma de Barcelona.

1.3.2. General remarks on the skull, mandible and incisors

Because of their fragility complete skulls and large skull fragments are quite rare in the rodent fossil record. In the studied sites only maxillary fragments have been recovered in a few cases. These maxillary fragments still retain some of the cheek teeth but are so fragmented that no measurements were taken, and only the position of certain morphological features (such as the anterior root of the zygomatic or the posterior margin of the incisive foramen) in relation the upper cheek teeth series was noted.

Complete mandibles or large mandibular fragments have been recovered more frequently than skull fragments in the localities studied. The mandible is divided into two portions: the mandibular body or corpus which bears the dentition, and the ramus which is usually thinner (see fig. 1.2.). Frequently the ramus is broken just behind the tooth row. The mandibular ramus bears three processes: a ventrally situated angular apophysis, a posterodorsally situated articular (or condyloid) process, and an anterodorsally situated coronoid process. A large depression occupied by the masseter muscle can be recognized on the external side of the ramus: the masseteric fossa. The masseteric ridges define the boundaries of the masseteric fossa. These ridges may extend far anteriorly until the level of the first lower cheek tooth. The masseteric ridges merge at their messial end, so they define a "V". A inflation, called the masseteric tubercle, may be recognized at the point where both ridges merge. The cheek teeth are separated from the incisor by a large diastema. The mental foramen is situated close to the diastema. On the inner side of the corpus a tiny insertion scar for the mylohyoid muscle may be observed just below the tooth row. On the inner side of the ramus the insertion areas for the pterygoid muscles can be recognized as shallow to deep fossae on the articular (insertion area for the external pterygoid) and angular (insertion area for the internal pterygoid) apophyses. The temporal muscle is inserted in a depression between the tooth row and the ramus. The mandibular foramen situated behind the tooth row on the inner side of the ramus. The following measurements taken for rodent mandibles:

1. Length of the postcanine series at occlusal and alveolar level.
2. Symphysis height.
3. Height of mandibular body at the lingual side (perpendicular to the alveolar level), at the level of each one of the cheek teeth.
4. Breadth of mandibular body (perpendicular to mandibular height), at the level of each one of the cheek teeth.

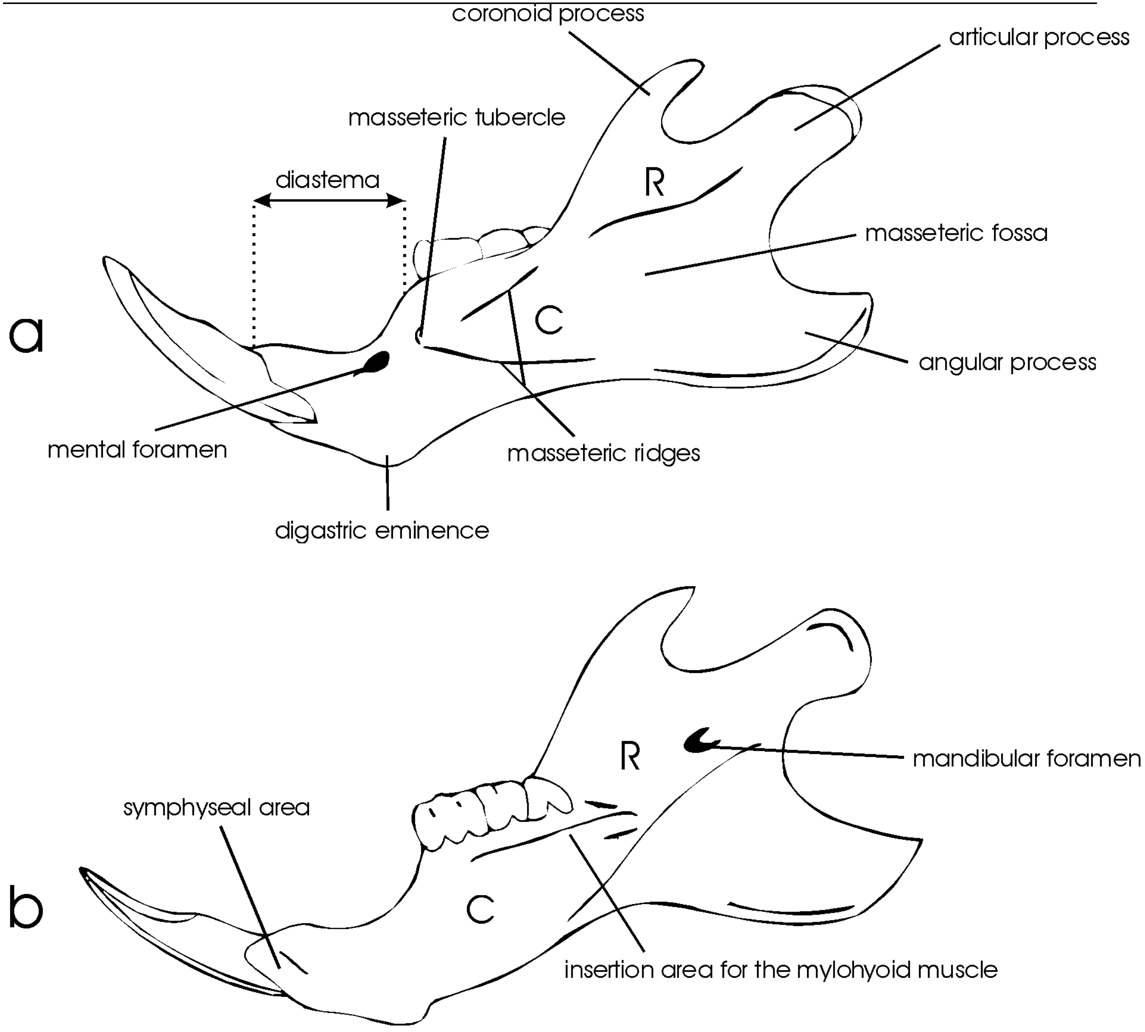


Figure 1.2. Nomenclature of elements of the mandible of rodents. a) Buccal view of a left mandible of *Rattus rattus* (rat). b) Lingual view of a right mandible of *Rattus rattus*. R = Ramus; C = Corpus. The figures are not to scale.

Rodent incisors are very common in screen-washed samples. However, since they are often found isolated it is really difficult to ascribe them to any of the species identified on the basis of cheek teeth. We have only described the incisors still inserted into the mandibles or found in close association to cheek teeth series. For the incisors up to four measurements have been taken (see fig. 1.3.). Nevertheless, in the case of the incisors still inserted into the mandibles the total length of the incisor (L in fig. 1.3.) could not be measured. The degree of curvature, the shape of the wear surface, the extension of the enamel into the lateral side and the ornamentation of the enamel on the anterior surface of the rodent incisors are the main diagnostic characters noted in their description. The enamel ornamentation may consist on parallel longitudinal ridges or grooves.

1.3.3. Family Sciuridae

Main anatomical characteristics

The sciurid skull is sciuromorphous and the rostrum is generally short. There are postorbital processes preceded by small knotches. The auditory region is relatively

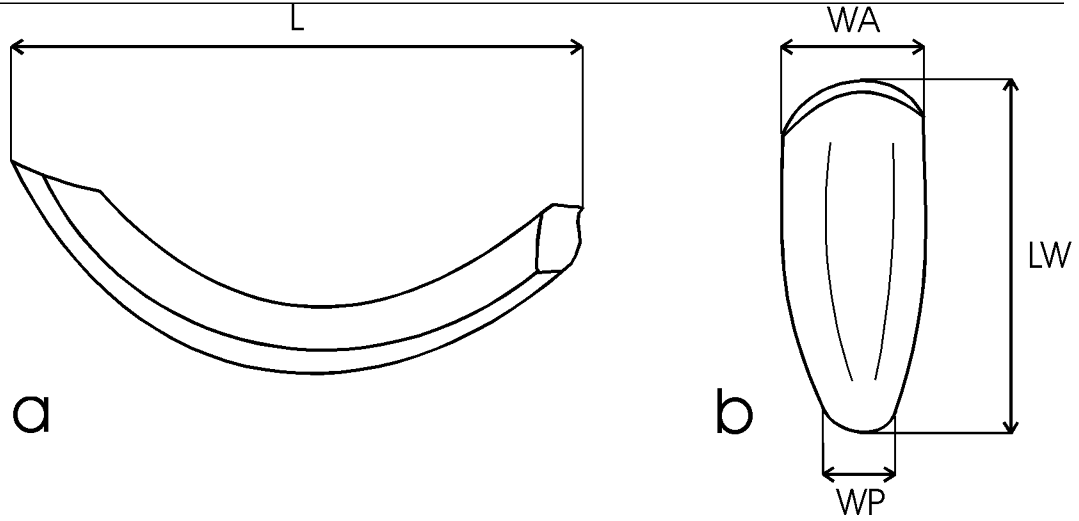


Figure 1.3. Measurements taken for rodent lower incisors. a) Buccal view of a left rodent incisor. b) The tip of the same incisor in occlusal view. L = Total length of the incisor; LW = Total length of the wear facet; WA = Anterior width of the wear facet; WP = Posterior width of the wear facet.

specialized (Lavocat & Parent, 1985). The presence of a distinct meato-cochlear bridge and a functional stapedial artery are characteristic of sciurids. The mandible is sciurognathous, with the anterior end of the masseteric fossa reaching the level of P_4/M_1 junction. The angle of the mandible is generally curved inward. The dental formula of the Sciuridae is $\frac{1-0-2/1-3}{1-0-1-3}$ although many genera have lost the third upper premolar. The incisors are generally compressed and possess uniserial enamel. Cheek teeth are rooted and usually brachyodont. The dental pattern of the upper cheek teeth presents three main cusps (protocone, paracone and metacone), while lower cheek teeth present four main cusps (metaconid, protoconid, hypoconid and entoconid) (see fig. 1.4.). The cusps on the lower cheek teeth, and particularly the entoconid, tend to be weak except in certain flying squirrels.When present, P^3 is either a conical and functional cutting tooth or a peg-like one, as in chipmunks and tree squirrels.

The axial skeleton is quite conservative and the tail is usually long (including 15-26 vertebrae). There are different ratios between the bones of the limbs and those of the digits in different groups of squirrels according to their type of locomotion (arboreal or terrestrial) (Vianey-Liaud, 1985). From their earliest history three adaptive types are recognized among squirrels: the ground squirrels (burrowing and diurnal), the tree squirrels (arboreal and diurnal) and the flying squirrels (arboreal and nocturnal) (De Bruijn, 1999). The flying squirrels present a characteristic patagium for gliding locomotion which is supported by a long cartilage attached to the carpals.

Origin, diversity and classification of the Sciuridae

Squirrels first appear in Europe as immigrants of the Grande Coupure at the beginning of the Early Oligocene (Vianey-Liaud, 1974) together with the probably related Aplodontidae. Sciurids are believed to have evolved from North American ischyromyids and later dispersed into Europe (but see Heissig, 2003 for a different interpretation). The oldest known squirrels from North America, namely *Douglassia* and *Protosciurus* (Emry & Korth, 1996), are recorded on the Early Oligocene. Both genera are protrogomorphous, while the zigomasseteric structure of the first European

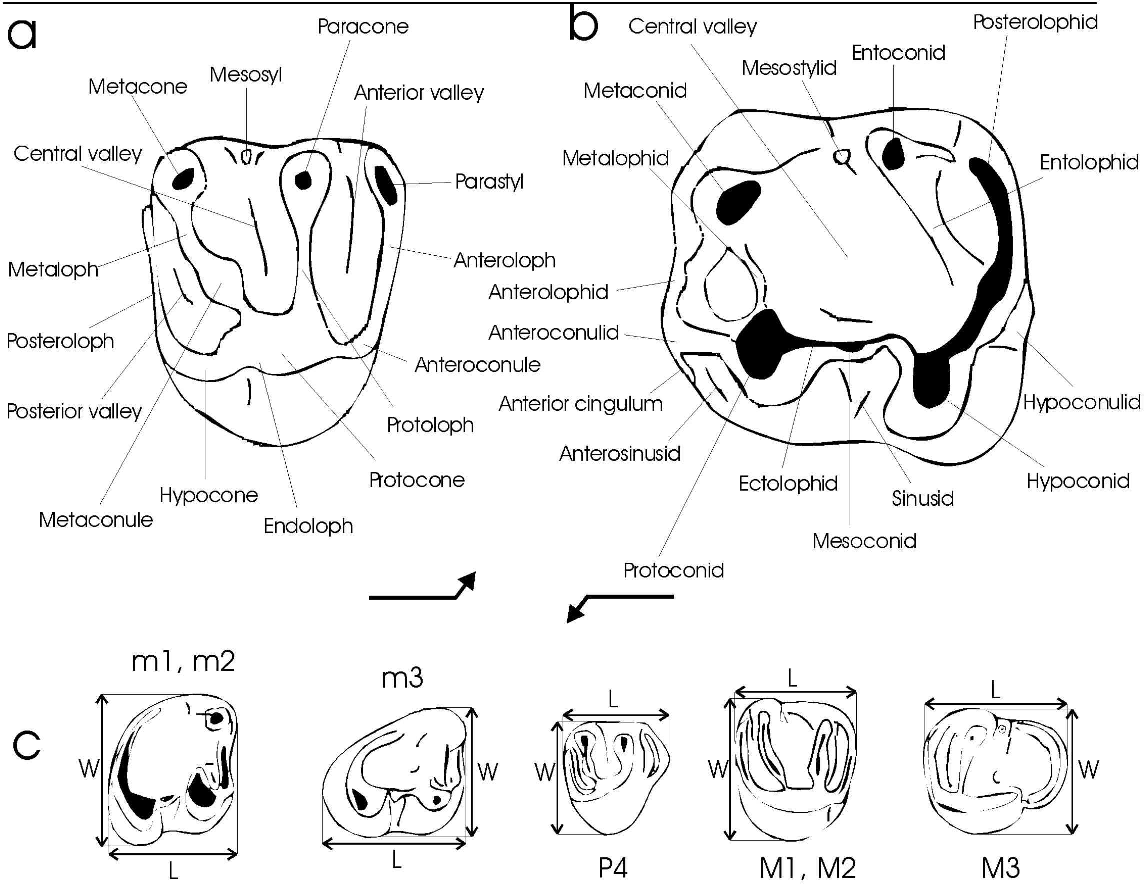


Figure 1.4. Nomenclature of dental morphology and measurement method for the cheek teeth of the Sciuridae. a) Nomenclaure of morphological elements for upper cheek teeth; b) for lower cheek teeth. The arrows point towards the mesiobuccal corner of the teeth. c) Measurement method for isolated cheek teeth. Upper-case letters indicate upper cheek teeth while lower-case letters indicate lower cheek teeth. L = mesiodistal length; W = buccolingual width. a) and b) modified after Aldana Carrasco, 1991 (fig. 2); c) modified after Van de Weerd, 1976 (fig. 27, p. 152).

squirrel, *Palaeosciurus goti*, is clearly sciuromorphous as in all other members of the family (Vianey-Liaud, 1974, Vianey-Liaud, 1985). The postcranial skeleton of *Douglassia* shows that it was arboreal (Emry & Thorrington, 1982). The oldest record of flying squirrels (*Oligopetes* from the MP 22 of Germany) in Europe are also Early Oligocene in age (Heissig, 1979). The interrelationships among the flying squirrels united as Pteromyinae (ranked to the family level and named Petauristidae after certain authors) are inadequately understood. De Bruijn (1999) has proposed that this family is in fact polyphyletic. However, molecular studies (Mercer & Roth, 2003) have provided a strong support for flying squirrel monophyly suggesting that they evolved from a particular group of tree squirrels (comprising most of the New World tree squirrels).

De Bruijn (1999) has given several criteria for the distinction amongst the three adaptive types of squirrels (see above) on the basis of the morphology of their cheek teeth. However, the validity of these dental traits has been questioned by Thorington *et al.* (2005) who focussed on flying squirrels. These authors compared the diagnostic features of the cheek teeth of flying squirrels and compared them to those of other squirrels, demonstrating that the features that have been used to distinguish fossil flying squirrels are also found in some tree squirrels. According to Thorrington *et al.* (2005) recent flying squirrels present a number of distinguishing morphological features in their carpal and tarsal bones and at the proximal and distal ends of their long bones. some of these morphological structures are obligatory features required for gliding locomotion in squirrels and hence are diagnostic of flying squirrels. In this work we will still retain the fossil species of putative flying squirrels in the subfamily Pteromyidae, although we assume that a study of the postcranial material of these species (if available) should either confirm or discard their attribution to this subfamily.

McKenna & Bell (1997) recognize three subfamilies within the Sciuridae: Cedromurinae, Sciurinae and Pteromyinae. The Cedromurinae include Late Eocene to Early Oligocene primitive forms from North America (*Oligospermophilus*, *Cedromus*) The Pteromyinae only include flying squirrels, while the ground and tree squirrels are distributed amongst numerous tribes within the Sciurinae. The molecular studies by Mercer & Roth (2003) have recognized the existence of three main clades: a clade comprising the flying squirrels (Pteromyinae) and certain tree squirrels (*Sciurus*, *Microsciurus* and *Tamiasciurus* amongst others); a second clade embracing the morphologically diverse array of tree squirrels in the Indo-Malayan region (traditionally placed together in the tribe Callosciurini = Nannosciurini); and a third clade including two distinct tribes of ground squirrels, the Holartic Marmotini (including *Spermophilus* and *Tamias*) and the African and Central Asian Xerini (including *Xerus* and *Atlantoxerus*), plus all the tree squirrels of Africa as well as the Chinese rock squirrel *Sciurotamias*. The genera *Ratufa* (Indian giant squirrel) and *Sciurillus* (Neotropical pygmy squirrel) appear as unrelated outgroups to the rest of the squirrels. Accordingly, Mercer & Roth (2003) suggest that these genera diverged early in the history of the Sciuridae. Part of these results fit with the classification of McKenna and Bell (1997) while others clearly do not. In this work the classification of squirrels is based on McKenna & Bell (1997) (see table 1.1.).

1.3.4. Family Castoridae

Main anatomical characteristics

The castorids are characterized by a generally low, broad and robust skull. The zygomatic arch is also broad and the zygomasseteric structure is sciuromorphous, with the infraorbital foramen low in the rostrum. The skull lacks the postorbital processes present in the Sciuridae. The interorbital foramen is posterior to the optic foramen. The mandible is sciurognathous and shows a digastric eminence which may be quite developed. The dental formula is $\frac{1-0-2/1-3}{1-0-1-3}$ and the cheek teeth are lophodont, forming series of transverse or oblique re-entrant valleys which evolve into elongated fossettes of enamel as wear progresses. The cheek teeth are mesodont to very hypsodont. The dP^3 and P^3 are only present in the subfamily Agnotocastorinae. Castorids are intermediate- to large-sized rodents, with robust or massive skeletons. Some lineages have developed fossorial or semiaquatic adaptations.

There are different interpretations concerning the homologies of the tubercles and lophs of the castorid cheek teeth (for a review of the alternative interpretations see Hugueney, 1999). The different patterns of Neogene castorids (tetralophodont in castorines, and lamellar or S-patterns in castoroidines) appear to be derived from a primitively pentalophodont pattern ("*Theridomys* plan", where the lophs are numbered 1, 2, 3, 4, 5 and the synclines I, II, III, IV from mesial to distal) (Stehlin & Schaub, 1951). According to this interpretation, the second syncline has disappeared, by fusion

- Family Sciuridae Fischer de Waldheim, 1817
    - † Subfamily Cedromurinae Korth & Emry, 1991
    - Subfamily Sciurinae Fischer de Waldheim, 1817
        - Tribe Sciurini Fischer de Waldheim, 1817
            - † *Douglassia* Emry & Korth, 1996
            - † *Protosciurus* Black, 1963
            - *Sciurus* Linnaeus, 1758
        - Tribe Xerini Murray, 1866
            - † *Heteroxerus* Schaub, in Stehlin & Schaub, 1951
            - *Atlantoxerus* Forsyth Major, 1893
            - *Xerus* Hemprich & Ehrenberg, 1832
        - Tribe Marmotini Pocock, 1923
            - † *Palaeosciurus* Pomel, 1853
            - *Marmota* Blumenbach, 1779
            - † ***Spermophilinus*** De Bruijn & Mein, 1968
            - *Spermophilus* F. Cuvier, 1825
            - *Tamias* Illiger, 1811
        - Tribe Ratufini Moore, 1959
            - *Ratufa* Gray, 1867
        - Tribe Nannosciurini Forsyth Major, 1867
            - *Callosciurus* Gray, 1867
            - *Rhinosciurus* Gray, 1843
        - Tribe Protoxerini Moore, 1959
        - Tribe Funambulini Pocock, 1923
        - Tribe Tamiasciurini Pocock, 1923
            - *Tamiasciurus* Touessart, 1880
    - Subfamily Pteromyinae Brandt, 1855
        - † *Oligopetes* Heissig, 1979
        - † ***Miopetaurista*** Kretzoi, 1962
        - † *Blackia* Mein, 1970
        - † *Forsythia* Mein, 1970
        - † *Albanensia* Daxner-Höck & Mein, 1975
        - *Pteromys* G. Cuvier, 1800
        - *Hylopetes* Thomas, 1908
        - *Glaucomys* Thomas, 1908

Table 1.1. Classification of the family Sciuridae used in this work (see text for details). The genera that appear in the systematic part of this work (chapter 4) are in bold. Other genera mentioned in the text are also included.

of the paracone and the mesoloph as revealed by the Oligocene and Early Miocene castorines of the genus *Steneofiber* (Hugueney, 1975). Consequently, the second loph of the tetralophodont castorines corresponds to the protoloph plus the mesoloph. The dental nomenclature follows Hugueney (1999) and additional fossetes/ids are named as proposed by Crusafont *et al.* (1948) (see fig. 1.5.). Because of their marked hypsodonty the morphology of many castorid cheek teeth changes with increasing wear (the flexi become closed and define fossetes and the striae become shorter or disappear). The measurements of the occlusal surface of the teeth may also vary according to wear because in many genera teeth are not cylindrical but rather piriform. Accordingly, wear stages have been defined by certain authors (Crusafont *et al.*, 1948; Aldana Carrasco, 1991) for some genera in order to facilitate the description and comparisons of cheek teeth. The wear stages defined by Aldana Carrasco (1991) for *Chalicomys* are the ones used in this work (see figure 1.6.). For all the cheek teeth we measured mesiodistal length (L) and buccolingual width (W) at the occlusal surface; for isolated teeth we also measured maximum crown height (at the hypostria/-iid side) (H), as well as hypostria/-iid height (HH) from crown base (see fig. 1.5.). Variations in the shape and

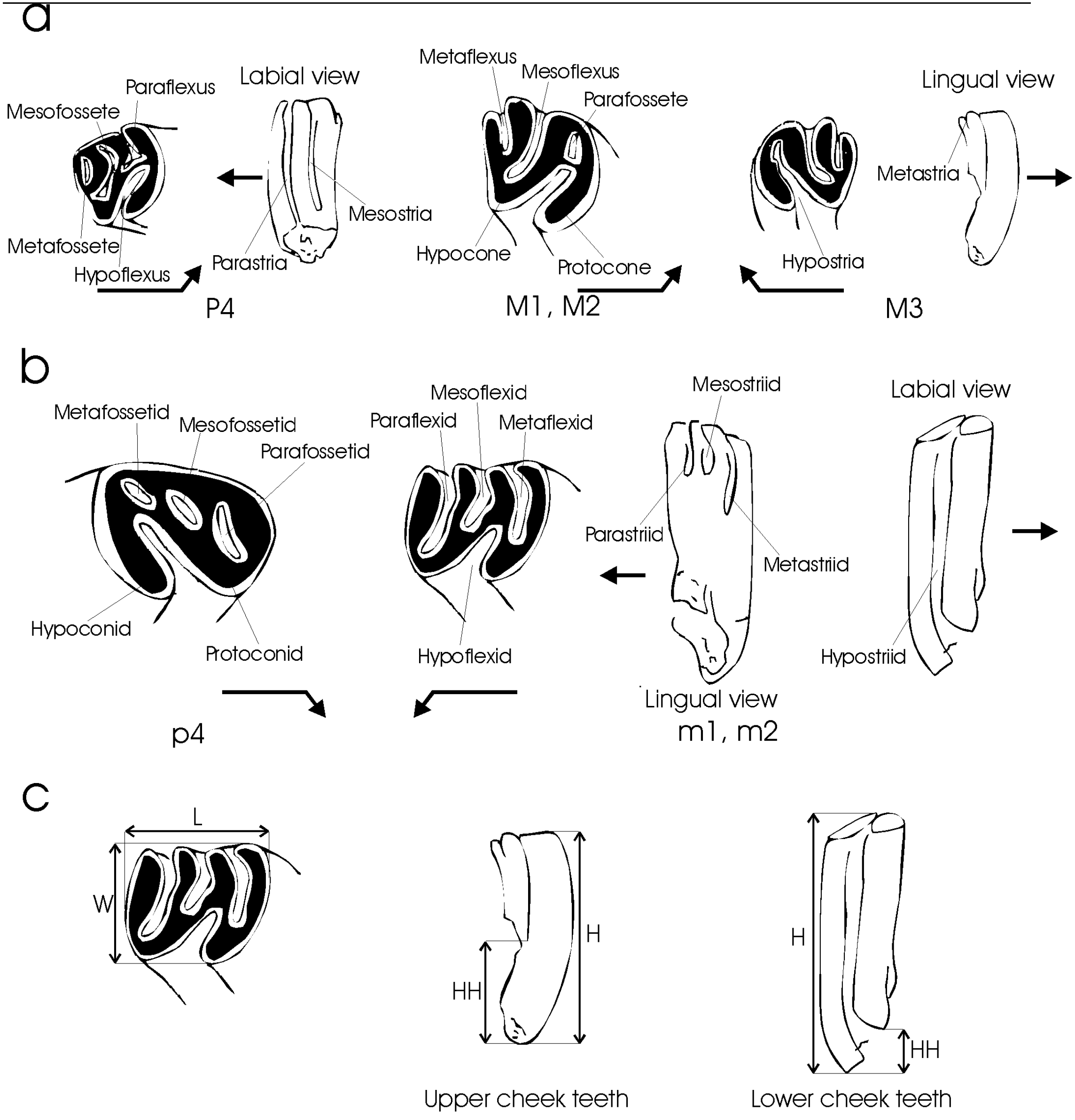


Figure 1.5. Nomenclature of dental morphology and measurement method for the cheek teeth of the Castoridae. a) Nomenclaure of morphological elements for upper cheek teeth; b) for lower cheek teeth. The arrows point towards the mesiobuccal corner of the teeth in occlusal view, and towards the mesial side in buccal and lingual views. Upper-case letters indicate upper cheek teeth while lower-case letters indicate lower cheek teeth. c) Measurement method for isolated cheek teeth. L = mesiodistal length; W = buccolingual width; H = maximum high of the crown at the hypostria/-iid side; HH = hypostria/-iid high from the base of the crown. All figures modified after Aldana Carrasco, 1991 (fig. 1).

ornamentation of the incisors, and particularly of the lower incisor, where given a great taxonomic value by Stirton (1935); nevertheless other authors (such as Korth, 2001) question the validity of these characters.

In this work we describe a castorine femur and dentognathic material. The nomenclature for the elements of the femur is presented in figure 1.7 In the case of the diaphysis we measured the anterioposterior and mediolateral diameters. In the case of the femoral head and neck the anterioposterior and the dorsoventral diameters were taken.

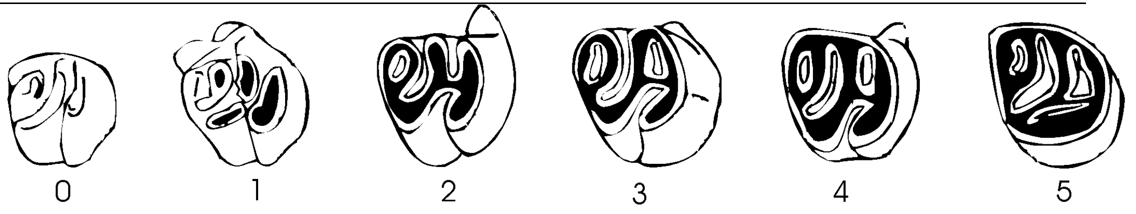
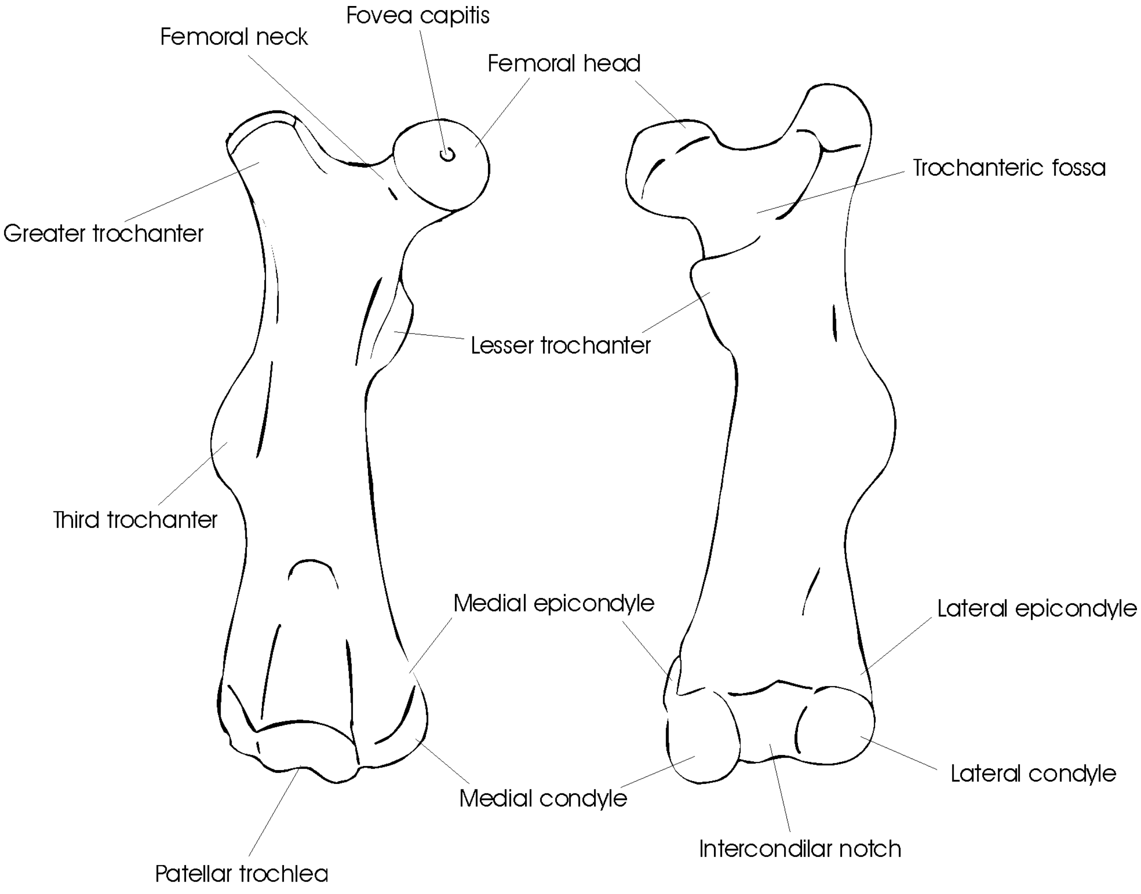


Figure 1.6. Successive wear stages in the beaver *Chalicomys* after Aldana Carrasco (1991). The P^4 of *Chalicomys catalaunicus* (see chapter 3) is given as example. Wear stages are as follows: 0) unworn; 1) moderately worn, no fossetes defined; 2) a single fossete (or fossetid in the lower cheek teeth) is present; 3) two fossetes are present; 4) three fossetes are present; 5) the wear nearly reaches the base of the crown. The figures are not to scale. Figures modified after Crusafont *et al.* , 1948 (fig. 11., p. 371).

Figure 1.7. Nomenclature of the elements of a castorine femur illustrated by a right femur of the extant *Castor canadensis*. Left: anterior view. Right: posterior view. The figures are not to scale.



Origin, diversity and classification of the Castoridae

Beavers are an exclusively Holartic family that has never invaded southern continents. At the present time they are only represented by the two species (or subspecies according to different authors) of the genus *Castor*, but their fossil record suggest a higher diversity during most of the history of this family. The Castoridae originated in the latest Eocene of North America (Korth, 2001). The rodent family believed to be the closest sister-group to the castorids is the Eutypomyidae, which are unknown from Europe and which display brachyodont and highly complex cheek teeth. The primitive castorids of the subfamily Agnotocastorinae (Late Eocene to Late Miocene of North America, and Oligocene to Late Miocene of Eurasia) share a number of sinplesiomorphies with the eutypomyids.

Simpson (1945) was the first to present formally a classification of the family, which was divided into two subfamilies: Castorinae and Castoroidinae. Martin (1987) presented a review of the "burrowing" beavers from the Arikareean (Early Oligocene) of North America, referring them to a new subfamily, the Palaeocastorinae. McKenna & Bell (1997) included all the castorid genera into the two subfamilies recognized originally by Simpson (1945). More recently Korth (2001) proposed a division of the family into four distinct subfamilies: Agnotocastorinae, Palaeocastorinae, Castoroidinae and Castorinae. The classification proposed by Korth (2001) is the one used in this work (see table 1.2.).

The first beaver that appears in Europe is the castorine *Steneofiber* from the Early Oligocene (Hugueney, 1975). All the subfamilies except the paleocastorines are also recorded from Europe. The agnotocastorines are represented by the genus *Anchitheriomys* and are clearly recognized by their great complexity of the occlusal pattern of cheek teeth (with a great number of crenulations and fossetes), and by the retention of the dP^3, even though the definitive premolar has been lost. The anterior surface of the incisors presents parallel ridges. The upper tooth rows are parallel. The premolars are subequal in size to molars. The angular process of the mandible is laterally directed (Korth, 2001). The castoroidines and the castorines share a number of autapomorphies such as the upper tooth rows strongly divergent posteriorly; the loss of dP^3 and P^3; the fourth premolars largest than molars; the nasal bones extending posteriorly on dorsal rostrum to the same point as premaxillaries; or the grooved palatal surface (Korth, 2001). The cheek teeth of both castoroidines and castorines become progressively hypsodont. The castoroidines differ from the castorines by their medially-directed angular apophysis. The castoroidines include the largest castorids that have ever existed, such as the North American Pleistocene giant beaver *Castoroides*, an animal of the size of a black bear. The smallest castorids, the genera *Monosaulax* and *Euroxenomys*, are also part of the castoroidines. Korth (2001) divides the Castoroidinae into two tribes: Castoroidini and Trogontheriini. The Castoroidini show a tendency towards an S-pattern in their cheek teeth and are recorded in North America since the Early Miocene and in Europe since the Late Miocene (*Dipoides*). Hugueney (1999) considered the genus *Schreuderia* from the Late Vallesian of the Vallès-Penedès Basin (Aldana Carrasco, 1991; 1992) to be a subgenus of the North American *Eucastor*. In the opinion of Korth (2001) *Schreuderia* is a Castorine and not a Castoroidine (see discussion in chapter 3). The Trogontheriini include the genus *Trogontherium* from the Pleistocene and the small-sized *Euroxenomys* which is commonly recorded on Miocene sites (MN 4 to MN 12/MN 13) (Hugueney, 1999). The Trogontheriini present a lamellar pattern in their cheek teeth and an elongated M^3. The subfamily Castorinae is first known from the early Oligocene of Europe. The members of this subfamily present increasingly hypsodont cheek teeth with a tetralophodont pattern. The flexi on cheek teeth progressively remain open to the base of the crown, indicating longer striae. Some species present thin to developed layers of cement in the synclines of the cheek teeth. The skeleton is massive and presents adaptations for a semiaquatic lifestyle in many species (broadened limb bones and digits, broadened caudal vertebrae, the second toe of pes modified and used for grooming). The humerus and the femur are massive and broadened, with powerful insertion areas for the main muscles.

Family Castoridae Hemprich, 1820
† Subfamily Agnotocastorinae Korth & Emry, 1997
† Tribe Agnotocastorini Korth & Emry, 1997
† *Agnotocastor* Stirton, 1935
† Tribe Anchitheromyini Korth, 2001
† *Anchitheromys* Roger, 1898
† Subfamily Palaeocastorinae Martin, 1987
† *Palaeocastor* Leidy, 1896
† Subfamily Castoroidinae Allen, 1897
† Tribe Castoroidini, 1877
† *Monosaulax* Stirton, 1935
† *Eucastor* Leidy, 1858
† *Dipoides* Schlosser, 1902
† *Castoroides* Foster, 1838
† Tribe Trogontheriini Lyschev, 1973
† *Euroxenomys* Samson & Radulesco, 1973
† *Trogontherium* Fischer de Waldheim, 1809
Subfamily Castorinae Hemprich, 1820
† *Steneofiber* Geoffroy Saint-Hilaire, 1833
† ***Chalicomys*** Kaup, 1832
† *Schreuderia* Aldana Carrasco, 1992
Castor Linnaeus, 1758

Table 1.2. Classification of the family Castoridae used in this work (see text for details). The genera that appear in the systematic part of this work (chapter 3) are in bold. Other genera mentioned in the text are also included.

1.3.5. Family Gliridae

The Latin authors Plinius the Elder and Varron reported that *glires* (singular: *glis*) were considered as delicacies for Romans, who used to cook candied animals with honey. Accordingly the generic term *Glis* has a long history and was subsequently used by Linnaeus (1758) for naming the order Glires. Later, Thomas (1897) defined the family Gliridae (dormice) according to the type genus *Glis* Brisson, 1762 (the edible dormouse). Wahlert *et al.* (1993) used the name Myoxidae for the family because they argued that the name *Glis* Brisson, 1762 does not fulfill the requirements of the International Code of Zoological Nomenclature. Consequently McKenna & Bell (1997) used this family name in their classification of mammals. In 1998 the Commision on Zoological Nomenclature decided in favor of the use of Gliridae for preservation on Brisson's generic name *Glis* (Daams, 1999). Since *Glis* is the type genus of the family, this family should be named Gliridae according to the principle of coordination[10] (art. 36 ICZN, 1999).

Main anatomical characteristics

Glirids are sciurognathous and myomorphous (except for some early forms which are protrogomorphous and for the extant African genus *Graphiurus*, which is hystricomorphous). The skull is usually robust and the neurocranium is broadened. The tympanic bulla is large and divided by three complete radial septa in all living forms except *Glirulus*, which presents several septa (Wahlert *et al.*, 1993). The dental formula is $\frac{1-0-2/1-3}{1-0-1/0-3}$ although only the early subfamily Gliravinae retains the P^3. The enigmatic recent genus *Selevinia* does not present lower premolars and retains a deciduous fourth upper premolar. The cheek teeth are low crowned except in certain

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[10] Following the same principle Muirhead's Glirini (1819) should be the base for Gliridae instead of Thomas (1897), in accordance the authorship of the family name is attributed to Muirhead.

Miocene genera such as *Armantomys* which show a tendency towards hypsodonty. The cheek teeth pattern is defined by several low ridges which tend to be parallel. The main cusps cannot be distinguished in many genera The terminology of the elements of the cheek teeth and the measurement method used in this work follows Daams (1981) (see fig. 1.8.). Recent genera may be arboreal or ground dwelling (such as the mouse-tailed dormouse, *Myomimus*). All present long tails which are furry in arboreal species. One fossil species, *Glirulus* aff. *lissiensis* from the Late Miocene of France, presented a patagium similar to those of flying squirrels and used for gliding (Mein & Romaggi, 1991). Note that this species is referred by dental characters to the same genus as the living non-gliding Japanese species *Glirulus japonicus*. Many dormice are nocturnal and their eyes are large. The ones living in temperate regions hibernate, and this ability to winter dormancy is emphasized by their common name both in English (dormice) and German (Sibenschläfer). Dormice feed on fruit and seeds, although they also include small animals in their diets (particularly in the case of certain genera such as *Eliomys*).

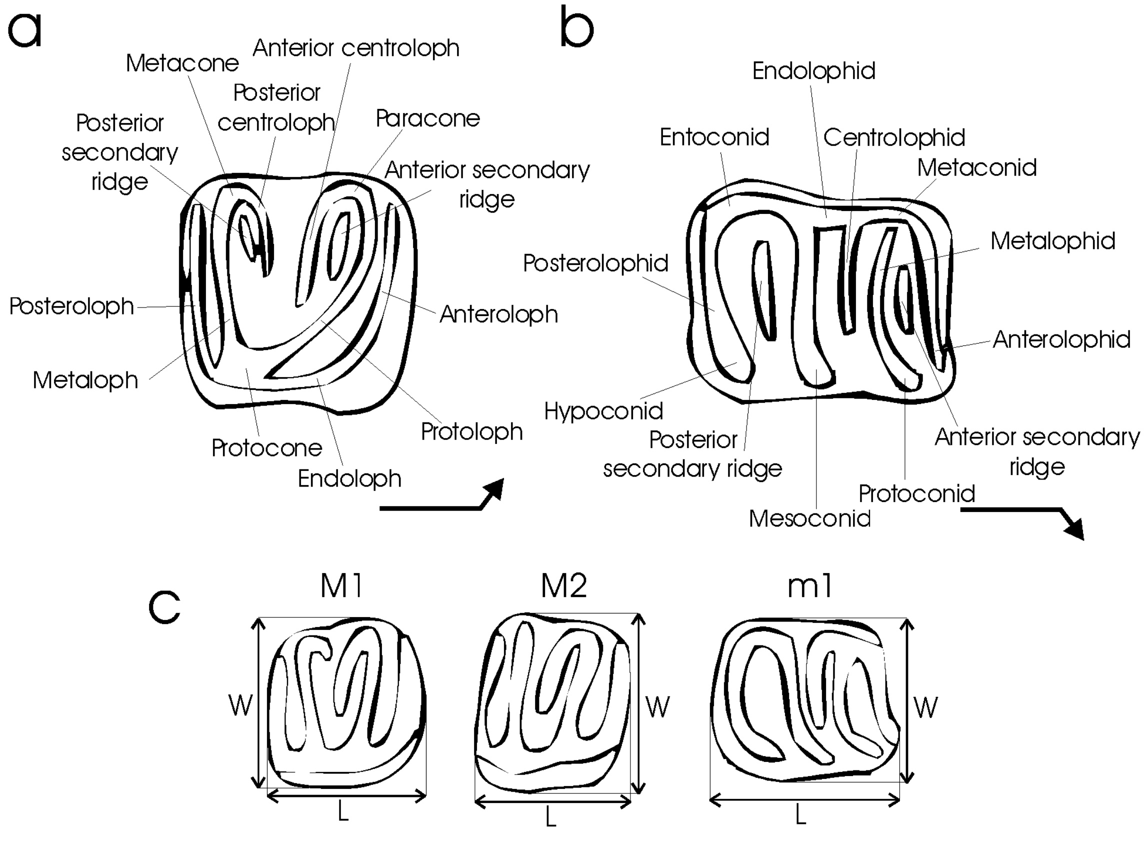

Figure 1.8. Nomenclature of dental morphology and measurement method for the cheek teeth of the Gliridae. a) Nomenclaure of morphological elements for upper cheek teeth; b) for lower cheek teeth. The arrows point towards the mesiobuccal corner of the teeth. c) Measurement method for isolated cheek teeth. Upper-case letters indicate upper cheek teeth while lower-case letters indicate lower cheek teeth. L = mesiodistal length; W = buccolingual width. a) and b) modified after Daams, 1981 (fig. 3., p. 18); c) modified after Daams, 1981 (fig. 2, p. 18).

Origin, diversity and classification of the Gliridae

The Gliridae are a monophyletic family that is represented by only 27 species in the extant fauna. The geographic range of the family (both fossil and extant) is limited to Europe, Asia and Africa. It is one of the oldest extant rodent families with a fossil record dating back to the Early Eocene. The living dormice are relics of a once very successful and diverse family. Glirids are always present in European Paleogene rodent assemblages, but almost never dominant. In the Early Miocene a massive adaptive radiation took place in Europe and they defined there the major part of many rodent assemblages (Hartenberger, 1994; Daams & De Bruijn, 1995; Daams, 1999). Their diversity and relative abundance in fossil rodent assemblages started to decline by the Middle Miocene and reduced markedly by the late Middle Miocene (Hartenberger, 1994; Daams & De Bruijn, 1995; Daams, 1999). From the Turolian (Late Miocene) onwards the Gliridae are represented in Europe Asia and Africa by a few genera only, excluding the insular forms, a situation that has essentially continued until the present.

As currently understood, the glirids descended in Europe from early Paleogene ischyromyids, and most probably from advanced small-sized microparamyines (Hartenberger, 1971; Hartenberger, 1994; Escarguel, 1999; Dawson, 2003). The genus *Eogliravus* represents the earliest and most primitive glirid taxon which is known from isolated cheek teeth from several Early Eocene (MP 10) French sites and recently by a extraordinarily preserved specimen from Messel, Germany (early Middle Eocene) (Storch & Seiffert, 2007). The Messel specimen consists in a virtually complete and articulated skeleton, also preserving the outline of the pelage and the gut contents, of *E. wildi*. The postcranial morphology, the proportions of the limb segments, the bushy tail and the small body size (length of the body and tail about 12 cm) indicates that *E. wildi* was a gracile arboreal animal. The very large orbits suggest a nocturnal activity, while the preserved gut content consist of various vegetable matter (Storch & Seiffert, 2007). Therefore this early dormouse was well adapted to an arboreal or scrub environment, the major habitat of their recent relatives. The cheek teeth of the older species of *Eogliravus* still show a paramyid-like pattern with cusps higher than those of later glirids, low and interrupted crests and a well marked hypocone (Hartenberger, 1971). The zygomasseteric structure is protrogomorphous and there is no distinct anterior bony processes for the insertion of the superficial masseter. The Eocene and Early Oligocene genus *Gliravus* is also protrogomorphous (Vianey-Liaud, 1985; 1989). In another Eocene genus, *Glamys*, Vianey-Liaud (1989) has observed that the zygomatic plate was tilted upwards and the infraorbital foramen enlarged. This author designates this condition, which is also exhibited by most glirids, as “pseudo-myomorphous” because it is not homologous to the myomorphous condition of muroid rodents. The particular myomorphous condition of extant glirids differs from that of muroids because the infraorbital foramen is rather small as compared to that of muroids. Therefore, glirids should not be included together with muroids and dipodoids within the suborder Myomorpha on the basis of this trait. Thaler (1966) considered the Gliroidea (Gliridae and Seleviniidae, see below) to be an early offshoot of primitive rodents, clearly separated from muroid ones. The taxonomic consequence was the proposal by Thaler (1966) of the suborder Glirimorpha. Despite this fact, McKenna & Bell (1997) place the infraorder Glirimorpha Thaler, 1966 within the suborder Myomorpha. The extant African dormouse *Graphiurus* exhibits a hystricomorphous condition which is thought to have derived from a protrogomorphous one. According to Hartenberger (1998) this point indicates that the origin of the *Graphiurus* group occurred early in the glirid history, during the Early Miocene or even earlier. This appreciation is markedly in contrast with molecular data, which suggest an early date for the divergence and radiation of *Graphiurus*, with the colonization of Africa by this lineage at ca. 8-10 Myr ago (Montgelard *et al.*, 2003). The subfamily Graphiurinae only include the genus *Graphiurus*, which is diversified into 14 species which inhabit subequatorial Africa. Many recent glirid genera (such as *Glis*, *Muscardinus* or *Myomimus*) are recorded in the Middle Miocene, and may be considered "living fossils".

The classical systematic view for recent forms considers the Gliridae (including the subfamilies Glirinae and Graphiurinae) to be the sister group of the Seleviniidae and includes both families within the superfamily Gliroidea (Simpson, 1945; Grassé & Dekeyser, 1955). The Seleviniidae, which only include the genus *Selevinia* from a restricted desert area of east Kazakhstan (around the Lake Balkhash) (Holden, 1993), appear to be the most derived and specialized gliroids. The juveniles present a dP^4, while the adults only show a three single-rooted molars. Incisors are very large, and the auditory bulla is inflated as in many desert mammals (Grassé & Dekyser, 1955; Hartenberger, 1998). None of the recent morphological or molecular (Wahlert *et al.*, 1993; Daams & De Bruijn, 1995; Montgelard *et al.*, 2003) studies has included *Selevinia* because of its currently endangered status and restricted geographical range. Therefore there is not a strong support for their inclusion within the Gliridae as proposed by Wahlert *et al.* (1993). Wahlert *et al.* (1993) applied cladistic analysis to a matrix of 43 cranial and 11 dental characters of recent Gliridae (Myoxidae in Whalter *et al.*, 1993). Their results support the hypothesis that the Gliroidea are monophyletic and the sister taxon to the Muroidea and the Dipodoidea; these three superfamilies would define the suborder Myomorpha, which is considered monophyletic. Three subfamilies are distinguished by Wahlert *et al.* (1993): Graphiurinae; Leithiinae, consisting of the tribes Leithiini (*Eliomys* and *Dryomys*) and Seleviniini (*Myomimus* and *Selevinia*); and Glirinae (Myoxinae in Wahlert *et al.*, 1993). The classification of Gliridae by McKenna & Bell (1997) recognizes the tribe Seleviniini within the subfamily Leithiinae, which in its turn includes *Dryomys*, *Eliomys* and related forms. The Seleviniini are divided into two subtribes, the Seleviniina (including *Selevinia*) and the Myomimina, including *Myomimus*. These authors advocate for a division of the Gliridae (Myoxidae in McKenna & Bell, 1997) into four subfamilies: the extinct Gliravinae, the Graphiurinae, the Leithiinae and the Glirinae (Myoxinae in McKenna & Bell, 1997).

Recent molecular studies (Montgelard *et al.*, 2003) have identified three evolutionary lineages that broadly correspond to the three extant subfamilies recognized by Wahlert *et al.* (1993) and McKenna & Bell (1997). The classification by Wahlert *et al.* (1993) encompasses a broad suit of characters of recent Gliridae; however, there is no attempt to review the fossil taxa and only a few remarks regarding the protrogomorphous condition of *Gliravus* are made (Wahlert *et al.*, 1993: 25). Fossil genera represent most of the dormice diversity and should not be overlooked in any study regarding the relationships within this family. Several classifications which are based on the morphology of the cheek teeth have also considered the fossil forms (De Bruijn, 1967; Daams, 1981; Daams & De Bruijn, 1995). The most recent of this classifications is that by Daams & De Bruijn (1995) which recognizes up to five subfamilies: Gliravinae, Glirinae, Dryomyinae, Myomiminae and Bransatoglirinae. Two of these subfamilies, the gliravines and the bransatoglirines, are known only from the fossil record. Daams & De Bruijn (1995) completely disagree with the conclusions of Wahlert *et al.* (1993), particularly on the revival of the nomen Leithiinae Lydekker, 1896 and Seleviinini Bashanov & Belosludov, 1939, to replace Dryomyinae de Bruijn, 1967 and Myomiminae Daams, 1981. These authors emphasize that the genus *Leithia* presumably has a sciuromorphous skull and an angular process of the lower jaw that is not perforated, therefore it does not match the requirements for Leithiinae (sensu Wahlert *et al.*, 1993). Accordingly, these authors revalidate the nomen Dryomyinae and include *Leithia* within this family. This decision may be a violation of the principle of priority since the genus *Leithia* is not transferred to any different subfamily by these authors; they just change the subfamily name. Leithiinae has priority over Dryomyinae and the latter nomen should be considered a junior synonym. The genus *Selevinia* is not considered by Daams & De Bruijn (1995) in their review, mainly because they did not have access to material of this genus. No material of this genus was available to Wahlert and co-workers (1993), nevertheless these authors revalidate the nomen Seleviniini Bashanov and Belosludov, 1896. Wahlert *et al.* (1993) point out several characters (extracted from the drawings and original descriptions of the genus) that allow the inclusion of *Selevina* not only within the Gliridae, but also emphasize a close relationship to *Myomimus* on the basis of three sinapomorphies: relatively long incisive foramina, rather small infraorbital foramen and tail covered with short hairs. *Selevina* lacks the premolars in the adult, while in *Myomimus* the premolars are somewhat reduced (Wahlert *et al.*, 1993). Storch (1995) has also suggested a close relation between both genera on the basis of similar dental and cranial characters. In our opinion *Selevina* is insufficiently known, and a detailed revision of the original material should be undertaken before assigning it to any of the recognized subfamilies of the Gliridae (or even to the family Gliridae). Therefore, the tribe Selviniini of Wahlert *et al.* (1993) only includes the extant *Myomimus* besides several fossil genera. If *Selevinia* is excluded this tribe should be named Myomimini Daams, 1981. *Graphiurus* was included by Daams & De Bruijn (1995) within the Dryomiminae, although morphological and molecular data seem to indicate that it should better be placed in a separate family: the Graphiurinae. In our opinion the dental characters listed by Daams & De Bruijn (1995) do not justify the creation of a distinct subfamily for the genus *Bransatoglis*. Daams & De Bruijn (1995) note that none of the dental features occurs exclusively in the Bransatoglirinae, although their combination is characteristic (Daams & De Bruijn, 1995: 25). Daams (1981) had assigned *Bransatoglis* to the Dryomiminae (= Leithiinae); however these authors state: "new information clearly demonstrates its independent evolutionary history [from the Dryomyinae]. We therefore think that the systematic position of the group within the dormice is best expressed by formally giving it the rank of subfamily" (Daams & De Bruijn, 1995: 25). We believe that these arguments are not convincing and therefore is preferable to follow Daams (1981) and place *Bransatoglis* within the Leithiini in the Leithiinae (= Dryomyinae of Daams, 1981). The classification of the dormice used in this work is presented in table 1.3. The basis of this classification is a combination of the diagnostic characters recognized by Wahlert *et al.* (1993) and Daams & De Bruijn (1995). Nevertheless, we must note that we introduce this classification mainly for practical reasons and because any of the recently proposed classification is found to be fully satisfactory. We sincerely expect that future "formal" classifications of the Gliridae will take into account whatever is known on the cranial morphology of fossil dormice and will tend to reconcile those classifications based on cranial and dental morphology for this family of rodents.

Suborder Glirimorpha Thaler, 1966
    Family Gliridae Muirhead, 1819
        † Subfamily Gliravinae Schaub, 1958
                † *Eogliravus* Hartenberger, 1971
                † *Gliravus* Schaub, in Stehlin & Schaub, 1951
            Subfamily Glirinae Muirhead, 1819
                Tribe Glirini Muirhead, 1819
                    Glis Brisson 1762
                Tribe Muscardinini Palmer, 1899
                    † ***Glirudinus*** De Bruijn, 1966
                    † *Myoglis* Baudelot, 1966
                    Muscardinus Kaup, 1829
                    † *Paraglirulus* Engesser, 1972
                    Glirulus Thomas, 1906
            Subfamily Leithiinae Lydekker, 1896
                Tribe Leithiini Lydekker, 1896
                    † ***Bransatoglis*** Hugueney, 1967
                    † ***Microdyromys*** De Bruijn, 1966
                    † *Tempestia* Van de Weerd, 1976
                    Eliomys Wagner, 1840
                Tribe Myomimini Daams, 1981
                    † *Peridyromys* Schaub, in Sthelin & Schaub, 1951
                    † *Miodyromys* Kretzoi, 1943
                    Myomimus Ognev, 1924
                    † *Armantomys* De Bruijn, 1966
                    † *Ramys* García Moreno & López Martínez, 1986
            Subfamily Graphiurinae Winge, 1887
                    Graphiurus Smuts, 1832
            Gliridae ? incertae sedis
                † *Plioselevinia* Sulimski, 1962
                Selevinia Belosdulov & Bashanov, 1939

Table 1.3. Classification of the family Gliridae used in this work (see text for details). The genera that appear in the systematic part of this work (chapter 4) are in bold. Other genera mentioned in the text are also included.

1.3.6. Superfamily Muroidea

Content of the superfamily Muroidea

The content and classification of the muroid rodents represents a major problem for both paleontologists and neontologists. This group has been treated variously as a family (family Muridae), with the major groups arranged as subfamilies, or as a superfamily (superfamily Muroidea), with groups raised to the familial status. Most paleontologists (see for example Flynn *et al.*, 1985; Jacobs, 1994; Hartenberger, 1998; Freudenthal & Martín Suárez, 1999) interpret the Muridae in a restricted sense, including this family (together with a dozen of families which include the Cricetidae, the Arvicolidae and the Gerbillidae) into the superfamily Muroidea. In their classification of mammals McKenna & Bell (1997) considered the broad definition of the family Muridae, ranking the major groups as subfamilies. This arrangement has been followed only by a limited number of paleontologists (see for example De Bruijn, 2001). McKenna & Bell (1997) include the superfamilies Dipodoidea (jumping mice, birch mice and jerboas) and Muroidea within the infraorder Myodonta (which in its turn is part of the suborder Myomorpha). Both superfamilies share a common dental pattern (the “cricetid plan” sensu Schaub, 1925), and close relationships between both groups have been suggested on the basis of morphological (Schaub, 1958; Emry, 1981; Flynn *et al.*, 1985; Luckett & Hartenberger, 1985) and molecular data (Huchon *et al.*, 2002). The main differences between both superfamilies imply the retention of the P^4 in most of the dipodoids (in the living dipodoid genus *Napeozapus* the P^4 is lost). The earliest muroids also retained a P^4 or dP^4 (see below). The zygomasseteric structure of the skull is hystricomorphous in the dipodoids, while all muroids, except the earliest ones (which are hystricomomorphous), present a myomorph zygomasseteric structure. The hystricomorphous condition shows a particularity in the case of dipodoids: a bony septum isolating a neurovascular canal occurs in the infraorbital foramen. As far as dentition and the zygomasseteric structure are concerned, the muroids appear to be more derived than the dipodoids.

According to McKenna & Bell (1997) the superfamily Muroidea includes two families: the Symimyidae and the Muridae. The Symimyidae are a family of Middle to Late Eocene North American muroids which only include two genera: *Simymys* and *Nonomys*. Both genera present a hystricomorphous skull with a separate neurovascular canal as in dipodoids but the muroid dental formula of only three upper and three lower molars. These genera have often been included within the Dipodoidea by certain authors (Emry & Korth, 1989; Wang & Dawson, 1994) on the basis of the particular structure of the infraorbital foramen, although dental features have been used to support the affinities of *Nonomys* with the muroids (Emry, 1981). We consider the Symimyidae to be part of the Dipodoids. If the symimyids are placed within the dipodoids the Muroidea only include the family Muridae in the classification after McKenna & Bell (1997). Therefore, we are inclined to regard the subfamilies included within the Muridae as families which would define the superfamily Muroidea. The superfamily Muroidea would include then more than 20 families (considering both fossil and extant ones). Many of these families include one or a few genera (such as the Platacanthomyidae [spiny dormice], the Anomalomyidae or the Spalacidae [mole rats]), while others encompass a considerable number of forms (the Muridae [Old World rats and mice] and the Sigmodontidae [New World rats and mice]). A high number of subfamilies and tribes exist in many cases (Sigmodontidae, Arvicolidae [voles and lemmings], Muridae, Cricetodontidae).

Main anatomical characteristics. The "cricetid plan"

The Muroidea are small- to medium-sized sciurognathous rodents (fossil insular forms attained considerable sizes). Muroids are distributed worldwide except for the Antarctica. Certain families have a broad distribution that may cover the entire Old World (Muridae) or the whole Holartic region (Arvicolidae) for example. Many muroids are mouse-like, rather unspecialized rodents with long tails. However, a number of genera and families show adaptations for a fossorial life-style (such as the spalacids, the myospalacids [zokors], and many arvicolids) and are characterized by the presence of robust fore limbs with long claws or by the presence of enlarged incisors when these are also used for digging (this is particularly true for the spalacids which present robust and extremely protruding incisors which can be used for digging without the mouth having to be opened). The ears, eyes and tail are reduced in these fossorial forms. In the case of the recent blind mole rats (family Spalacidae) the eyes are completely and permanently hidden under their skin. Certain forms are adapted to a jumping locomotion (such as many Gerbillidae [jirds and gerbils] or the murid *Notomys* [hopping mouse]. These jumping muroids present elongated hind limbs and long tails that are used to keep balance. Finally, many other muroids are adapted to a semiaquatic life-style, such as the muskrat (*Ondatra zibethicus*; family Arvicolidae), the African swamp rats (genus *Malacomys*; family Muridae); or the South American fish-eating rats and mice (subfamily Ichthyomyinae). Many of these semiaquatic forms present webbed feet and laterally flattened tails used for swimming. All the muroids, except the earliest ones are myomorphous. Incisors, particularly the lower ones, are ornamented with thin parallel ridges on the lateral half of the anterior surface in many forms, such as in most of the older ones. Certain Oligocene genera, such as *Paracricetodon* or *Pseudocricetodon*, present pinnate ridging, consisting in multiple parallel ridges. Some species of *Eucricetodon* and many Miocene genera (*Eumyarion*, *Cricetodon*, *Hispanomys*) present two longitudinal ridges on the incisor, while the number of ridges is one in *Ruscinomys* and none in *Copemys*, *Megacricetodon* and many *Democricetodon* species. The incisor enamel is uniserial.

The Muroidea are characterized by the following dental formula $\frac{1-0-1/0-2/3}{1-0-0-2/3}$, although the occurrence of a P^4 (or dP^4) is only known to occur in one fossil species: the Middle Eocene *Pappocricetodon antiquus* from China (Wang & Dawson, 1994). The third molars, and particularly the upper ones, are very reduced in many muroids and they have even disappeared in some of them such as in the murid *Hydromys chrysogaster* (Australian water rat). In most muroids the molars are rooted, although a significant number of them (including most arvicolids and the gerbil *Rhombomys*) present unrooted, evergrowing molars. Muroids display the typical "cricetid plan" (Schaub, 1925) or variations of it because of the development of additional cusps or ridges. The "cricetid plan" basically consists in four major cups besides additional cusps (anterocone or anteroconid) at the messial part of the first molars (see fig. 1.9., for measurements taken see fig. 1.10c.). The first molars are generally the longest, while the third molars are reduced, particularly on their distal half. The second molars are square shaped. The lingual cups of the upper molars and the labial cusps of the lower ones display a more or less marked crescentic form an are linked by a longitudinal to oblique ridge. They are also joined to the opposite cusps by transverse or oblique ridges. Additional transverse ridges (mesoloph/id, posteroloph/id, etc.) may be also present. Primitively the upper molars are three-rooted (certain forms may develop additional roots). The M^1 and M^2 present a robust and flattened lingual root besides two cylindrical buccal ones. In the M^1 the mesiobuccal root, placed below the anterocone, is very long and points obliquely forward. The M^3 presents three cylindrical roots: two messial ones, besides a distal one that points backwards. The lower molars present only two roots: mesial and distal. These roots are always straight, robust and usually flattened, except in the case of the mesial root of the M_1 and the distal one of the M_3, which are cylindrical and oblique.

It seems appropriate to introduce here a number of terms that are commonly used in the description of muroid molars. The connection between opposite cusps may be attained by the means of an anterior ridge, a posterior ridge, a transverse ridge or a double one. Considering for example the paracone and the protocone, if the protolophule (see fig. 1.9a.) points obliquely forward and it is connected to the anterolophule in front of the protocone it is said to be "anterior". The "transverse" protolophule joins the paracone to the protocone. The "posterior" protolophule is connected to the longitudinal ridge or endoloph behind the protocone. The "double" protolophule presents an anterior and a posterior arm. The arms of the prolophule may present different degree of development and they may not be complete. Concerning the length of the

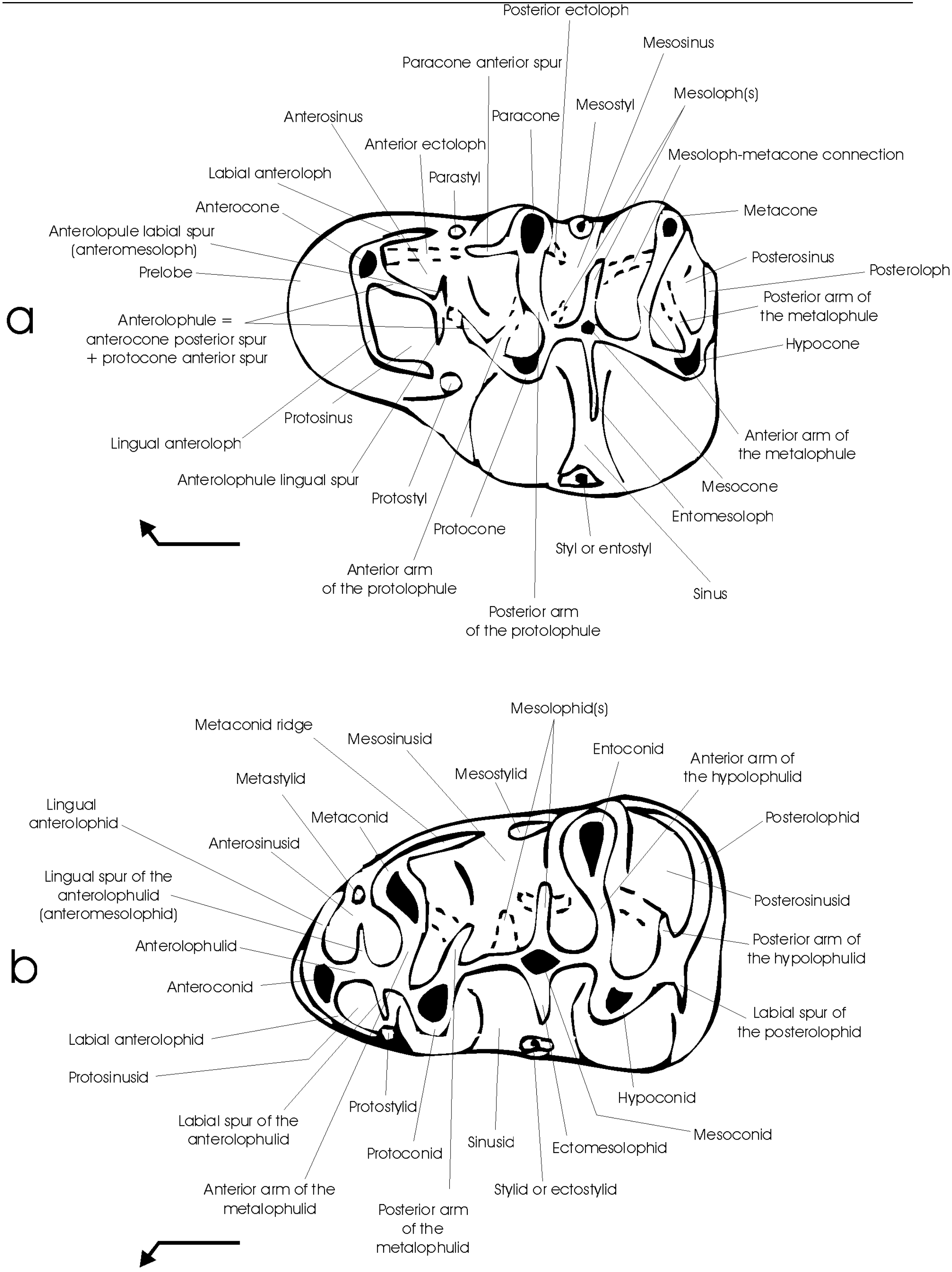

Figure 1.9. Nomenclature of dental morphology for the molars of the Muroidea. a) Nomenclaure for morphological elements of upper molars; b) for lower molars. The arrows point towards the mesiobuccal corner of the teeth. The terminology used for the description of the M^3 is presented in figure 1.10. All figures modified after Freudenthal *et al.*, 1994 (fig. 2., p. 61) and Mein & Freudenthal, 1971a (fig.1, p.3).

transverse ridges (mesoloph/-id, ectomesoloph/-id, posteroloph/-id, etc.) five situations exist: long, medium sized, short, vestigial and absent. Considering for example the mesolophid (see fig. 1.9b.), it is considered to be "long" when it reaches the lingual border of the molar. The "medium-sized" mesolophids comprise the stages which are more or less half the length of the mesosinusid. When the mesolophid can still be clearly recognized although it does not reach half the length of the mesosinusid it is said to be “short”. The “vestigial” mesolophid is recognized as a small protuberance of the longitudinal ridge. Finally, regarding the orientation of the valleys (particularly the sinus/-id) three different situations are described: proverse (the valley points obliquely forwards), transverse and retroverse (the valley points obliquely backwards).

The muroid M^3 is a moderately to highly reduced element in many forms. This often makes the interpretation and description of its morphology quite difficult, so even an specific terminology involving some of the M^3 morphological elements has been proposed by Freudenthal & Daams (1988) (see figs. 1.10a-b.). Many of the morphological elements were named by Freudenthal & Daams (1988) based in supposed homologies and interpretations that are not accepted by all paleontologists. Nevertheless, the use of this terminology seems appropriate in order to facilitate the descriptions, even if there is not a general agreement in the interpretation of the homologies. These morphological elements exclusive of the M^3 include the neo-entoloph, which is a short longitudinal connection between the protocone and the hypocone resulting from the rotation of the protocone. The centrocone may be an homologous of the mesocone. The centroloph is a more or less transverse ridge connecting the hypocone to the postero-buccal margin of the molar. Freudenthal & Daams (1988) proposed that the centroloph is derived from the fusion of the anterior metalophule and the distal part of the longitudinal ridge. The axioloph is an axial connection between the paracone and the hypocone, fundamentally composed of the posterior protolophule and the distal part of the ancient longitudinal ridge according to Freudenthal & Daams (1988).

The dental variation and evolution of the basic plan concerns the relative size of the teeth, the shape of the cusps and addition or simplification of ridges. Most muroid families have modified this pattern in an important way, and the basic “cricetid plan” is only found in some of the living cricetids, sigmodontids and nesomyids (family Nesomyidae, Malagasy mice and rats). For example the murids present a fully functional additional lingual row of cusps in their upper molars. In the lower ones a third row of usually lower cusps may be added labially. The longitudinal crest is lacking in the upper molars and very reduced (or lacking) in the lower ones. In the arvicolids the longitudinal ridge is retained with a zigzag arrangement of triangular cusps, but the number of cusps is greatly increased in many forms.

Origin, diversity and classification of the “cricetids”

Muroids first appeared in Asia during the Middle Eocene. These earliest muroids have been recovered from China and are assigned to the genus *Pappocricetodon*. *P. antiquus* from the Middle Eocene deposits in southeastern China presents uniserial incisor enamel pattern and a large and rounded infraorbital foramen with no vental constriction (Wang & Dawson, 1994). This is a hystricomorphous zygomasseteric structure that differs from that of dipodoids by the absence of the bony septum isolating the neurovascular canal (Wang & Dawson, 1994). On all the recovered maxillae there is a small circular alveolus just anterior to the anterobuccal alveolus of M^1, indicating the presence of a small P^4 or dP^4 that has not been recovered yet. The presence of this dental element is further evidenced by the presence of a small contact facet on the anterior surface of many M^1 (Wang & Dawson, 1994). The first molars are not

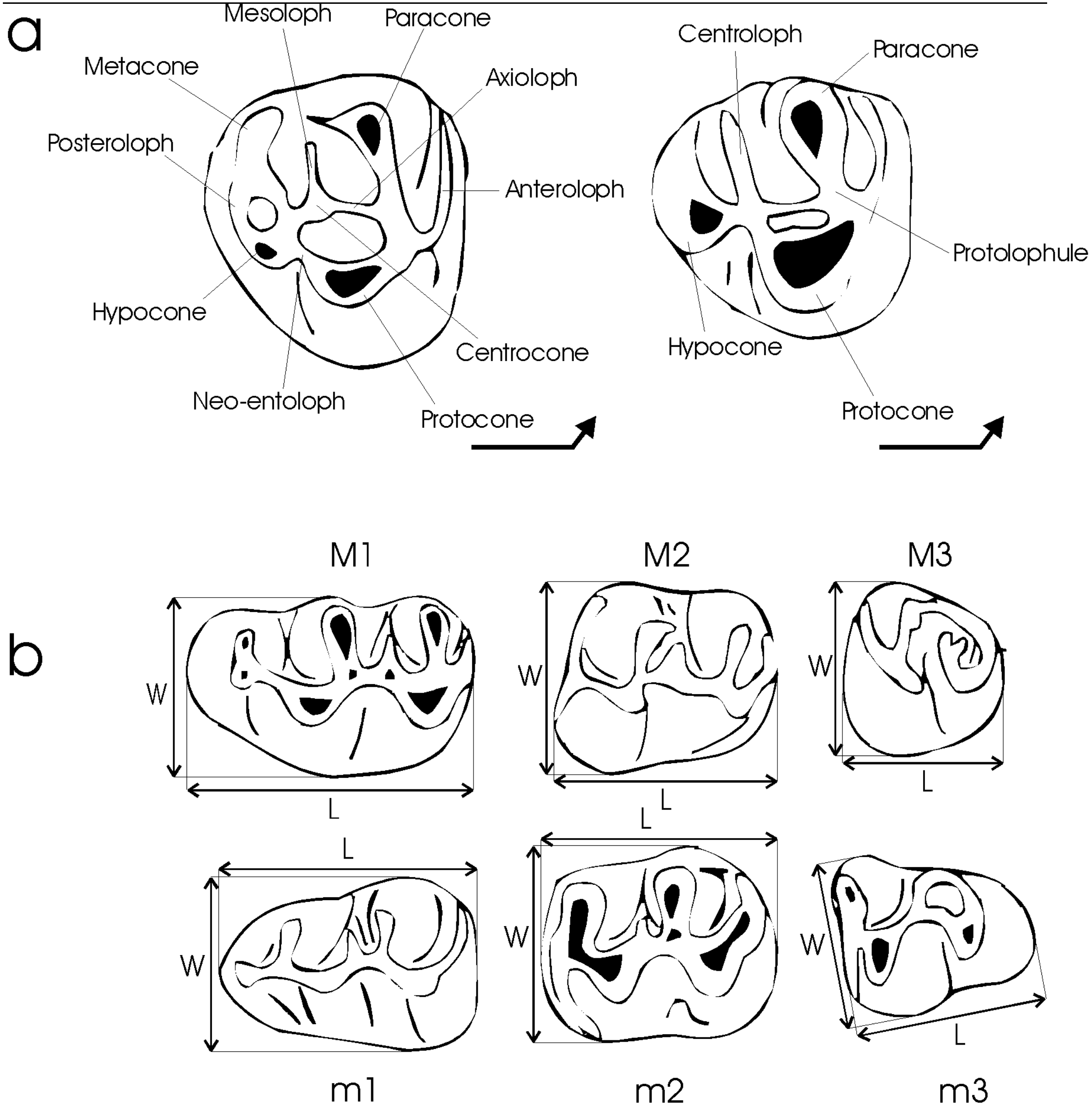

Figure 1.10. a) and b) Terminology of parts of the muroid M^3. The arrows point towards the mesiobuccal corner of the teeth. c) Measurement method for isolated muroid molars. Upper-case letters indicate upper cheek teeth while lower-case letters indicate lower cheek teeth. L = mesiodistal length; W = buccolingual width. a) and b) modified after Freudenthal & Daams, 1988 (fig. 3, p. 139); c) modified after Daams & Freudenthal, 1988b (fig. 1, p.42).

elongated, so their shape, particularly in the case of the M^1 is very similar to those of the second molars. The anterocone and the anteroconid are reduced. The dental pattern of these early muroids may be derived from that of sciuravids. Sciuravids are basically primitive rodents, combining the primitive dental formula (including two upper premolars besides a lower one) with a protrogomorphous zygomasseteric structure and a siurognathous mandible. Their incisor enamel is pauciserial. Certain Early Middle Eocene North American sciuravids (*Armintomys*, *Elimys*) are probably hystricomorphous and show a transitional incisor enamel from pauciserial to uniserial (Wang & Dawson, 1994). The P^3 has disappeared in *Elimys* and the P^4 is reduced, furthermore the upper molars are longer than wide and resemble those of *Pappocricetodon* and early muroids and dipodoids (Emry & Korth, 1989; Wang & Dawson, 1994). Therefore, the Sciuravidae are the most likely sister group to the Myodonta (Wang & Dawson, 1994).

Soon after their appearance in the Asian fossil record, the first muroids also occur in North America by the Late Eocene. These are referred to the family Eumyidae and are characterized by the presence of a ventrally constricted, myomorphous infraorbital foramen with a strongly inclined anterior plate (Flynn *et al*., 1985). The anterocone and the anteroconid are well developed and the first molars are elongated. By the same time a radiation of early muroids occurred during the Early Oligocene in Asia (Flynn *et al*., 1985; Lindsay, 1994; Wang & Dawson, 1994; Dawson, 2003) involving the appearance of many new genera such as *Cricetops* and *Eucricetodon*. These Asian genera still show an enlarged infraorbital foramen, more similar to that of hystricomorphous rodents (Flynn *et al*., 1985; Wang & Dawson, 1994), but the anterocone and the anteroconid are well developed. Evidence for a pre-Oligocene expansion of the range of cricetids into eastern Europe comes from the Late Eocene (Priabonian) of Romania, where *Pseudocricetodon* and *Atavocricetodon* have been found (Baciu & Hartenberger, 2001). *Pseudocricetodon* first occurs in Europe in the late Early Oligocene after the “Grande Coupure” (Vianey-Liaud, 1972; 1975; 1985; Hartenberger, 1989; Dawson, 2003). By the Middle Oligocene several muroid genera (such as *Eucricetodon*, *Paracricetodon*, *Pseudocricetodon* and *Melissiodon*) occur in Europe. Three of these genera *Eucricetodon*, *Pseudocricetodon* and *Melissiodon* range into the Early Miocene (Hartenberger, 1989).

Most mammal paleontologists include many of the Oligocene and Early Miocene muroids in the extant family Cricetidae (hamsters) (see for example Chaline & Mein, 1979; Hartenberger, 1985; Flynn *et al*., 1985; Hartenberger, 1998). The content of the family Cricetidae varies according to the opinion of the authors. Many authors consider the sigmodontids, nesomyids, arvicolids and gerbillids (as well as other extant and fossil groups) as subfamilies within the cricetids (for example Hartenberger, 1985). Other workers restrict the family (or subfamily) Cricetidae to the living hamsters (for example McKenna & Bell, 1997). Recent molecular studies have shed new light on the relationships between muroid rodents. Jansa & Weskler (2004) used DNA sequences form the first exon of the IRBP from every recognized muroid subfamily[11] (except the plathacantomyines) to infer phylogenetic relationships between and among major lineages of muroid rodents. Their results show the existence of five major lineages: 1) a basal clade containing the fossorial rodents in the subfamilies Spalacinae, Myosplaciane and Rhizomyiinae; 2) a clade of African and Malgasy genera comprising the Cricetomyinae, Dendromurinae and Nesomyinae amongs others; 3) a clade of Old World taxa including the Lophiomyinae, the Murinae and the Gerbillinae amongst others; 4) a clade uniting the subfamilies Cricetinae, Sigmodontinae and Arvicolinae; 5) and a last clade including *Calomyscus*, which in the opinion of these authors may be the sole living member of the Miocene Cricetodontinae. The major groups recognized by this molecular study may correspond to major muroid families. For example, the group including the Sigmodontinae, the Cricetinae and the Arvicolinae fits rather well with the content of the family Cricetidae according to certain authors (Hartenberger, 1985). Neverhteless, the internal structure of these groups does not appear to be well resolved, since the main subfamilies represent within-node basal politomies. In our opinion many of the fossil groups of Oligocene and Miocene muroids are not particularly close related to living Cricetidae. Therefore, we place them in distinct families and subfamilies following the classifications proposed by Mein & Freudenthal (1971b), Ünay-Bayraktar (1989), Freudenthal *et al.* (1992) and McKenna & Bell (1997). Throughout the text we will refer to these muroids as “cricetids” (always in quotation marks) in an informal way because this term is widely used in the paleontological literature. The classification

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[11] These authors always refer to the groups of muroids as subfamilies within the family Muridae.

for the European Oligocene and Miocene muroids used in this work is presented in table 1.4.

Table 1.4. Classification of the European Oligocene and Miocene muroids used in this work (see text for details). The genera that appear in the systematic part of this work (chapter 4) are in bold. Other genera mentioned in the text are also included. This classification only concerns the Oligocene and Miocene families and subfamilies present in the European record, a complete classification covering the whole content of the superfamily Muroidea is not provided. The Muridae, Gerbillidae and Arvicolidae include a significant number of subfamilies and tribes which do not have Miocene representatives.

- Superfamily Muroidea Illiger, 1811
  - † Family Paracricetodontidae Mein & Freudenthal, 1971
    - † Subfamily Eucricetodontinae Mein & Freudenthal, 1971
      - † *Eucricetodon* Thaler, 1966
      - † ***Eumyarion*** Thaler, 1966
    - † Subfamily Pseudocricetodontinae Engesser, 1987
      - † Tribe Pseudocricetodontini Engesser, 1987
        - † *Pseudocricetodon* Thaler, 1969
      - † Tribe Heterocricetodontini Ünay-Bayraktar, 1989
        - † *Heterocricetodon* Schaub, 1925
      - † Tribe Paracricetodontini Mein & Freudenthal, 1971
        - † *Paracricetodon* Schaub, 1925
      - Pseudocricetodontinae incertae sedis
        - † *Adelomyarion* Hugueney, 1969
  - † Family Melissiodontidae Schaub, 1925
    - † *Melissiodon* Schaub, 1920
  - † Family Cricetodontidae Schaub, 1925
    - † Subfamily Megacricetodontinae Mein & Freudenthal, 1971
      - † ***Megacricetodon*** Fahlbusch, 1964
    - † Subfamily Copemyinae Jacobs and Lindsay, 1984
      - † ***Democricetodon*** Fahlbusch, 1964
    - † Subfamily Cricetodontinae Schaub, 1925
      - † *Cricetodon* Lartet, 1851
      - † *Deperetomys* Mein & Freudenthal, 1971
      - † *Byzantinia* De Bruijn, 1976
      - † ***Hispanomys*** Mein & Freudenthal, 1971
      - † *Ruscinomys* Depéret, 1890
  - Family Cricetidae Fischer de Waldheim, 1817
    - † *Cricetulodon* Hartenberger, 1965
    - † *Kowalskia* Fahlbusch, 1969
    - † *Apocricetus* Freudenthal, Mein & Martín Suárez, 1999
    - † *Rotundomys* Mein, 1965
    - † *Microtocricetus* Fahlbusch & Mair, 1975
  - † Family Microtoscoptidae Kretzoi, 1955
    - † *Microtoscoptes* Schaub, 1934
  - † Family Baranomyidae Kretzoi, 1955
    - † *Baranomys* Kormos, 1933
  - Family Arvicolidae Gray, 1821
    - Subfamily Arvicolinae Gray, 1821
      - † *Promimomys* Kretzoi, 1955
  - Family Gerbillidae Gray, 1825
    - † Subfamily Myocricetodontinae Lavocat, 1961
      - † *Myocricetodon* Lavocat, 1952
      - *Calomyscus* Thomas, 1905
    - Subfamily Gerbillinae Gray, 1825
      - Tribe Gerbillini Gray, 1825
        - † *Pseudomeriones* Schaub, 1934
    - Subfamily Taterillini Chaline, Mein & Petter 1977
      - † *Protatera* Jaeger, 1977
  - Family Dendromuridae G. M. Allen, 1939
    - *Dendromus* Smith, 1829
  - Family Muridae Illiger, 1811
    - † *Progonomys* Schaub, 1938

- † *Huerzelerimys* Mein, Martín Suárez & Agustí, 1993
- † *Occitanomys* Michaux, 1969
- † *Stephanomys* Schaub, 1938

Family Plathacantomyidae Alston, 1876

- † *Neocometes* Schaub & Zapfe, 1953

Family Spalacidae Gray, 1821

- † *Pliospalax* Kormos, 1932

† Family Anomalomyidae Schaub, 1925

- † *Anomalomys* Gaillard, 1900
- † *Prospalax* Mehely, 1908

Muroidea incertae sedis.

- † *Blancomys* Van de Weerd, Adrover, Mein & Soria, 1977

Chapter 2

Geographical and geological background. Biostratigraphy and biochronology

2.1. The Middle to Late Miocene sedimentary record of the Vallès-Penedès Basin

2.1.1. Introduction

The progressive convergence between Africa and Europe implied the development of several marginal basins in the Western Mediterranean as an indirect result of the subduction processes that occurred in eastern areas. One of these basins is the Catalan-Balearic Basin (also known as the Valencia Trough). The compressive structures are common at the SE margin of this basin and are related to the Alpine thrust belts. On the contrary, in the NW margin estensional structures predominate. Part of this NW sector is not covered by water and defines a belt of approximately 60 km wide at the Catalan coastline. In this region the distension processes resulted in the reactivation during the Oligocene of the pre-Tertiary faults of the basement, which were NE-SW to NNE-SSW oriented (Roca & Guimerà, 1992; Roca & Desegaulx, 1992;Bartrina *et al.*, 1992).

By the latest Oligocene – Early Miocene the Catalan continental margin experienced a first phase of rifting and half graben generation. The sediment infilling of the half-grabens also started at that time. By the Late Burdigalian, after the cortical cooling, a phase of thermal subsidence started. From then on, the basins defined at the first phase were progressively filled with sediments (Roca & Guimerà, 1992; Roca & Desegaulx, 1992;Bartrina *et al.*, 1992).

The Vallès-Penedès Basin is one of these NNE-SSW oriented half-grabens, which measures about 100 km in length by 12-14 km in breadth depending on the area. It is placed at the Catalan continental margin (the NW margin of the Valencia Trough) (see fig. 2.1.). It was generated in relation to the rifting of the NW Mediterranean and stretches between two parallel mountain ranges (Pre-littoral and Littoral ranges), which constitute the so-called Catalan Coastal Ranges (Bartrina *et al.*, 1992; Cabrera & Calvet, 1990; Roca & Desegaulx, 1992; Roca & Guimerà, 1992; Cabrera *et al.*, 2004). The southeast dipping Vallès and Penedès major fault segments bound the Vallès-Penedès basin and define moderate to high in altitude footwall blocks to the NW (Pre-littoral Range) and hangingwall blocks to the SE, which include the syntectonic basin fill and some northwestward tilted basement blocks, whose uplifted sides constitute the Littoral Range. Tectonic subsidence of the basin was controlled by these faults, their listric geometry being responsible for the accentuated asymmetry of the half-graben infill, with thickened sedimentary sequences (more than 3000 m) developing at the north-western active margin. Basin tectonic subsidence coupled with rift shoulder uplift along the Pre-littoral Range (Gaspar Escribano *et al.*, 2004; Cabrera *et al.*, 2004) probably sustained an inherited elevated Paleogene relief (1500 m; López Blanco *et al.*, 2000) along the north-western margin of the Vallès-Penedès basin during most of the Miocene.

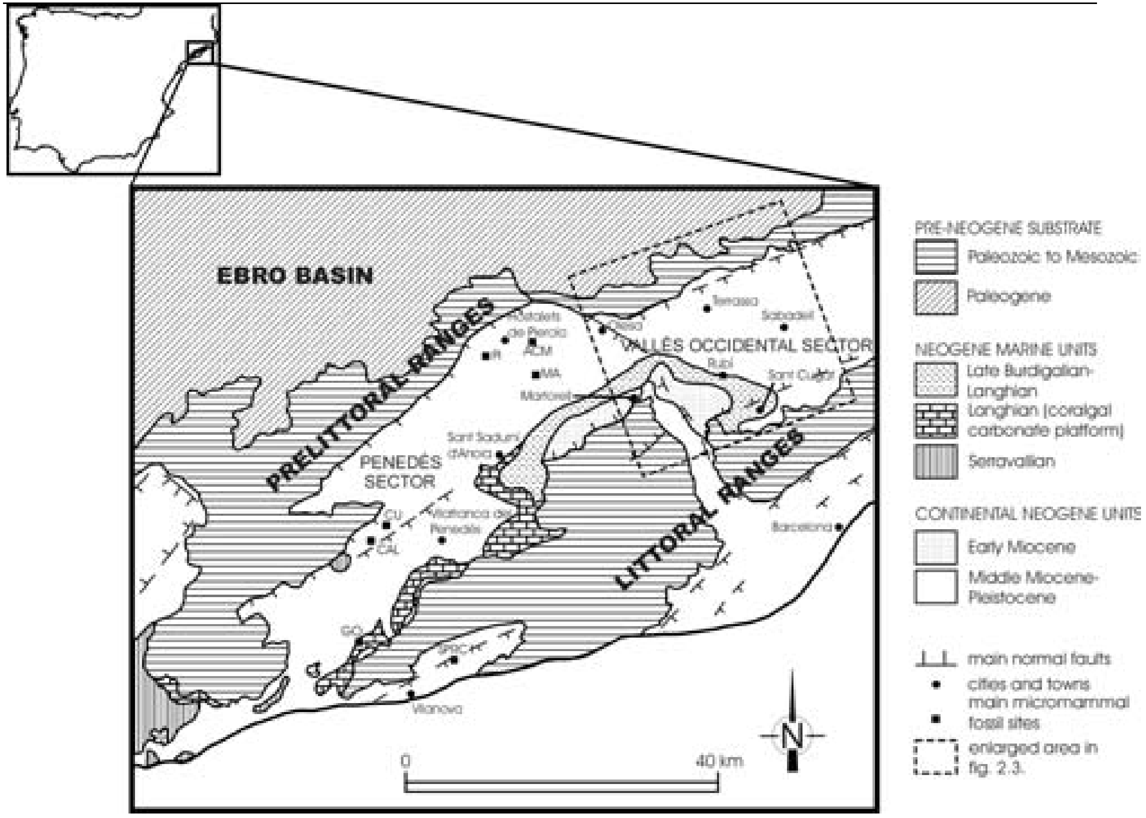

Figure 2.1. Schematic geological map of the Vallès-Penedès Basin showing the main geological units and some of the Late Miocene mammal sites (modified after Garcés, 1995 and Agustí *et al.*, 1985). The area enclosed by the dashed square is enlarged in fig. 2.3. ACM refers to the Abocador de Can Mata series, see appendix 2.1. at the end of this chapter for the acronyms of the remaining localities.

2.1.2. Major stratigraphic units of the Vallès-Penedès Basin

The Miocene deposits of the Vallès-Penedès Basin have been traditionally divided in three major stratigraphic units: the Lower Continental Complexes, the Marine and Transitional Complexes and the Upper Continental Complexes. The outcrops fo these units range from the Burdigalian to the Tortonian (or from the Ramblian to the Turolian, if we consider continental land mammal ages). The sedimentary record is limited by two stratigraphic unconformities. The first one is believed to be a pre-rift or sin-rift unconformity and is always associated to colluvial deposits and/or paleosoils that usually cover it. The second unconformity is Mesinian in age, and can be appreciated throughout the Valencia Trough. This unconformity affects the Cenozoic units and the pre-Tertiary basement as well (Ryan & Cita, 1978). The main characteristics of the three Miocene complexes of the Vallès-Penedès Basin can be summarized as follows (for more detailed descriptions see for example Cabrera, 1981; Cabrera & Calvet, 1990; Cabrera & Calvet, 1996):

- Lower Continental Complexes. Their sedimentation probably started by the Early Burdigalian (Ramblian) or even earlier, by the Latest Oligocene-Early Miocene and finished by the Early Langhian (earliest Aragonian, at about 16 Ma). They are predominantly defined by reddish terrigenous deposits corresponding to proximal, medial and distal facies of alluvial fans. These formations mainly outcrop at the southern margin of the basin, even thought the northern alluvial fans were in all probability more well developed. Ramblian lutites, limestones and gypsums corresponding to distal fan and shallow lacustrine areas outcrop at certain places (Costa Blanca Unit, nearby Martorell and Rubí). Other lacustrine facies, Aragonian in age, may also include some interbedded lignites (Subirats, Can Martí Vell).

- Marine and Transitional Complexes. The origin of these units is related to the marine transgression that occurred by the Middle Miocene (Late Burdiaglian to Serravallian, Haq *et al.*, 1987). This event implied the invasion of part of the basin by sea through its southwestern margin. At the time of maximum transgression sea water reached the Vallès Occidental (Sant Cugat and Cerdanyola). By the Late Burdigalian (earliest Aragonian) several restricted lagoons developed at the Baix Penedès area, resulting in the sedimentation of important evaporite formations such as the Vilobí Gypsums. From the latest Burdigalian until the Early Serravallian (Early-Late Aragonian) facies corresponding to terrigenous and terrigenous/carbonate platform-bay were deposited at El Penedès and El Camp areas. During the transgression maximum, coinciding with the greater extension of sea water as far as the Vallès Oriental, reef formations developed at the areas protected or isolated from the siliciclastic inputs (such as the Sant Pau d'Ordal reefs; Bessedik & Cabrera, 1985).

- Upper Continental Complexes. Their sedimentation started by the Early Serravallian (at about 15 Ma) and lasted until the latest Tortonian (Aragonian-Middle Turolian). The lithological characteristics of this unit are very similar to those of the Lower Continental Complexes, but the Upper Continental Complexes are only linked to alluvial fans of northern origin. The geometry of the sedimentary bodies is unequal, their thickness (which can be close to 1000 m near the Vallès-Penedès Fault) progressively decreasing southwards. Yet another difference with the Lower Continental Complexes is related to the sediment color, which is not predominantly reddish, but also yellowish to pale tan, grayish or ochre. Several different alluvial fan systems may be recognized (figs. 2.2. and 2.3.; see Cabrera & Calvet, 1990 and also Garcés, 1995 for a detailed description of these units), although we will only focus in four of them (and specially on the Hostalets de Pierola one) which have delivered most of the fossil mammal sites (see appendix 2.1. for site acronyms, and additional information regarding magneto- and biostratigraphical data):

    - Hostalets de Pierola System. Since we will pay special attention to this system in the following sections, no comments will be added here.

    - Olesa-Les Fonts System. The proximal facies of this system, which was active from the Aragonian until the Turolian (Cabrera & Calvet, 1991), are situated in the surroundings of Olesa de Montserrat. This is the larger system and covers a radius of about 14 km, so its distal facies reach the southern margin of the basin. In the Viladecavalls and Terrassa area its proximal facies are interbedded with those of the Terrassa-Viladecavalls Alluvial Fan System. These proximal facies consist in polygenic conglomerates with a clear dominance of Paleozoic clasts, although Triassic and Paleogene rock fragments are also common. The sites of Trinxera Sud Autopista 2 (TSA2), Creu Conill 20 and 22 (CCN20, CCN22) are located in the distal facies of this system, while Ceràmiques

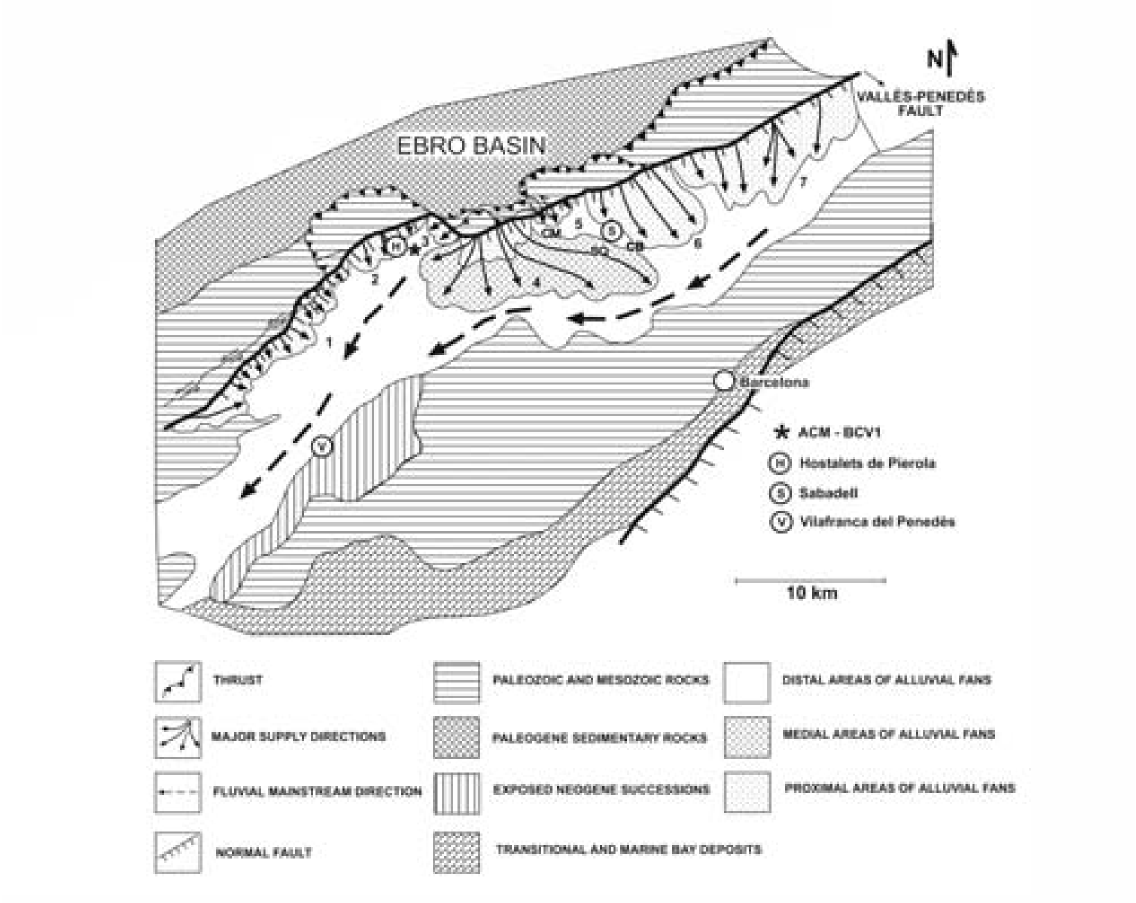

Figure 2.2. Paleogeographical map of the Vallès-Penedès Basin during the latest Serravalian (i. e. Late Aragonian, MN 7+8) indicating the position and extent of the main alluvial fan systems as well as their source area. Alluvial fan systems are numbered as follows: 1 = Torrelles de Foix; 2 = Hostalets de Pierola; 3 = Collbató; 4 = Olesa-Les Fonts; 5 = Terrassa-Viladecavalls; 6 = Castellar del Vallès; 7 = Granollers. The position of the Abocador de Can Mata (ACM) series and the Barranc de Can Vila 1 (BCV1) site is indicated by an asterisk. Furthermore, we have also indicated the situation of other close-aged sites mentioned in the text: Sant Quirze (SQ), Castell de Barberà (CB) and Can Missert (CM).

Viladecavalls (CV) and La Tarumba 1 (LTR1) are situated in the interfan areas between the Terrassa-Viladecavalls and Olesa-Les Fonts systems.

- Terrassa-Viladecavalls System. It was probably active during the same period than the Olesa-Les Fonts Alluvial Fan System, so its development was linked to the growing of this latter system. Its proximal areas are located very close to the northern margin of the basin and outcrop in the surroundings of Viladecavalls and Terrassa. These facies are mainly defined by polygenic breccias exclusively composed of Paleozoic clasts. This alluvial fan system is much more smaller than the Olesa-Les Fonts one. The mammal sites of Can Missert (CM), Trinxera Nord Autopista (TNA) and Torrent de Febulines 3 (TF3) are situated in the distal facies of this system which outcrop at the south and southeast of Terrassa.

- Castellar del Vallès System. This system is also contemporary to the Olesa-Les Fonts Alluvial Fan System, and like this one also covers an important area, nearly reaching the southern margin of the basin. Its proximal areas are situated near Castellar and Matadepera and consist in polygenic rudites, mainly composed of Paleozoic clasts. Its distal facies are defined by lutites of different colours, although grayish and ochre shades are very common. The well known mammal sites of Castell de Barberà (CB) and Can Llobateres (CL) are located at the distal facies of this system near to Sabadell.

The Upper Continental Complexes were sedimented in a time of distensive efforts and reached their maximum development during the Vallesian, once the rifting phase had finished. It is also possible that certain of these units prograded over the southeastern margin of the basin (Garcés, 1995).

2.2. The Miocene fossil sites from the area of Els Hostalets de Pierola

2.2.1. Historical background

The fossiliferous potential of the area of Els Hostalets de Pierola was discovered by Marius Guerín. Eventually, during the decade of 1920s, Guerín collected an isolated right M^2 of a great ape. This teeth, however, was mistaken for a suid, not being “rediscovered” until much latter it in the collections of the Museu i Laboratori de Geologia del Seminari de Barcelona (Van der Made & Ribot, 1999). Later on, the paleontologist Ramon Bataller surveyed the area and discovered several fossiliferous points that delivered mostly small mammal remains. Bataller described the sites and the recovered material in his monograph “Els Ratadors Fòssils de Catalunya” (Bataller, 1938) (see chapter 1). Further field work at this area would be carried by Crusafont and co-workers during the 1950s and 1960s, resulting in the discovery of more than twenty sites (Crusafont & Truyols, 1954a; Golpe-Posse, 1974). These loosely-defined “localities”, however, are not paleontological localities in a strict sense, because they do not correspond to a single stratigraphic level (except for Can Mata I) (Agustí *et al.*, 1984). For this reason, these historical “localities” have been traditionally grouped into “Lower Hostalets” (Aragonian levels) and “Upper Hostalets” (Vallesian ones) (Crusafont & Truyols, 1954a; Golpe-Posse, 1974; Agustí *et al.*, 1984).

By the early 1970s, a clandestine rubbish dump began to develop in the area of Els Hostalets de Pierola, situated between the farm-houses of Can Mata de la Garriga and Can Vila. This was later conditioned and legalized in 1985 under the name of Abocador de Can Mata, currently exploited by the company CESPA Gestión de Residuos, S. A. When an extension of it began to be planned, a paleontological intervention was devised, in order to control the removal of Miocene sediments by the excavators, as well as to carry out excavations and micromammal sampling when necessary. The record of associated litho- and magnetostratigraphical information was also taken into account. Such excavations began in November 2002, and are still on course. To date, thousands of large and small mammal remains have been recovered, and about 90 fossiliferous localities have been sampled (Alba et al., 2006, 2007 in press, In press). These new sites are named after the names of the different sectors of the rubbish dump, preceded by the acronym ACM (Abocador de Can Mata) (see fig. 2.4.). The works also marginally affected a ravine next to Can Vila, resulting in the discovery of an important fossiliferous locality (the so-called Barranc de Can Vila 1; BCV1) which has delivered a remarkably complete fossil great ape (Moyà-Solà *et al.*, 2004) (see chapters 4 and 5).

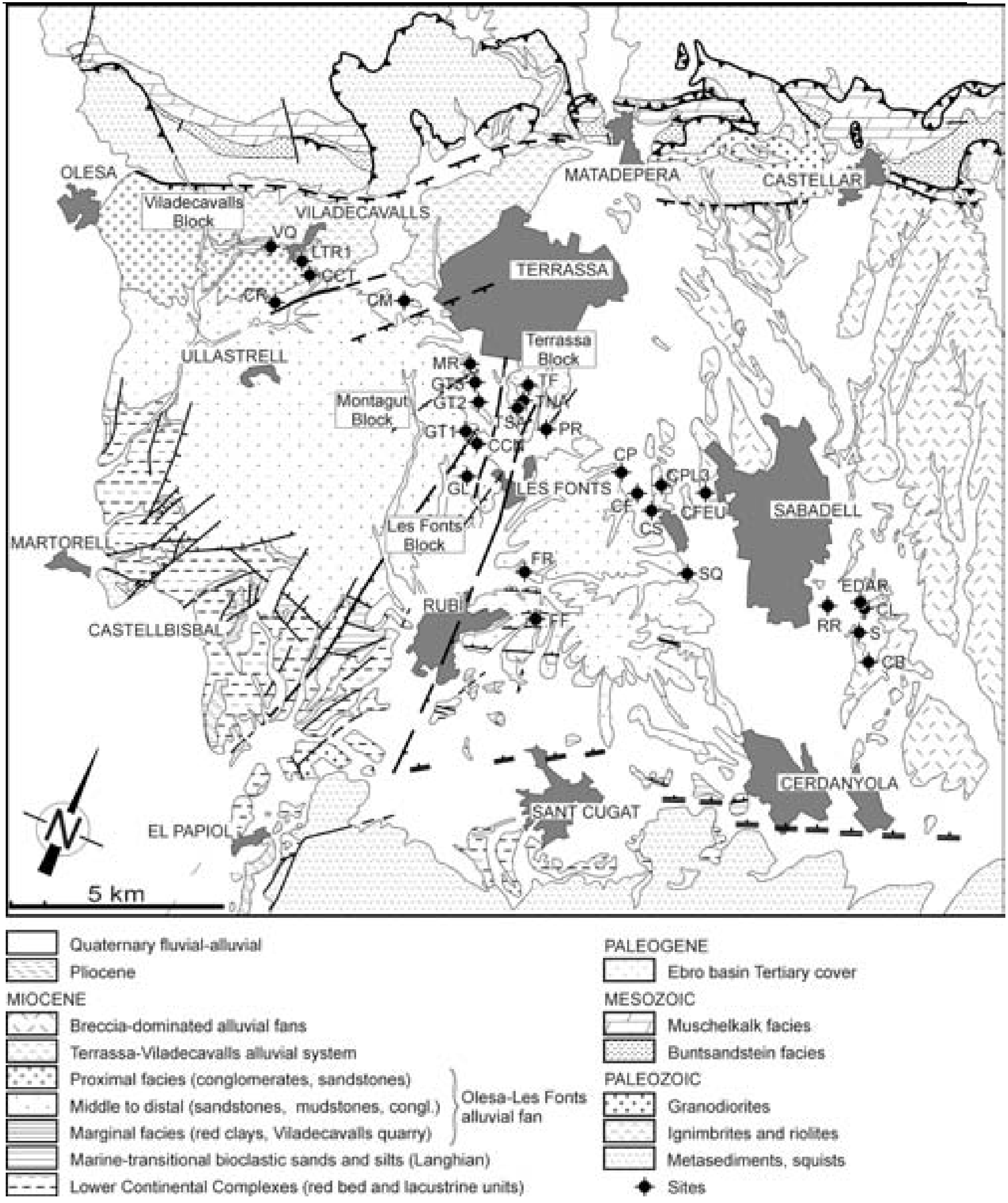

Figure 2.3. Detailed geological map of the Vallès-Penedès (modified from Garcés, 1995). It corresponds to the area marked with a dashed square in fig. 2.1. The main geological units and the facies of the different alluvial fan systems are indicated. The fossil sites that have delivered rodents are indicated as well as the magnetostratigraphic sections sampled by Garcés (1995). Acronyms for magnetostratigraphic sections and localities are as follows (for additional information regarding their chronological position and faunal content see appendix 2.1.): FF = Font del Ferro section; FR = Can Ferran section; SQ = Sant Quirze (Trinxera del Ferrocarril site and Sant Quirze A, B and G); CB = Castell de Barberà; S = Santiga; EDAR = sites of the Estació Depuradora d'Aigües Residuals del Riu Ripoll; CL = Can Llobateres section; RR = Riu Ripoll; CS = Can Casablanques; CFEU = Can Feu; CF = Can Feliu; CPL3 = Can Pallars de Llobateres 3; GL = Can Guilera section; CCN = Creu Conill section; GT1 = Can Guitart 1 section; GT2 = Can Guitart 2 section; GT3 = Can Guitart 3 section; TSA = Trinxera Sud Autopista sites; TNA = Trinxera Nord Autopista sites; TF = Torrent de Febulines section; MR = Les Martines section; CM = Can Missert; CR = Can Coromines section; CCT = Can Tarumbot section; LTR1 = La Tarumba 1; VQ = Pedrera de Viladecavalls section.

2.2.2. Geological setting

The Middle Miocene sequences in the area of els Hostalets de Pierola consist of red to brown mudstones, sandstones, breccias and conglomerates. Coarse-grained deposits can be grouped into two types on the basis of clast composition and fabrics. First, monogenic siliciclastic breccious conglomerates with clasts of Paleozoic phyllites and quartz; and second, polygenic, well-rounded conglomerates with a variety of clasts of Paleozoic rocks as well as Mesozoic and Paleogene limestones and sandstones. These observations indicate that sediments were deposited in the distal to marginal, inter-fan zones of two major coalescing alluvial fan systems. Some sediment corresponds to a short-radius alluvial fan system (Els Hostalets de Pierola System) that was sourced from the NW Pre-littoral range by very close, local catchments dominated by Palaeozoic metamorphic rocks. Others correspond to a coalescing and radially extensive alluvial fan system (Olesa-Les Fonts System), sourced from the NE by more extensive catchments in the Pre-littoral Range, where a variety of metamorphic Palaeozoic and sedimentary Mesozoic and Palaeogene rocks cropped out (see fig. 2.2.).

The area of els Hostalets de Pierola is characterized by thick (300 m) Middle to Late Miocene sedimentary sequences that resulted from a high rate of continued accumulation (see fig. 2.5.), most likely controlled by its proximity to the actively subsiding north-western margin. In addition, it is also possible that the existence of a fault release zone between the Penedès and the Vallès fault segments may have preferentially focused sediment supply towards this area. High subsidence rates determined sediment trapping at the foot of the marginal faults as well as the rapid transitions from proximal-middle alluvial fan coarse-grained sediments to distal-marginal and inter fan mud-flat mudstones. The combination of high rates of both subsidence and sediment supply must have favoured rapid burial in a mudstone dominated sedimentary environment, with a positive effect on the preservation potential of vertebrate remains. No major hiatuses neither major faults appear to affect the succession.

The mudstone dominated alluvial successions at Els Hostalets de Pierola (see fig. 2.5.) show widespread evidences of pervasive, although changing in intensity processes of soil formation. The overall dominant pale tan, reddish-brown, grayish mottled and pale yellowish mudstones suggest that, under shallow burial, these sediments were affected by oscillating water table conditions, which resulted in the development of a vadose zone where Eh changes may be significant. As a consequence, the alluvial sediments were affected by alternating reducing and oxidizing conditions, which resulted in the mentioned color shades. Intensely red paleosoil horizons are thin and scarce and record punctuated episodes of accentuated water table lowering with development of very well aerated, oxidizing conditions. Widespread early diagenetic carbonates also occur in the fine grain dominated alluvial successions studied. This early diagenetic carbonate generation took place in a variety of conditions, under the influence of both meteoric water and more evolved, carbonate rich groundwaters. The widespread occurrence, among others, of Mesozoic carbonates and Paleogene carbonate conglomerates in the Pre-littoral Range catchments would account for the high groundwater calcium bicarbonate content. This high carbonate solute content would have triggered incipient carbonate cementation of the coarse grained alluvial facies, as well as the development of widespread nodular pedogenic and lenticular groundwater calcretes.

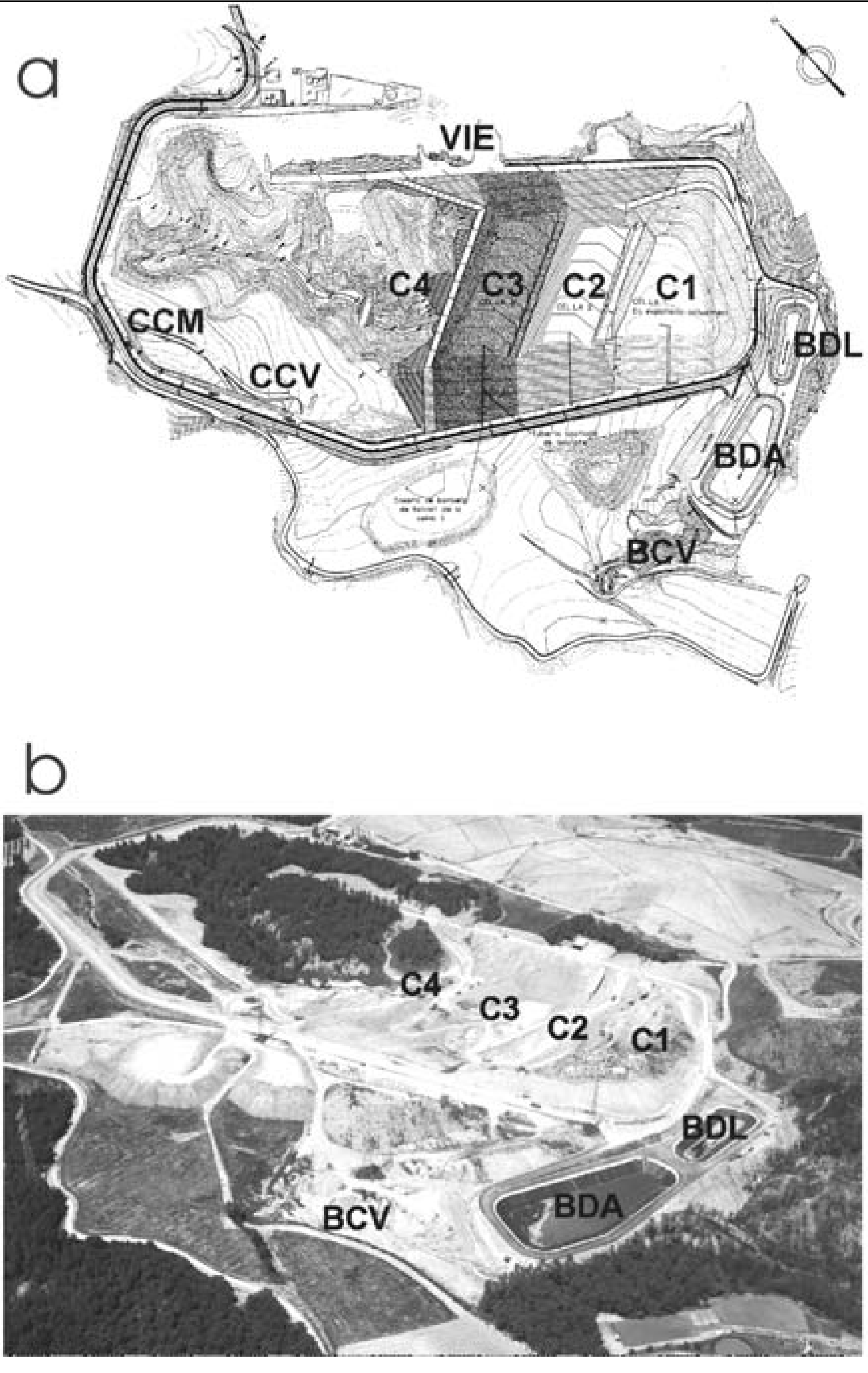

Figure 2.4. a) situation map of the different sectors of the Abocador de Can Mata (ACM) works (base map kindly handled by CESPA Gestión de Residuos, S. A). Acronyms: C1: cel·la 1 (cell 1); C2: cel·la 2 (cell 2); C3: cel·la 3 (cell 3); C4: cel·la 4 (cell 4); BDA: bassa de decantació d'aigües pluvials (rain water decant pond); BDL: bassa de lixiviats (lixiviate pond); CCM: camí de Can Mata (Can Mata track); CCV: camí de Can Vila (Can Vila track); BCV: Barranc de Can Vila (Can Vila ravine); RP: rasa de desguàs d'aigües pluvials (rain water drainage furrow); VIE: vial intern d'explotació (inner track for exploitation). b) aerial photograph of the ACM works by 2004, note that the three first cells have been build and that the first one is being filled with rubbish (picture kindly handled by Magí Miret).

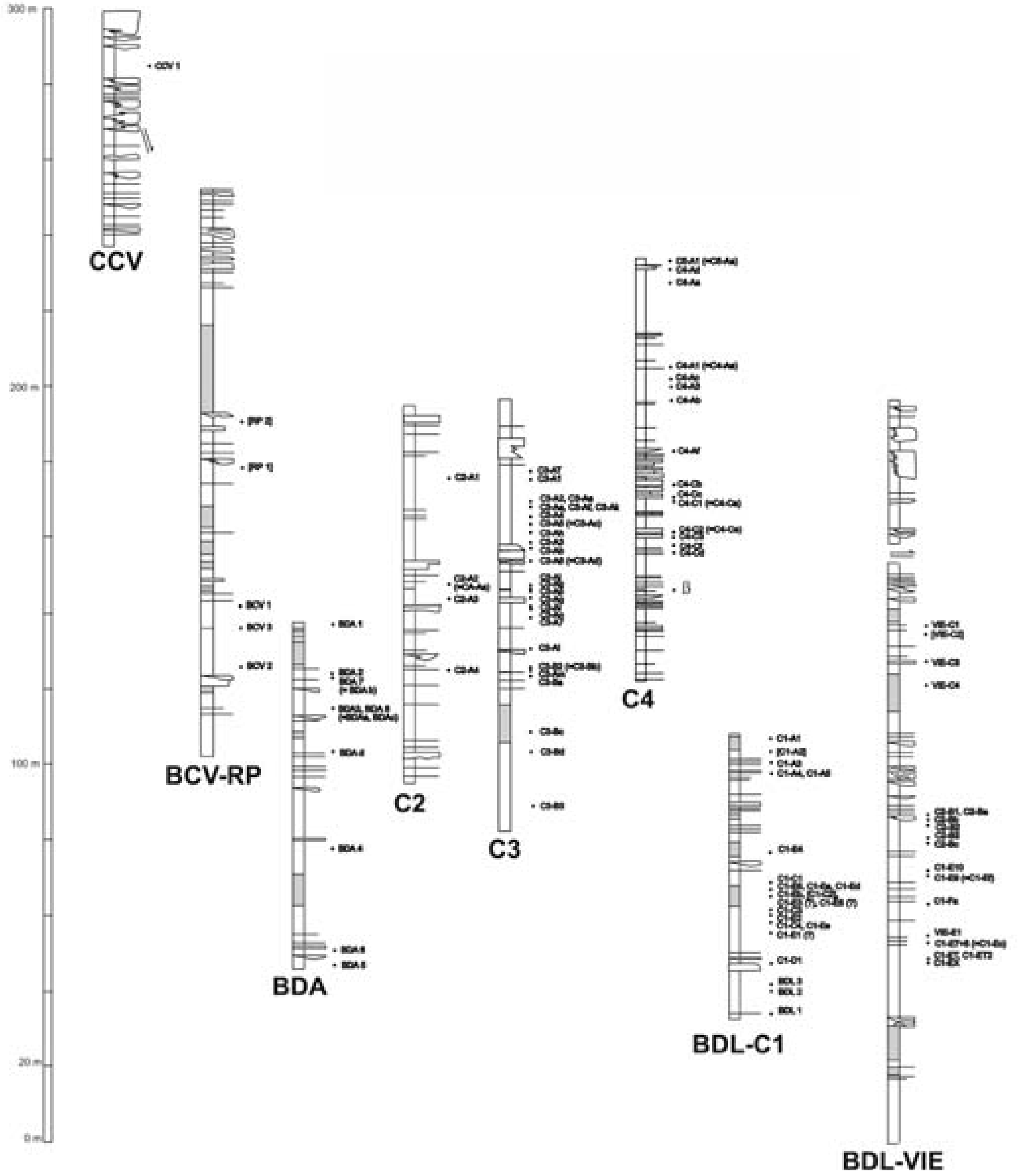

Figure 2.5. Stratigraphic columns for the different sectors of the Abocador de Can Mata (ACM) and their correlation on the basis of lithostratigraphic and preliminary bio- and magnetostratigraphical data. The fossils sites that have delivered micro- and/or macromammals are indicated on the right of the columns. For acronyms and situation of the different sectors in the ACM area see fig. 2.4.

2.2.3. The fauna

The ACM series includes a set of different localities, belonging to different parts of the area affected by the extension works of the rubbish dump (fig. 2.3.). These sites are distributed along 300 m of stratigraphic series, obviously representing a considerable time-span. In the case of macromammals the lithostratigraphic position of the main concentrations of bones (such as C3-Ak, C4-A1 = C4-Ae, and C4-C2 = C4-Ce) was accurately recorded. On the contrary there is some degree of uncertainity in the exact stratigraphic position of the macromammal remains found isolated during the excavation works (Alba *et al.*, 2007 in press). In the case of micromammals there is an excellent lithostratigraphic control of the sites, and the amount of sediment collected for screenwashing is never lower than 1500 kg (larger samples are collected in special cases). This has resulted in the recovery of about 1300 small mammal cheek teeth, an amount that shall surely increase in the future, once sieving and sorting of the accumulated sediments is finished.

The synthetic taxonomic list of the ACM sites includes more than 70 species, including some birds and reptiles, but mostly small and large terrestrial mammals (see appendix 2.2.). Whereas many of these species had been previously recorded from the area of els Hostalets, a significant portion of the recovered taxa represent new citations. These are mostly attributable to the huge collecting effort, but also to the fact that the time interval being sampled is partially older than the one corresponding to Lower Hostalets. The intensive control of enormous quantities of excavated sediments has eventually led to the discovery of rare mammalian taxa, including many carnivores and primates. In fact, a previously unsuspected primate diversity has been already retrieved. In the following sections we quote the vertebrate fauna recovered from ACM and BCV1 (with an special reference to this site, since we will focus on it in chapters 4 and 5) and comparisons are made with the classical collection of Lower Hostalets.

Avifauna and Herpetofauna

The aviafauna and herpetofauna of both ACM and BCV1 are still to be studied in detail. Furthermore, most of the material is still being prepared, and in most cases only field identifications of unprepared remains are available. Remains from different birds and small reptiles (mainly anguids) have been recovered from both Hostalets Inferior and ACM (Crusafont & Villalta, 1952; Alba *et al.*, 2007 in press). Turtle remains are very common in ACM, being attributable to at least two different terrestrial testudinid species, including a middle-sized *Testudo* and the giant turtle *Cheirogaster* (Alba *et al.*, 2007 in press).

The macromammals

- Proboscidea. On the basis of some isolated dental material, the numerous and mainly fragmentary proboscidean postcranial bone fragments from BCV1 can be attributed to *Deinotherium giganteum*. This deinotheriid species has been found both in Hostalets Inferior (e.g. Crusafont & Truyols, 1954; Crusafont & Casanovas, 1973) and in ACM (Alba *et al.*, 2007 in press), where it is very common. Although the deinothere remains from the classical "locality" of Can Vila were attributed to the taxon "*laevius*", either as a variety (Villalta & Crusafont, 1941a), subspecies (Villalta & Crusafont, 1944a) or distinct species (e.g. Crusafont & Truyols, 1954), this taxon is nowadays generally considered a synonym of *D. giganteum*. No gomphothere remains have been found in BCV1, whereas gomphotheriid remains from Can Vila were attributed to *Gomphotherium angustidens* by Crusafont & Truyols (1954) and to *Tetralophodon longirostris* by Crusafont & Casanovas (1973). In fact, as noted by Alba *et al.* (2007 in press), there is a lot of confusion regarding the classical citations of gomphotheriid proboscideans from Hostalets Inferior as a whole, since different authors have attributed the same remains to either one or the other of the two above-mentioned taxa. Material from locality BDA8 of ACM, about 25-30 m below BCV1 in stratigraphic series, permits to confirm the presence of *G. angustidens* in this area (Alba *et al.*, 2007 in press), albeit the simultaneous presence of *T. longirostris* at some point in the ACM stratigraphic series cannot be discarded for the moment.

- Perissodactyla. No perissodactyl remains have been found at BCV1. In the classical site of Can Vila, the rhinocerotids *Lartetotherium sansaniense* and *Alicornops simorrense*, were quoted by Crusafont & Truyols (1954) and Crusafont & Casanovas (1973), although the former is a very dubious citation. In fact, only *A. simorrense* and *Hoploaceratherium tetradactylum* are reasonably well documented in Hostalets Inferior (Santafé, 1978) and ACM (Alba *et al.*, 2007 in press). No chalicotheriid or equid remains were either found in classical Can Vila, although both *Chalicotherium grande* and *Anchitherium* sp. are present at lower levels from ACM (Alba *et al.*, 2007 in press).

- Artyodactyla. Artiodactyl ungulates are represented in BCV1 by several isolated teeth from the suid *Listriodon splendens*, some dental and postcranial remains of the moschid *Micromeryx flourensianus*, and some dental material and two shed antlers of the cervid *Euprox furcatus*. All these taxa, together with the tetraconodontine suid *Conohyus steinheimensis* (classically cited as *Hyotherium simorrense*) and the bovid *Protragocerus chantrei* had been previously cited from Can Vila (Villalta & Crusafont, 1941a, 1944a; Crusafont & Truyols, 1954; Crusafont & Casanovas, 1973). Other artiodactyl species documented in Hostalets Inferior and/or ACM, but found neither in BCV1 nor in Can Vila, include (Alba *et al.*, 2007 in press): the suids *Korynochoerus palaeochoerus* and *Albanohyus pygmaeus*, the palaeochoerid cf. *Taucanamo* sp., the tragulid *Dorcatherium naui*, and the bovids *Miotragocerus* cf. *monacensis* and cf. *Eotragus* sp.

- Carnivora. With regard to carnivore remains, the findings from BCV1 are relatively meager as compared with many other ACM localities, where several partial crania from different taxa have been thus far recovered (Alba *et al.*, 2007 in press). Only three different taxa have been documented in BCV1 on the basis of the scanty available evidence. The presence of the hyaenid *Thalas*sic*tis montadai*, previously unknown from Can Vila but otherwise recorded at Hostalets Inferior (Villalta & Crusafont, 1941b, 1941c; Crusafont & Truyols, 1954; Crusafont & Casanovas, 1973), is documented at BCV1 by an isolated right dP_4. Albeit other ictitheriine hyaenids have been also documented from Hostalets Inferior and ACM, including *Protictitherium crassum* and *P. gaillardi* (Crusafont & Truyols, 1954; Crusafont & Casanovas, 1973; Alba *et al.*, 2007 in press), the deciduous carnassial from BCV1 can be attributed, on the basis of its size and morphology, to *Thalas*sic*tis*. The presence of the small viverrid *Leptoples*ic*tis* cf. *aurelianensis* is further documented at BCV1 by a left mandibular fragment with P_4-M_1; this species had been previously cited from Hostalets Inferior (Crusafont & Truyols, 1954; Crusafont & Casanovas, 1973), although Roth (1987) attributed this classical material to *L. filholi* (Gaillard, 1899). Finally, a small partial left lower canine from BCV1 belongs to an undeterminable Mustelidae. Only the mustelid *Palaeomeles pachecoi* Villalta & Crusafont, 1943b, recorded from Hostalets Inferior but not from ACM, had been previously cited from Can Vila (Villalta & Crusafont, 1944a, 1944b; Crusafont & Truyols, 1954; Crusafont & Casanovas, 1973). In fact, from the other four mustelid species previously recorded from Hostalets Inferior and/or ACM (Villalta & Crusafont, 1941b,c, 1944b; Crusafont & Truyols, 1954; Crusafont & Casanovas, 1973; Alba *et al.*, 2007 in press), including *Martes munki*, *M. delphinensis*, *Ischyrictis mustelinus* and *Trocharion albanense*, all except the former can be discarded on the basis of size, although the available evidence is not enough to confirm this taxonomic attribution. No other carnivores have been found at either BCV1 or Can Vila, albeit the ursid *Hemicyon goeriachensis*, the nimravid *Sansanosmilus jourdani*, and several species of the felid *Pseudaelurus* as well, have been previously quoted in the faunal lists of Hostalets Inferior and/or ACM (Villalta & Crusafont, 1941b, 1943b, 1944a, 1944b; Crusafont, 1952; Crusafont & Truyols, 1954; Crusafont & Casanovas, 1973; Ginsburg & Morales, 1998; Alba *et al*., 2007 in press).

- Primates. Finally, with regard to primates, some nomenclatural clarifications should be done regarding the identity of the *Sivapithecus occidentalis* Villalta & Crusafont, 1944 type material from Can Vila. Given stratigraphic uncertainties regarding the exact provenance of the Can Vila material, as well as the impossibility to directly compare the lower molars from Can Vila with the palate from BCV1, in the original description of *P. catalaunicus*, Moyà-Solà *et al.* (2004) considered the nomen "*occidentalis*", previously considered to be a synonym of *D. laietanus* (Villalta & Crusafont, 1944) (e.g. Andrews *et al*., 1996), to be a nomen dubium. This view has been later reinforced by other primate discoveries at ACM, because they show that the primate diversity in that area is actually higher than initially thought. Thus, besides *P. catalaunicus*, there are at least three other different species recorded from several stratigraphic levels at ACM (Alba *et al*., 2007 in press): a pliopithecoid and two hominoids. These remains are currently under study, but for the moment being, it can be tentatively asserted that the hominoid remains other than *Pierolapithecus* belong to two different hominid (i.e. great ape) species that cannot be attributed to *D. laietanus*. Among others, a considerably complete palate from locality C3-Ae records another *Dryopithecus* species, whereas a partial splachnocranium from C3-Aj most likely represents a new genus and species. This leaves the nomen *"S." occidentalis* with a doubtful taxonomic validity for the moment being, although further discoveries might finally prove it to be a valid taxon (see chapter 4). It is worth mentioning that the previous citation of *D. laietanus* from Can Mata I is neither reliable, being based on a single lower female canine of uncertain great ape affinities.

Insectivores, chiropterans and lagomorphs

- Insectivora. The insectivores have only been adequately studied in BCV1, while just preliminary identifications are available for the remaining sites. The Heterosoricidae are represented by *Dinosorex sansaniensis*. This species ranges in Europe from MN 4 to MN 9 (Ziegler, 1999), but according to the data compiled by Van den Hoek Ostende & Furió (2005), its presence in Spain is temporally restricted to the MN 7+8 and MN 9, and geographically confined to northeastern basins. The true shrews (family Soricidae) are only represented by very scarce material, nevertheless two different morphologies on the incisors recovered at BCV1 indicate that at least two different species are present. One of them shows a strong curvature on its dorsal side, which added to its rather small size and no fissidenty, suggests that it belongs to a Crocidosoricinae (sensu Reumer, 1987). The family Talpidae is represented by two different species: *Talpa minuta* and cf. *Proscapanus* sp. In Spain, *T. minuta* has only been reported in some Aragonian and Vallesian fossil sites of the Vallès-Penedès Basin. The Erinaceidae include three species: *Parasorex socialis*, which may be quite abundant in certain sites, such as BCV1; an unidentified form that differs from *Parasorex* in certain aspects of its dental morphology; and finally an undetermined erinaceid of noticeable size. The Dimylidae are represented by *P. chantrei*. As in the case of the heterosoricid *Dinosorex*, the occurrences of *Plesiodimylus* in Spain are restricted to Late Aragonian and Vallesian sites from north-eastern basins.

- Chiroptera: Some scanty bat remains have been recovered in ACM.

- Lagomorpha: The lagomorphs are not very abundant in the ACM sites, and most of the material can be referred to *Prolagus oeningensis*. Moreover a few remains of *Eurolagus fontannesi*, have been identified.

The rodents

As usual, rodents are by far the most diverse and abundant mammalian order the ACM sites and they are represented by nearly 30 species belonging to five different families: Sciuridae (6), Castoridae (1), Gliridae (6), Eomyidae (2), the "cricetids" (14, including one Anomalomyidae species). Only three of these have been recorded at BCV1 (the "cricetids", Gliridae and Sciuridae) (see chapter 4).

- Sciuridae. In BCV1 the Sciuridae include the ground squirrel *Spermophilinus bredai*, which is a common component in Middle and early Late Miocene small mammal faunas. The remains of flying squirrels are very rare and consist in just three teeth attributed to *Miopetaurista* cf. *crusafonti*. Besides *Spermophilinus*, a few remains of the ground squirrel *Heteroxerus* sp. and up to three other flying squirrels (*Albanensia albanensis albanensis*, *Miopetaurista neogrivensis* and ? *Blackia* sp.) have been identified in the ACM series (Alba *et al.*, 2007 in press). Like in BCV1, flying squirrels are always rare in ACM.

- Castoridae. The presence of beavers had never been previously reported from the Hostalets de Pierola area. In fact they are extremely rare, being only represented by a few cranial and postcranial remains attributed to a new species of the large-sized beaver *Chalicomys* (see chapter 3).

- Gliridae. This family follows the "cricetids" in diversity, but they are much less abundant. For example in BCV1 the "cricetids" represent more than 80 % of the recovered cheek teeth, while the Gliridae are less than the 5 %. The dormice include *Glirudinus undosus*, two species of the genus *Muscardiuns* (*M. sansaniensis* and *M. hispanicus*), *Microdyromys complicatus*, *Paraglirulus werenfelsi* and *Bransatoglis astaraciensis*. *Muscardinus sansaniensis* and *Microdyromys complicatus* are recorded for the first time from the Vallès-Penedès Basin from the lower levels of the ACM series (Alba *et al.*, 2007 in press; see also chapter 4).

- Eomyidae. This family is represented by a few minute teeth attributed to two different species: *Eomyops* cf. *oppligeri* and *Keramidomys carpathicus*.

- "Cricetids". As in most of the Middle Miocene rodent assemblages, "cricetids" are the most abundant and diverse rodents throughout the whole series. They include *Eumyarion leemani*, which may be the most abundant rodent in many sites, such as BCV1. *E. leemani* has only been reported from the Late Aragonian and Early Vallesian of the Vallès-Penedès Basin and from the Late Vallesian of the Czech Republic (Fejfar, 1990). *E. leemani* is also the dominant rodent in other Late Aragonian (Castell de Barberà) of the Vallès-Penedès Basin. The genus *Democricetodon* includes two medium-sized species *D. larteti* and *D. crusafonti* as well as two small-sized subspecies *D. brevis brevis* and *D. brevis nemoralis*. *D. brevis brevis* is recorded for the first time in the Vallès-Penedès Basin from the lower levels of the ACM series (Alba *et al*., 2007 in press; see also chapter 4). This subspecies is distributed across Central Europe and France. In the Vallès-Penedès Basin, a closely related form, *D. brevis nemoralis*, was described from the Late Aragonian site of Castell de Barberà (Agustí, 1981b) and has been reported from another C4-A3, which is in the upper third of the ACM series (Alba *et al*., 2007 in press). *D. larteti* is found in several Spanish and French sites (we follow Van der Meulen *et al*. (2003) in the synonymy of the genus *Fahlbuschia* with *Democricetodon*, see discussion in chapter 4). *D. larteti* is part of the evolutionary lineage *D. franconicus* – *D. crusafonti* (Van der Meulen *et al*., 2003). The last member of this lineage, *D. crusafonti*, is present in the latest Aragonian of the Vallès-Penedès Basin (including the upper levels of ACM; Alba *et al*., 2007 in press) and the earliest Vallesian (Agustí, 1978a). *D. larteti* is present in most of the sites of the ACM series, while *D. crusafonti* is only present at the upper part. The genus *Megacricetodon* may be quite abundant in some sites, being represented either by small-sized species (the subspecies *M. minor minor* or *M. minor debruijni*) or by larger-sized ones (*M.* cf. *crusafonti*, *M. gersii*, and *M. ibericus*) (Alba *et al*., 2007 in press). *M. gersii* and *M.* cf. *crusafonti* have only been identified in two test samples corresponding to the lowermost part of the series (BDL1 and C1-E7+8 = C1-Ec, respectively). In C1-E7+8 an anterior fragment of M_1 of a second *Megacricetodon* species has also been recovered. This specimen is conspicously larger than the ones attributed to *M. gersii*. Furthermore this tooth shows a divided anteroconid with the two cusps widely separated. The anterolophulid is divided and reaches each cusp separately. The two arms of the anterolophulid define an X-pattern with the crests that join the protoconid and the metaconid. This morphology resembles that of *M. ibericus* and clearly contrasts with *M. gersii* which shows a divided anteroconid but with both cusps close to one another. However, the intraspecific variation in the genus *Megacricetodon* may be enormous, so it will be necessary to wait for the final sample in order to asseverate the presence of this species in C1-E7+8. *M. ibericus* is unquestionably present in somewhat younger sites of the ACM series, such as C1-E9, where it may be very common. Finally, two (or probably three) different species of the genus *Hispanomys* have been identified (Alba *et al*., 2007 in press.). *H. decedens* has been certainly identified in some sites corresponding to the lower part of the series (such as C2-B2). This species is only known from La Grive (fissure M and probably other fissures, P. Mein pers. com.). The second species is *H. daamsi*, which has only been reported from the Late Aragonian site of Can Missert in the same basin (Agustí *et al*., 2005). This second species is present from younger sites of the ACM series. In BCV1 a few remains that may prove to belong to a third smaller-sized *Hispanomys* species have been recovered (see chapter 4). Quite surprisingly, no remains of the two cricetodontinin species found at Lower Hostalets, *Cricetodon* (*Pararuscinomys*) *lavocati*[12] (Freudenthal, 1967) and *Hispanomys dispectus* Agustí, 1980, have been identified. Maybe the old material was retrieved from upper levels and those species were not present at the lower ones or maybe they will appear once

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[12] Although a detailed revision of this species has not been attempted yet, it is likely that it would conclude that it should be better considered as a highly plesiomorphic *Hispanomys* species rather than the sole member of the subgenus *Pararuscinomys*.

sieving and sorting of the sediment of the several ACM sites is finished. *Cricetulodon hartenbergeri* has also been quoted from Lower Hostalets[13] (Agustí & Gibert, 1982a) on the basis of an isolated M^1 and an M^2, this last one already described by Schaub (1944, 1947a)[14]. However, we have not been able to find this material within the collections from Hostalets de Pierola kept in the Institut de Paleontologia M. Crusafont (Sabadell), so in the light of the scarce material recovered, that presumably precludes a reliable identification we consider dubious the presence of *Cricetulodon* in the Lower Hostalets.

- Anomalomyidae. This subfamily of high crowned and probably fossorial rodents is only represented by a few teeth that on the basis of morphology are attributed to *Anomalomys gaudryi*, although their size is slightly above the variation limits of this species.

2.3. Biostratigraphy and biochronology of the Late Aragonian and Vallesian mammal successions of the Vallès-Penedès Basin and correlation to other areas

The composite Late Aragonian to earliest Turolian mammal succession of the Vallès-Penedès Basin consists in more than 100 sites, many of them still unpublished. More than half of these sites are part of the ACM series. In these cases results are preliminary because many micromammal samples are still being processed and a great amount of the macromammal material is still waiting to be prepared. Several sites have provided both macromammals and micromammals in the ACM series and in other areas of the basin as well. The stratigraphic order of the localities and their correlation to other records is based on the interpretation of published and unpublished litho-, bio- and magnetostratigraphic data. In the case of certain old collections a degree of resolution above that of the biozone is not possible.

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[13] The remains of *Cricetulodon hartenbergeri* are erronously attributed to Upper Hostalets in the table of figure 10 of Agustí *et al.* (1997: 163). However, in the main text it is stated that they were recovered from Lower Hostalets (Agustí *et al.*, 1997: 164).

[14] Agustí (1981a) notes that the material described by Schaub (1947a) was lost, however, this author argues that on the basis of the original description the material can be attributed to *Democricetodon brevis nemoralis* (the M^1 is also attributed to this species). In his 1982 paper (Agustí & Gibert, 1982a) this author would transfer the mentioned tooth to *Cricetulodon hartenbergeri*.

2.3.1. A preliminary biozonation of the Late Aragonian of the Vallès-Penedès Basin

The land mammal biochronology of the latest Middle Miocene in Western Eurasia is a matter of constant debate, since no sufficiently long and continuous stratigraphic section covering this crucial interval has been published so far. There are many good sections covering the Aragonian in its type area, the Calatayud-Daroca Basin (Inner Spain), and most of them are magnetostratigraphically calibrated (Krijgsman *et al.*, 1994; Krijgsman *et al.*, 1996; Daams *et al.*, 1999a; Garcés *et al.*, 2003). However, the resolution of these calibration is poorer in the latest Aragonian, and particularly at the Aragonian/Vallesian boundary as well.

The chronological position of many European sites is based on the Mammal-Neogene (MN) biozones (Mein, 1975). The MN 6 and MN 7+8 define the Late Aragonian, that is, the latest Middle Miocene (Steininger, 1999; Agustí *et al.*, 2001). In 1990 a working group of the Regional Comittee of the Mediterranean Neogene Stratigraphy (RCMNS) decided to join the original MN units 7 and 8 (De Bruijn *et al.*,1992). This decision was taken after several participants of the meeting (held in Reisenburg in 1990) expressed their doubt concerning the stratigraphical position of the two reference sites: Steinheim (Germany) for MN 7 and Anwil (Switzerland) for MN 8. Furthermore only minor differences could be found between both faunas (De Bruijn *et al.*,1992). As a pragmatic solution the classical fauna of La Grive M (France) was chosen as the reference site for MN 7+8 (De Bruijn *et al.*,1992). Recent reviews have stated that Anwil is certainly older than La Grive M and in fact closer to Steinheim (Mein, 1999a). Recently Mein & Ginsburg (2002) have claimed that both biozones can be clearly distinguished at La Grive fissure fillings, and have proposed La Grive M as reference site for MN 7 and La Grive L3 as reference site for MN 8 (we will insist in this point in the following sections).

In the Vallès-Penedès Basin the Late Aragonian is represented by a considerable number of classical localities, such as Sant Quirze or Castell de Barberà, and a high number of unpublished sites, which include all the sites from the ACM series. Agustí (1981a, 1981b, 1982a) described the rodent fauna of the Middle Miocene classical sites of the Vallès-Penedès Basin and distinguished three different local biozones for this time period. The two first ones (*Pseudodryomys ibericus* and *Megacricetodon minor primitivus* zones) correspond to the Early Miocene, while the third one (*Fahlbuschia* [= *Democricetodon*] *crusafonti* zone) is correlated to the MN 8 (Agustí, 1981a, 1981b, 1982a). The type site for this biozone is the classical site of Sant Quirze, and characteristic taxa include *Megacricetodon ibericus*, *Hispanomys dispectus* and *Cricetodon lavocati* besides *D. crusafonti* (Agustí, 1981a, 1981b, 1982a). Other sites included in this biozone are the Lower Hostalets, Castell de Barberà and Can Feliu. Later on the first localities from the Vallès-Penedès Basin attributed to the MN 6 were reported by Agustí *et al.* (1985) (Can Almirall and Les Conilleres, from the Baix Penedès area). Nevertheless, for the moment being the rodent material from these localities remains to be studied in detail (except for the sciurids, which were described by Aldana Carrasco, 1991). More recently Garcés (1995) has added a site which may also correspond tot the MN 6: Rubí-Terrassa 3C (RT-3C), near Rubí, in the Vallès Occidental area. Considering the information provided by the sites of the ACM series a preliminary biozonation of the Late Aragonian of the Vallès-Penedès Basin is sketched:

- **Unnamed biozone (*Megacricetodon gersii/Megacricetodon crusafonti* zone?).** The faunas from the localities that may be placed within this biozone have not been accurately studied yet and the zone boundaries are not well defined. Two sites of the ACM series are included within this biozone: BDL1 and C1-E7+8. This biozone may be defined by the presence of *M. gersii* and/or *M. crusafonti* coupled to the absence of *M. ibericus* (although this species may coexist with *M. gersii* at C1-E7+8, see discussion in 2.2.3.). *Eumyarion medius* may also be characteristic of this biozone. This fits rather well with the definition of MN 6 according to Agustí *et al.* (2001), so this unnamed biozone may correspond to part or all of the MN 6 zone. Since C1-E7+8 is placed 52 m above the basal levels of the ACM series, the lowermost part of this series is regarded as MN 6. Unfortunately, only test samples are available from BDL1 and C1-E7+8, and the sites situated between them (BDL2, BDL3 and C1-D1) do not add any information since they have provided too few remains. Other sites that may also be placed within this biozone include La Gornal 1 and 2 (which are fissure infillings located at the Alt Penedès area), Can Almirall, Les Conilleres and RT-3C. The small mammal fauna from La Gornal has not been prepared yet, while provisional faunal lists for the other sites have been given (Agustí *et al.*, 1985; Garcés, 1995). According to Agustí *et al.* (1985) the rodent fauna from Les Conilleres includes *M. crusafonti* besides *Eumyarion medius* and is correlated to the MN 6. In contrast to the rest of localities Can Almirall is not placed within the Upper Continental Complexes, but in transitional facies of the Marine and Transitional ones. This locality has delivered a rich mammal fauna and some macromammal remains as well. The small mammals include amongst others *Cricetodon* aff. *jotae*, *Fahlbuschia* [= *Democricetodon*] cf. *crusafonti* and *Eumyarion medius* (Agustí *et al.*, 1985). The occurrence of *D. crusafonti* is very unlikely (pers. obs.), although according to Agustí *et al.* (1985) the presence of *Eumyarion medius* and *Cricetodon* aff. *jotae* allows a correlation to MN 6. The possible presence of the suid *Listriodon* at this site will further support this correlation, since this genus first appeared in Western Europe at the MN 6 (Agustí *et al.*, 2001). Agustí (pers. com. to Garcés, 1995) quoted *Eumyarion medius*, *Megacricetodon crusafonti*, *Megacricetodon minor* and *Cricetodon* cf. *albanensis* from RT-3C. RT-3C is a test sample and includes only 11 teeth (a revision of the material has added an $M^{1/2}$ of *Spermophilinus*). The absence of the hypoconid hind arm and a simplified tooth morphology suggests that the identification of *Eumyarion medius* is correct, although it should be better quoted as *E.* cf. *medius*. Nevertheless, *Cricetodon* cf. *albanensis* is identified on the basis of just one M^2, and the inference of the presence of two different *Megacricetodon* species is based on slight differences on the size and morphology of two M^1. Consequently, these identifications should be better regarded as *Megacricetodon* sp. (since the material is too poor to allow the distinction of two different species) and cf. *Cricetodon* sp. RT3-C is situated within the Font del Ferro magnetostratigraphic section, which is 80 m long. Garcés (1995) suggested two possible correlations for RT-3C: a first one to Chron C5AA, and a second alternative one to Chron C5An. The exposed additional data do not allow to choose between these two possibilities, although a correlation to C5AA is proposed here as more likely.

- ***Megacricetodon ibericus* + *Democricetodon larteti* zone.** This biozone is defined on the basis of the sites of the ACM series. Its lower limit lies above the site C1-E7+8 (at 54 m from the base of the series), and the first site unambiguously attributed to this biozone is C1-E9 (at 74 m). Its upper boundary is not so well constrained, although it is probably below 200 m, the site CCV1 clearly belonging to the following biozone. This zone is defined by the joint occurrence of *M. ibericus* and *D. larteti*, although they do not always appear associated in all the sites (for example in BCV1 we have only found *D. larteti*, while the genus *Megacricetodon* is represented by a small-sized species; see chapter 4). *M. ibericus* is first confidently reported from this biozone, while *D. larteti* maybe is present in older sites. Another rodent that probably appears at this biozone is *Eumyarion leemani*. In the sites from the lower part of this biozone (such as C2-B2) we record *Hispanomys decedens*, while in younger ones a different *Hispanomys* species is recorded (temptatively identified as *H. daamsi*). The range of *H. daamsi* extents to the following biozone. No classical sites from the Vallès-Penedès Basin are correlated to this biozone. The definition of this biozone fits well with the revised definition of the MN 7 according to Mein & Ginsburg (2002) (see discussion in section 2.3.3.).

- ***Megacricetodon ibericus* + *Democricetodon crusafonti* zone.** This biozone is considered to be equivalent to the "*Fahlbuschia crusafonti* zone" of Agustí (1981a, 1981b, 1982a). The lower boundary of this zone is probably situated below the 200 m at the ACM series. The CCV1 site (at 292 m) is clearly attributed to this biozone, and the C3-A2 site (for which only a fairly rich test sample is available) may be placed within it as well. If this is correct the lower boundary would be below 170 m. Its upper limit coincides with the arrival of hipparionine horses and the Aragonian/Vallesian boundary at about 11 Ma (see following section). In the Hostalets de Pierola area this transition is recorded in a point between the uppermost levels of the ACM series and Can Mata III, which is 100 m in stratigraphic series above CCV1 and is clearly Vallesian[15]. This biozone is defined by the appearance of *D. crusafonti* which coexists with *M. ibericus* from the previous biozone. Other rodents that first appear in the Vallès-Penedès record within this biozone include *Hispanomys dispectus*, *Hispanomys lavocati*, *Democricetodon brevis nemoralis* and *Muscardinus hispanicus*. The girafids of the genus *Palaeotragus* first appear within this zone (Can Missert, see Agustí *et al.*, 1985; Agustí *et al.*, 2005). The classical sites Sant Quirze, Castell de Barberà[16], Can Missert and probably Can Feliu and most of the sites that define the classical "Lower Hostalets" are correlated to this biozone. The definition of this biozone fits well with the revised definition of the MN 8 according to Mein & Ginsburg (2002) (see discussion in section 2.3.3.).

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[15] Unpublished magnetostratigraphic data indicate that Can Mata III may be correlated to chron C5n.3n, thus yielding an age of about 10.6 Ma for this site.

[16] Some authors have assigned a Vallesian age (MN 9) to this site (see for example De Bruijn *et al.*, 1992). This interpretation was based in the similarity of the rodent assemblage to that of Can Llobateres and in the finding of an *Hipparion* tooth by M. Pickford in a visit to the site with M. Crusafont. This tooth was found on the surface (J. Agustí pers. com.) and in all probability it is derived from upper levels. Concerning the rodent assemblage, the presence of *Cricetulodon*, which would indicate a Vallesian age, has not been reported from Castell de Barberà. Thus, this site is referred to the Late Aragonian.

2.3.2. Biozonation of the Vallesian succession of the Vallès-Penedès Basin: state of art

The Vallesian was defined by Crusafont (1950a) in the Vallès-Penedès Basin to designate the Late Miocene fossil mammal faunas characterized by the first entry of the three-toed equid *Hipparion* (sensu lato). Crusafont (1950a) established the interest and the need for defining a new subdivision for the Late Miocene, given the association in the Vallès-Penedès of this well characterized equid with typical Middle Miocene mammal assemblages. Crusafont (1950a) proposed the Vallesian as a stage and this author considered (at least in a broad way) the criterion of stratigraphic superposition of the fossil mammal localities in the Hostalets de Pierola classical sites, also considering Can Ponsic and Viladecavalls. Nevertheless, Crusafont (1950a) did not situate the fossil localities in a lithostratigraphic framework neither defined a stratotype for the upper and lower boundaries of the Vallesian. Anyway, the Vallesian was broadly accepted as a continental stage and was recognized in other areas, including all Europe and North Africa (Crusafont, 1950a had proposed the Vallesian as restricted to the Iberian Peninsula).

In 1950 Crusafont already proposed a subdivision of the Vallesian into two parts: a lower one including the Upper Hostalets and Can Ponsic and an upper one including the site of Viladecavalls. This subdivision was maintained by Mein (1975) and expressed as the zones MN 9 and MN 10, which correspond to the Early and Late Vallesian, respectively. Crusafont (1950a) based his subdivision of the Vallesian in the absence of certain taxa of Middle Miocene origin at Viladecavalls. Mein (1975) refined the definition of the Early and Late Vallesian. The MN 9 would be characterized by the first appearance of *Hipparion* s. l. as well as the cricetine *Cricetulodon*, besides the extinction of certain rodents such as *Megacricetodon*. The entry in the Iberian Peninsula of the first murids of the genus *Progonomys* and of certain bovids and suids (*Microstonyx*) would characterize the MN 10. Can Llobateres (Vallès-Penedès Basin) was chosen as the reference site for the MN 9, while the Masia del Barbo (Teruel Basin) was erected as the reference site for MN 10. The Turolian would be characterized by an important diversification of murids in the Iberian Peninsula. These subdivisions have survived subsequent revisions and have been maintained throughout the years.

Agustí (1981a, 1981b, 1982a) retained this division of the Vallesian in the type-area with slight changes. His “*Progonomys hispanicus* zone” would equal to the MN 10, while his “*Cricetulodon* zone” would comprise most of the Early Vallesian. Agustí (1981a, 1981b, 1982a) situated the Upper Hostalets in his “*Fahlbuschia crusafonti* zone” resulting of the extension of this biozone into the earliest Vallesian. The rodent fauna of Upper Hostalets is virtually identical to those of the Late Aragonian sites, so the Late Aragonian sites cannot be distinguished from the earliest Vallesian ones on the basis of rodents, only the presence of *Hipparion* s. l. would confirm their age. Later on, Agustí & Moyà-Solà (1991) would modify this zonation and would replace the “*Fahlbuschia crusafonti* zone” by two different zones: the “*Megacricetodon ibericus* zone”, corresponding to the MN 8; and the “*Megacricetodon ibericus* + *Hipparion* zone” or MN 9a. The rest of the MN 9 is the “*Cricetulodon* zone” or MN 9b. Agustí & Moyà-Solà (1991) recognize this subdivision of the Early Vallesian in the Calatayud-Daroca area (where MN 9a would correspond to local zone H and MN 9b to zone I) and in the Duero Basin.

The magnetostratigraphic survey of the Vallès-Penedès Basin started with the doctoral thesis by Miguel Garcés (1995) represented a qualitative jump in the biochronology of the Vallesian. This work consisted in an intensive magnetostratigraphic and biostratigraphic sampling along a SE-NW transect covering the whole width of the basin in the Vallès Occidental. The main results of this work include:

1) The chronology of the first appearance of *Hipparion* s. l. in the Vallès-Penedès Basin (Garcés, 1995; Garcés *et al.*, 1997a), defining the lower boundary of the Vallesian.

2) The magnetostratigraphic (Garcés, 1995; Garcés *et al.*, 1996) and biostratigraphic (Agustí *et al.*, 1997) characteritzation of the Vallesian in its type area.

3) The establishment of an stratotype for the Vallesian defined by the composite section sampled by Garcés (1995).

Agustí *et al.* (1997) subdivided the Vallesian into four different biozones whit well-defined, magnetostratigraphically-calibrated boundaries. These are the following:

- ***Megacricetodon ibericus* + *Hipparion* zone (MN 9a).** This zone is inherited from Agustí & Moyà-Solà (1991) and its lower boundary is defined by the first appearance of *Hipparion* s. l. at the locality of Creu Conill 20 (CCN20). The dispersal of this equid across the Old World was possible because of a global sea level fall of about 100 m (Haq *et al.*, 1987) which connected North America and Asia through Beringia. The First Appearance Datum (FAD) of *Hipparion* s. l. in the Vallès-Penedès Basin is placed at the base of Chron C5r.1n (11.1 Ma; Garcés *et al.* 1996, Garcés *et al.*, 1997a). This age is congruent with the radiometric dating of key sites in Central Europe that suggest ages close to 11.5 +/- 0.5 Ma for the *Hipparion* s. l. FAD (Bernor *et al.*, 1988). Rögl & Daxner-Höck (1996) estimated the age of this event to be 11.2 Ma, based on Central-Eastern Paratethys correlations. However, the chronologic estimates of the *Hipparion* s. l. FAD in the Daroca area (east-central Spain; Garcés *et al.*, 2003), in Sinap (Turkey; Kappelman *et al.*, 1996; Kappelman *et al.*, 2003; Bernor *et al.*, 2003), Siwaliks (Pakistan; Barry *et al.*, 1982; Barry *et al.*, 1985) and Ngororo formation (Kenya; Pickford, 2001) provide somewhat younger dates, ranging from 10.7 to 10.3 Ma, which might indicate that this dispersal was somewhat diachronic. The first-appearing hipparionine horses in the Vallès-Penedès Basin were associated to low diversity faunas dominated by *Megacricetodon ibericus* and to a lesser degree *Hispanomys* (Casanovas-Vilar *et al.*, 2006[17]; Agustí & Gibert, 1982a). However, the rodent association is basically identical to that of the preceding biozone and it is uncertain if the temporal absence of certain taxa (many dormice, flying squirrels, eomyids) may derive of taphonomic biases or may be related to local environmental conditions at specific sites. Nevertheless, Agustí *et al.* (1997) and Casanovas-Vilar *et al.* (2006) have suggested that the *Hipparion* s. l. dispersal may coincide with a short-lasting shift towards dryer conditions in the area (such shift is not detected in the Calatayud-Daroca Basin for instance; Casanovas-Vilar *et al.*, 2006). Amongst the macromammals the

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[17] Casanovas-Vilar *et al.* (2006) quote the presence of the following rodents: *Megacricetodon ibericus*, *Hispanomys dispectus*, *Democricetodon* cf. *sulcatus*, *Cricetulodon* n. sp., *Miodyromys hamadryas*, *Muscardinus hispanicus*, *Euroxenomys minutus* and *Spermophilinus bredai*. The identification of *Democricetodon* cf. *sulcatus* is based on two teeth (one of these damaged) and it should be better regarded as *Democricetodon* sp. (small-sized species). Concerning *Cricetulodon* n. sp., the reported material (an M_1 and an M^2) certainly belongs to a small *Megacricetodon*, so the presence of the *Cricetulodon* at the MN 9a is denied for the time being.

appearance of the felid *Machairodus* (recorded for the first time at CCN20) also occurred at the lower boundary of this zone. The upper boundary is defined by the appearance of the cricetinae *Cricetulodon*. Important mammal sites placed within this biozone include CCN20, CCN22 and Upper Hostalets (Can Flaquer).

- ***Cricetulodon* zone (MN 9b).** This biozone is also inherited from Agustí & Moyà-Solà (1991) and its lower boundary is defined by the sudden appearance in high numbers of the cricetine *Cricetulodon* at many sites (Can Ponsic, Santiga, Ballestar and others). *Cricetulodon* is clearly present from the middle part of Chron C5n (at approximately 10.4 Ma) in the sections of Can Coromines (CCR-2 and CCR-3) and Can Guitart 2 (RT-8) (Agustí *et al*., 1997). This genus is an eastern immigrant, since it is recorded earlier in Turkey (Bayraktepe, MN 7+8; Koufos, 2003). The appearance of *Cricetulodon hartenbergeri* coincided with the disappearance of *Megacricetodon ibericus* and *Democricetodon crusafonti*. The rodent fauna from this biozone is very similar to that of the *Megacricetodon ibericus* + *Democricetodon crusafonti* zone (MN 8) and includes a high diversity of dormice, while the eomyids and the flying squirrels are present again. *C. hartenbergeri* is the species present in the older sites within this biozone (Santiga, Can Ponsic and probably the EDAR[18] set of sites), while in the younger ones (Can Llobateres 1, Can Pallars de Llobateres 3) it is replaced by *C. sabadellensis*. For the moment being this species has only been reported from the Vallès-Penedès Basin. At the classical site of Can Llobateres 1 a few teeth of a murid (Muridae incertae sedis after Mein *et al*., 1993) and one molar of a small-sized *Rotundomys* species (Agustí, 1981a) have also been recovered. These taxa are more characteristic of the following biozone.

- ***Progonomys* + *Cricetulodon* zone.** The lower boundary of this biozone is marked by the first occurrence of the murid *Progonomys* in the basin at 9.7 Ma (Garcés *et al*., 1996; Agustí *et al*., 1997). The first murid, *Antemus*, appeared the Middle Miocene in Pakistan (Jacobs, 1977) while the genus *Progonomys* species originated in that area at about 12 Ma (Jacobs *et al*., 1990; Flynn *et al*., 1995). The first occurrence of *Progonomys* in Turkey is dated at 10.135 Ma (Kappelman *et al*., 2003), but this genus apparently needed about 0.4 Ma to reach Spain, where it is recorded at MN 10. The pre-MN10 record of murids in Spain consist in a few teeth recovered from Can Llobateres 1 (assigned to Muridae incertae sedis by Mein *et al*., 1993) and one M_3 recovered from Pedregueras 2C (late MN 9, Calatayud-Daroca Basin), which cannot be identified to the genus level according to Freudenthal & Martín Suárez (1999). After their arrival in Spain the mice will characterize the rodent assemblage and evolve into several endemic genera during the Vallesian and the Turolian. Recently Aguilar *et al*. (2004) have suggested a much older age for the Aragonian/Vallesian boundary and particularly for the *Progonomys* dispersal. According to these authors *Progonomys* was already present in the MN 9 zone at about 11.4 Ma and did not experience a 2 million year delay in its putative prochoresis from Asia. This conclusion is based on the interpretation of a the short (10 m thick) Ecotet section in which two micromammals sites (Jujurieux 1 and 2) are associated with transitional marine facies that have yielded calcareous nannoplankton and plnaktonik foraminifera belonging to zones NN 6-NN 8 and

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[18] The EDAR (Estació Depuradora d'Aigües Residuals) set of sites include ten new localities that are situated close to the Can Llobateres classic site. This new localities were discovered as the result of the works for the construction of a water treatment plant, although provisional faunal lists have been published (Checa Soler & Rius Font, 2003) the abundant small mammal remains still wait to be prepared.

N14-15. The micromammal sites have not delivered neither *Hipparion* s. l. nor *Progonomys*. On the basis of the presence of *Democricetodon* cf. *nemoralis* in Jujurieux 1 and *Megacricetodon debruijni* (although Aguilar *et al.*, 2004 comment that the few remains recovered from this "cricetid" may either belong to *M. minutus* or *M. minor*) in Jujurieux 1 and 2 the sites are attributed to MN 9. These authors state that *Cricetulodon* (which characterizes the MN 9 in Spain) is only rarely found in French deposits, so they do not consider the presence of this genus as a valid criterion for distinguishing this biozone in France. We have shown in a previous section *Democricetodon brevis nemoralis* and *Megacricetodon minor debruijni* are already present in the Late Aragonian (*Megacricetodon ibericus* + *Democricetodon crusafonti* zone) sites of the Vallès-Penedès Basin, although they persist in the Early Vallesian, after the arrival of the hipparionine horses. The poor data presented by Aguilar *et al.* (2004) neither suggest an MN 9 age for these sites nor add any new information concerning the dispersal of *Progonomys*. Aguilar *et al.* (2004) further reinterpreted several sections, including Bou Hanifia (Algeria) and Kastellios Hill (Greece). In both sections the hipparionine horses occur altogether with *Progonomys* so they have been regarded as Late Vallesian (Krijgsman *et al.*, 1996). However, according to the marine-continental correlations presented by Aguilar *et al.* (2004) they should be referred to the Early Vallesian and that would imply an earlier dispersion of *Progonomys*. However, the mammal site of Bou Hanifia is about 100 m above the marine levels assigned to the N14, suggesting a considerably younger age. In the case of Kastellios Hill the revision of the planktonik foraminifera suggests to this authors that the lower part of the section is referable to N14 and/or N15 instead of N16 as originally suggested by De Bruijn & Zachariasche (1979). Finally, Aguilar *et al.* (2004) also reinterpret the relatively short section of Can Llobateres (which includes two sites: CL1 referred to the MN 9b and CL2 assigned to the MN 10), and conclude that it also may be nearly two million years older, since the presence of *Hipparion* s. l. and *Progonomys* is also congruent with this dating. The magnetostratigraphic section of Can Llobateres (Garcés, 1995; Agustí *et al.*, 1996; Garcés *et al.*, 1996) includes two reverse polarity intervals separated by a normal polarity one. CL2 includes a small sample of seven rodent teeth, five of them attributed to *Progonomys* sp, and is placed in the normal interval, thus it has been correlated to Chron C4Ar.2n (9.7 Ma) according to Garcés (1995), Agustí *et al.* (1996), Garcés *et al.* (1996). This correlation is supported by a litho-, magneto- and biostratigraphic correlation to the Les Fonts and Montagut composite sections of the same basin. The correlation to Chron C5r.2n (ca. 11.5 Ma) suggested by Aguilar *et al.* (2004) can only be supported assuming that the correlation with these composite sections is wrong and also assuming that *Progonomys* was already present prior to 11 Ma. As exposed, both situations are very unlikely in the view of the existing data.

The appearance of *Progonomys* in the Vallès-Penedès coincided with an important decrease in diversity known as the Vallesian Crisis (Agustí & Moyà-Solà, 1990. We will focus in this event, which had important effects on both micro- and macromammals and involved the disappearance of certain taxa, in chapters 6 and 7. The presence of a yet undescribed *Cricetulodon* species (*Cricetulodon* sp. nov. in Agustí *et al.*, 1997) besides one or two *Progonomys* species characterizes this zone. A small-sized *Rotundomys* species is also present at some sites. Important sites referred to this biozone include: Can Llobateres 2 (CL2), Rubí-Terrassa 7 (RT7), La Tarumba 1 (LTR1), Camí de Can Tarumbot 1 and 2 (CCT1, CCT2) and Ceràmiques Viladecavalls (CV). The last record of great apes in the Vallès-Penedès Basin occurs within this zone (LTR1).

- ***Rotundomys bressanus* zone.** The lower boundary of this biozone is defined by the first record of *Rotundomys bressanus*, an hypsodont cricetinae with a lophodont-sigmodont dental pattern, at Chron C4Ar.2r between 9.2-9.3 Ma (Creu Conill 10, Can Turu, Trinxera Nord Autopista, Trinxera Sud Autopista) (Agustí *et al.*, 1997). Amongst the rodents a second *Rotundomys* species is recorded in certain sites, such as Torrent de Febulines 3 (TF3). The murid *Progonomys woelferei* first appears within this biozone. Some large mammal species mostly characteristic of the later Turolian faunas appear in the *Rotundomys* zone: *Hipparion* cf. *mediterraneum*, *Tragoportax gaudryi*, *Indarctos atticus* and *Paramachairodous orientalis* (Moyà-Solà, 1983; Pons-Moyà, 1988). The great apes have apparently disappeared from the area by this time, instead the crouzeline pliopithecid *Egarapithecus narcisoi* is recorded from Torren de Febulines (Moyà-Solà *et al.*, 2001). The upper boundary of this zone is defined by the appearance of *Occitanomys* sp. A at the Piera site, which marks the beginning of the Turolian at about 8.7 Ma (Agustí *et al.*, 2001).

2.3.3. Geographical range of the proposed biozones and correlation to the continental record of other basins

Some of the proposed biozones may extent beyond the Vallès-Penedès Basin into other Spanish basins and into France as well. Previous works have already stressed this point (such as Agustí, 1981a and 1982a, and Agustí & Moyà-Solà, 1991) and even a mammal zonation for all the Iberian Peninsula has been proposed (Agustí & Moyà-Solà, 1991). Here we will discuss the geographical extension of our proposed biozones and their correlation with other continental records, particularly with that of the Calatayud-Teruel Basin (see fig. 2.6. for a graphical summary of the proposed correlations). The proposal of a zonation valid for all the Iberian Peninsula for the considered time interval is beyond this work scope.

The Late Aragonian

Three different bizones are proposed for the Late Aragonian record of the Vallès-Penedès Basin: an unnamed biozone characterized by the presence of *Megacricetodon gersii* and probably *M. crusafonti* as well; the *Megacricetodon ibericus* + *Democricetodon larteti* zone; and the *Megacricetodon ibericus* + *Democricetodon crusafonti* zone. The first biozone, although not well known for the moment, corresponds to the MN 6 on the basis of the presence of *M. gersii* and *M.* cf. *crusafonti*. The occurrence of *Eumyarion medius*, also recorded from Sansan, the reference site for this biozone (Baudelot, 1972), further supports this interpretation. On the basis of the presence of *M. gersii* this zone could be correlated with local zones F or G1 of the type Aragonian in the Calatayud-Daroca Basin (Daams *et al.*, 1999a). The substitution of *M. gersii* by *M. crusafonti* would be diagnostic for zone G2 according to Daams *et al.* (1999a). Apparently, in our sites this situation is reversal and *M.* cf. *crusafonti* (if the adscription of the BDL1 material is right) is recorded before *M. gersii* (C1-E7+8). The study of the new material from the lower part of the ACM series (once processed) will surely shed more light on this contradiction between both records. For the moment being it may be better not to insist in this question.

The *Megacricetodon ibericus* + *Democricetodon larteti* zone can be correlated with the lower part of the zone G3 of the Calatayud-Daroca Basin. The presence of the transitional assemblages *M. crusafonti-M. ibericus* characterizes this biozone according to Daams *et al.* (1999a). These authors already pointed that *Fahlbuschia* [= *Democricetodon*] *crusafonti* appears in the upper part of zone G3, but they did not further subdivide this zone. In the ACM series *M. ibericus* is unquestionably present at C1-E9 associated with *D. larteti*. This *M. ibericus* population shows a relatively smaller size than the type population from Upper Hostalets (see Agustí, 1980a), but there is no clear reason to consider it a different species or a transitional form between *M. crusafonti* and *M. ibericus*. Van der Meulen *et al.* (2003) have quoted the presence of *D. larteti* from certain sites included in zone G3 (Villafeliche 9, Alcocer 2 and the several sites from Toril). We correlate this sites to the *Megacricetodon ibericus* + *Democricetodon larteti* zone.

The *Megacricetodon ibericus* + *Democricetodon crusafonti* zone may be correlated with the upper part of zone G3. Las Planas 5H and Nombrevilla 2, 9 and 10 are referred to this biozone since they all present *D. crusafonti*, although coexisting with *M. crusafonti-M. ibericus* transitional assemblages, and the hipparionine horses are absent.

It is interesting to consider the implications of this local biozonation for the definition of the MN zones. As commented in an previous section, De Bruijn *et al.* (1992) decided to join the MN 7 and MN 8 zones because of the uncertain stratigraphical position of the two reference sites coupled with the fact that only minor differences appeared to exist between the faunas of these two sites. Recently Mein & Ginsburg (2002) claimed that both biozones can be distinguished in La Grive fissure fillings, further proposing La Grive M as reference site for MN 7 and La Grive L3 as reference site for MN 8. The MN 7 would be characterized by the presence of certain taxa including *Megacricetodon gregarius* and *D. larteti* amongst others, while in the MN 8 the putative descendant of *D. larteti*, *D. crusafonti*, would be present besides other taxa such as *Megacricetodon minutus*, *Megacricetodon* aff. *ibericus* and *Dryopithecus fontani* (Mein & Ginsburg, 2002). This division is consistent with our data, since it is supported by a distinction between two biozones depending on the *Democricetodon* species present. The other characteristic taxa cited by Mein & Ginsburg (2002) are very rare or have not been recorded in the Vallès-Penedès Basin. Thus, on the basis of the species of occurrence of *D. larteti* or *D. crusafonti* this biozonation may be applied to the Calatayud-Daroca Basin and France. For the moment being this distinction cannot be extended to other Iberian basins such as the Madrid and Duero Basins. In the first case because of the

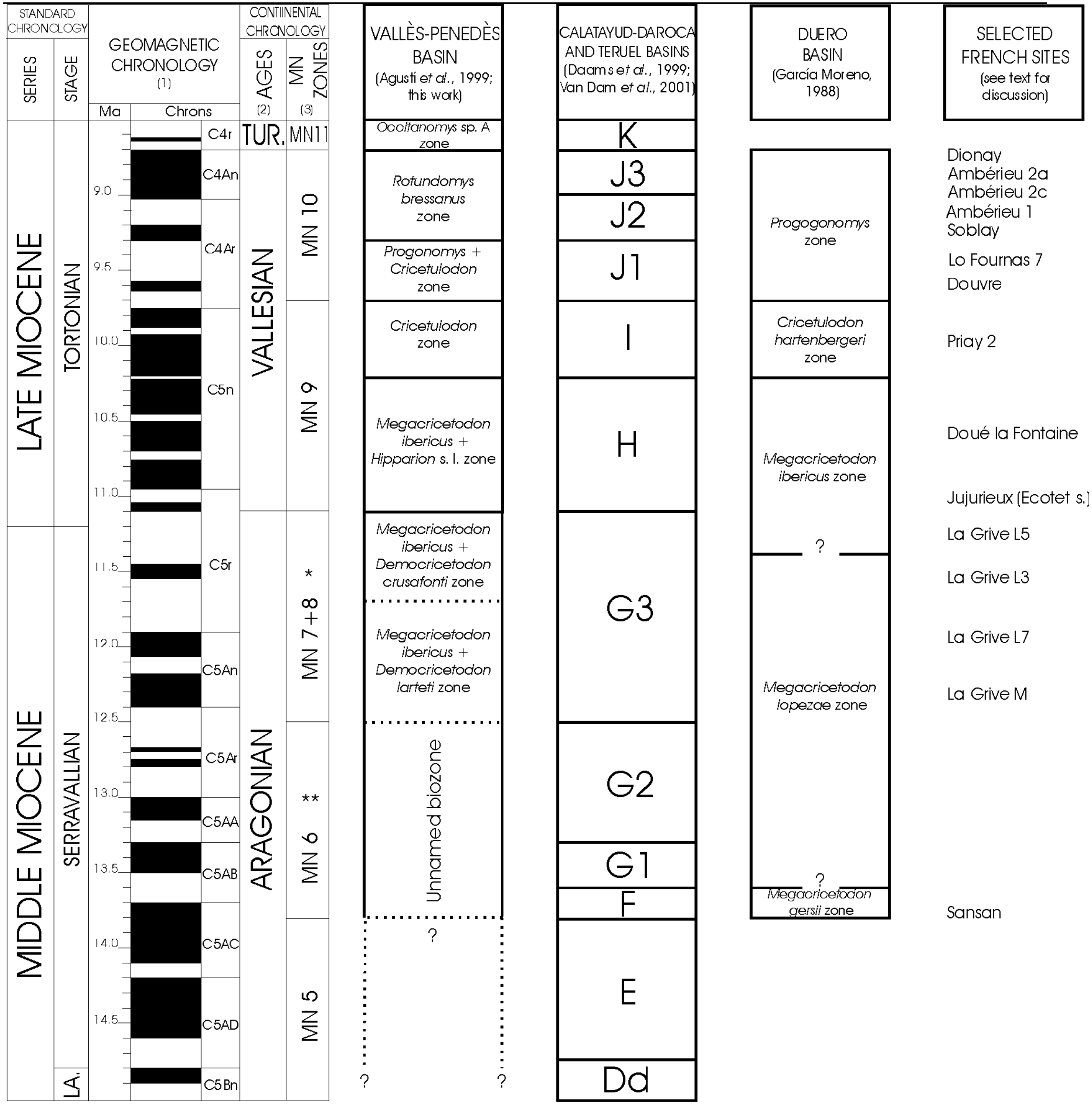

Figure 2.6. Graphical scheme of the proposed correlations between Vallès-Penedès, Calatayud-Daroca and Teruel and Duero basins local biozones. The correlation to selected French sites is also presented as well as a correlation to MN zones and the Geomagnetic Polarity Time Scale (GPTS). In the case of the Vallès-Penedès local biozones, solid lines indicate magnetostratigraphical correlations, while pointed lines indicate biostratigraphical correlations. Question marks are used for uncertain boundaries.[1] after Woodburne & Swisher, 1995; [2] and [3] after Agustí *et al.*, 2001; * indicates the maximum age for the MN 9 lower boundary, while ** indicates the maximum age for the MN 7+8 lower boundary.

presence of an important hiatus coinciding with this time interval (Peláez-Campomanes *et al.*, 2003), while in the second one this is due to the absence of *Democricetodon* from the sites of this basin (García Moreno, 1988). Thus, the MN 7 and MN 8 (although not exactly as defined by Mein & Ginsburg, 2002[19]) may be distinguished in France and northeastern to north-central Spain. In the rest of Europe there is apparently no way to divide the MN 7+8 in two independent zones.

The Early Vallesian

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[19] As many other paleontologists (which according to Lindsay & Tedford, 1990 would be included in a "stratigraphic school of though") we consider that MN zones should be defined on the basis of the occurrence of easily identifiable widespread taxa, instead in considering the whole fauna present at reference sites ("faunal school of thought"). *Hippotherium*, *Progonomys* and, within a more restricted geographic area, *D. larteti* and *D. crusafonti* appear to achieve these requirements.

The *Megacricetodon ibericus* + *Hipparion* (s. l.) zone (Agustí *et al.*, 1997) is equivalent to zone I of the Calatayud-Daroca Basin, which is precisely characterized by the joint occurrence of these taxa (Daams & Freudenthal, 1981; Daams & Freudenthal, 1988a; Daams *et al.*, 1999a). Since the local biozonation of the Calatayud-Daroca Basin has also been extended to the Madrid Basin (Peláez-Campomanes *et al.*, 2003) this biozone may also be recognized there. However, for the moment being the Early Vallesian in this latter basin is not well represented, and no micromammal sites have been reported (Peláez-Campomanes *et al.*, 2003). The *Megacricetodon ibericus* + *Hipparion* (s. l.) can be confidently identified in the Duero Basin (upper part of the *M. ibericus* zone of Garcia Moreno, 1987).

In its turn, the *Cricetulodon* zone (Agustí *et al.*, 1997) equals to zone I (Daams & Freudenthal, 1981; Daams & Freudenthal, 1988a; Daams *et al.*, 1999a) and is characterized by the entry of the cricetine *Cricetulodon* (besides the glirid *Ramys multicrestatus* in the Calatayud and Teruel areas). This zone can be confidently recognized in the Calatayud-Daroca and Teruel basins, and in the Duero Basin as well (*Cricetulodon hartenbergeri* zone of García Moreno, 1988).

In France the Early Vallesian is represented by a few sites including the sites from the Ecotet section (Aguilar *et al.*, 2004) as well as several other localities (Mein, 1999b), most of them being located in fissure fillings from southern France (Aguilar *et al.*, 1999). Many of these sites have delivered a poor and yet undescribed fauna that does not include *Megacricetodon ibericus*, *Hipparion* s. l. or *Cricetulodon*. Accordingly their correlation with the proposed biozones is not possible. However, the site of Priay 2 (Ain County) has delivered *Cricetulodon* (Mein, 1999b) and may be correlated to MN 9b.

The Late Vallesian

The Late Vallesian (MN 10) is equivalent to the *Progonomys hispanicus* zone of Van de Weerd (1976) in the Teruel Basin and to the same named zone of García Moreno (1988) in the Duero Basin. Van Dam (1997) and Van Dam *et al.* (2001) named the zones recognized at the Teruel-Alfambra region with letters following the order established by Daams & Freudenthal (1981) for the Calatayud-Daroca area. The record in the Calatayud-Daroca area ends at zone I, which is also identified in the Teruel Basin, consequently the following biozone should be named zone J (Van Dam, 1997; Van Dam *et al.*, 2001). Zone J equals to the *Progonomys hispanicus* zone of Van de Weerd (1976) although Van Dam (1997) and Van Dam *et al.* (2001) further subdivided this zone into three subzones: J1, from the entry of *P. hispanicus* to the entry of *P. cathalai*; J2, characterized by the total range zone of *P. cathalai*; and J3, from the entry of *Huerzelerimys minor* to the entry of *Parapodemus lugdunensis*. The genus *Rotundomys*, so useful for the subdivision of the Late Vallesian in the Vallès-Penedès Basin is not recorded in inner Spain. However, different *Progonomys* species were quoted by Agustí *et al.* (1997) from the Late Vallesian of the Vallès-Penedès (*P. hispanicus*, *P. woelferi*, *P.* aff. *hispanicus* and *P.* sp.). The study of most of these remains has not been attempted yet, however preliminary data suggest that the zonation devised by Van Dam (1997) and Van Dam *et al.* (2001) cannot be expanded to the Late Vallesian of the Vallès-Penedès Basin.

Rotundomys bressanus is well-known from French sites such as Soblay, Dionay, Ambérieu 1, 2a and 2c (Mein, 1999b). These sites may be correlated to the *R. bressanus* zone of the Vallès-Penedès Basin. Instead, the genus *Cricetulodon* is rare in France, and the joint occurrence of *Progonomys* and *Cricetulodon* has been just recorded at Lo

Fournas 7 (Pyrénées Orientales County; Aguilar *et al.*, 1999) and Douvre (Ain County, Mein, 1999). In both cases *Cricetulodon* (*Cricetulodon* sp. in Lo Fournas 7 and *Cricetulodon bugesiensis* in Douvre) is associated to *Progonomys* and *Rotundomys montisrotundi*. Lo Fournas 7 and Douvre may be tentatively correlated to the *Progonomys* + *Cricetulodon* zone of the Vallès-Penedès Basin.

2.4. Conclusions

The Vallès-Penedès Basin is a classical area for the study of the Miocene mammal successions of Europe. The nearly the whole Miocene epoch is recorded in the sediments of the Vallès-Penedès Basin, mostly belonging to alluvial fan continental deposits. Part of the Middle Miocene, mainly corresponding to the Langhian stage and maybe the earliest Serravallian, is represented by marine and transitional facies. Recently the number of mammal sites known has increased spectacularly as the result of the magnetostratigraphic survey of the Vallès Occidental area, and more importantly by the field work at the Abocador de Can Mata (ACM) series, near els Hostalets de Pierola. A thick and continuous section (300 m) covering the Late Aragonian an (in the near future) the Early Vallesian is being sampled and for the moment being has delivered nearly 100 mammal sites. The preparation and study of the material are still in course, however, preliminary results allows us to suggest a new biozonation for the Late Aragonian of the Vallès-Penedès Basin that may be also applied to the successions of Calatayud-Daroca Basin (Inner Spain) and the La Grive fissure fillings (France). Further field work, and the study of the material will refine these preliminary conclusions.

Appendix 2.1.

The rodent sites from the Upper Continental Complexes of the Vallès-Penedès Basin. Locality acronyms refer to those used in figures and maps. The sites from the ACM (Abocador de Can Mata) series are not included. The position of each site in the defined biozones (see section 2.3.) is given. In the case of these sites for which magnetostratigraphical data are available we have also indicated the section they belong and the geomagnetic Chron were they are placed. The presence of macromammal remains is also indicated.

Acronym	Locality	Magnetostratigraphic section	Biozone	Chron	Macrovertebrates
CAL	Can Almirall	-	unnamed? (MN 6?)	-	X
CB	Castell de Barberà	-	*M. ibericus* + *D. crusafonti*	-	X
CC	Can Coromines	Can Coromines (CC)	*Cricetulodon*	-	
CCN 10	Creu Conill 10	Creu Conill (CCN)	*Rotundomys bressanus*	C4Ar.1n	
CCN 20	Creu Conill 20	Can Guitart 1 (GT-1)	*M. ibericus* + *Hipparion* s. l.	C5r.1n	X
CCN 22	Creu Conill 22	Can Guitart 1 (GT-1)	*M. ibericus* + *Hipparion* s. l.	C5r.1r	X
CCR 2	Can Coromines 2	Can Coromines (CR)	*Cricetulodon*	C5n.1r	
CCR 3	Can Coromines 3	Can Coromines (CR)	*Cricetulodon*	C5n.1r	X
CCT 2	Camí de Can Tarumbot 2	Can Tarumbot (CCT)	*Progonomys* + *Cricetulodon*	C4Ar.2r	
CCT 3	Camí de Can Tarumbot 3	Can Tarumbot (CCT)	*Progonomys* + *Cricetulodon*	C4Ar.2r	
CF	Can Feliu	-	*M. ibericus* + *D. crusafonti* ?	-	X
CFEU	Can Feu	-	*Cricetulodon*	-	X
CL 1	Can Llobateres 1	Can Llobateres (CL)	*Cricetulodon*	C4Ar.3r	X
CL 2	Can Llobateres 2	Can Llobateres (CL)	*Progonomys* + *Cricetulodon*	C4Ar.2r	X
CM	Can Missert	-	*M. ibericus* + *D. crusafonti*	-	X
CP	Can Ponsic	-	*Cricetulodon*	-	X
CPL3	Can Pallars de Llobateres 3	-	*Cricetulodon*	-	
CS	Can Casablanques	-	*Progonomys* + *Cricetulodon*	-	X
CTU	Cal Turu	Pedrera de Viladecavalls (VQ)	*Rotundomys bressanus*	C4Ar.1r	
CU	Les Cunilleres	-	unnamed? (MN 6?)	-	
CV	Ceràmiques Viladecavalls	Pedrera de Viladecavalls (VQ)	*Rotundomys bressanus*	C4Ar.1n	X
EDAR 2	Est. Dep. Aigües Residuals del Riu Ripoll 2	-	*Cricetulodon*	-	X
EDAR 3	Est. Dep. Aigües Residuals del Riu Ripoll 3	-	*Cricetulodon*	-	X
EDAR 6	Est. Dep. Aigües Residuals del Riu Ripoll 6	-	*Cricetulodon*	-	X
GO1	La Gornal 1	-	unnamed? (MN 6?)	-	
GO2	La Gornal 2	-	unnamed? (MN 6?)	-	
HI	"Lower Hostalets de Pierola"	-	*M. ibericus* + *D. crusafonti*	-	X
HS	Upper Hostalets de Pierola (= Can Flaquer and nearby sites)	-	*M. ibericus* + *Hipparion*	-	X
LTR 1	La Tarumba 1	La Tarumba (LT)	*Progonomys* + *Cricetulodon*	C4Ar.2r	X
MA	Masquefa	-	unnamed? (MN 6?)	-	
PI	Piera	-	MN 11	-	X
PR	Can Perellada	-	*Rotundomys bressanus*	-	X
RK 11	Autopista de Rubí-Terrassa Km 11	Can Guitart 2 (GT-2)	*M. ibericus* + *Hipparion*	C5n.2n	
RK 27	Autopista de Rubí-Terrassa Km 27	Can Guitart 2 (GT-2)	*M. ibericus* + *Hipparion*	C5n.2n	X
RR	Riu Ripoll	-	*Progonomys* + *Cricetulodon*	-	
RT 10	Autopista de Rubí-Terrassa 10	Can Guitart 3 (GT-3)	*Progonomys* + *Cricetulodon*	C4Ar.2r	X
RT 12	Autopista de Rubí-Terrassa 12	Les Martines (MR)	*Cricetulodon*	C4Ar.3r	
RT 3B	Autopista de Rubí-Terrassa 3B	Can Ferran (FR)	*M. ibericus* + *Hipparion*	C5n.2n	

RT 3C	Autopista de Rubí-Terrassa 3C	Font del Ferro (FF)	unnamed? (MN 6?)	C5AA?	
RT 6E	Autopista de Rubí-Terrassa 6E	Can Guilera (GL)	*M. ibericus* + *Hipparion*	C5n.2n	
RT 7	Autopista de Rubí-Terrassa 7	Creu Conill (CCN)	*Progonomys* + *Cricetulodon*	C4Ar.3r	
RT 8	Autopista de Rubí-Terrassa 8	Can Guitart 2 (GT-2)	*M. ibericus* + *Hipparion*	C5n.2n	
S	Santiga	-	*Cricetulodon*	-	X
SPRC1	Sant Pere de Ribes Pedrera C1	-	unnamed? (MN 6?)	-	
SQ	Sant Quirze (trinxera ferrocarril)	-	*M. ibericus* + *D. crusafonti*	-	X
SQA	Sant Quirze A	-	*M. ibericus* + *D. crusafonti*	-	
SQB	Sant Quirze B	-	*M. ibericus* + *D. crusafonti*	-	
SQG	Sant Quirze G	-	*M. ibericus* + *D. crusafonti*	-	
TF3	Torrent de Febulines 3	Torrent de Febulines (TF)	*Rotundomys bressanus*	C4An	X
TF (M)	Torrent de Febulines M	Torrent de Febulines (TF)	*Rotundomys bressanus*	C4An	X
TSA1	Trinxera Sud Autopista 1	-	*Rotundomys bressanus*	-	
TSA2	Trinxera Sud Autopista 2	Torrent de Febulines (TF)	*Rotundomys bressanus*	C4Ar.1r	X
TSA3	Trinxera Sud Autopista 3	-	*Rotundomys bressanus*	-	
TNA	Trinxera Nord Autopista	Torrent de Febulines (TF)	*Rotundomys bressanus*	C4Ar.1r	X
TNA2	Trinxera Nord Autopista 2	-	*Rotundomys bressanus*	-	
VI	Viñedos	-	unnammed? (MN 6?)	-	
VK7	Viladecavalls Km 7	Pedrera de Viladecavalls (VQ)	*Rotundomys bressanus*	-	

Appendix 2.2.

Synthetic faunal list of the fossil vertebrates found at the Abocador de Can Mata (ACM) series and Barranc de Can Vila 1 (BCV1) site. It is based only in the material recovered during the 2002-2003, 2004 and 2005 field campaigns. It should be noted that not all the macromammals that are quoted in the taxonomic list of ACM lived at the same time.

Class AMPHIBIA
- cf. Amphibia indet.

Class AVES
- Gen. et sp. indet.

Class REPTILIA
- Order TESTUDINES
  - Family Testudinidae
  - *Cheirogaster bolivari* (Hernández-Pachecho, 1917)
  - *Testudo* cf. *catalaunica* Bataller, 1926
- Order SQUAMATA
  - Family Lacertidae
    - Lacertidae Gen. et sp. indet.
  - Family Gekkonidae
    - Gen. et sp. indet.
  - Family Amphisbaenidae
    - Gen. et sp. indet.
  - Family Anguidae
    - cf. *Pseudopus* sp.
  - Family Colubridae
    - Gen. et sp. indet.

Class MAMMALIA
- Order INSECTIVORA
  - Family Soricidae
    - Gen. et sp. indet.
    - Crocidosoricinae indet.
  - Family Talpidae
    - *Talpa minuta* Blainville, 1840
    - cf. *Proscapanus* sp.
  - Family Erinaceidae
    - *Parasorex* cf. *socialis* (von Meyer, 1865)
    - Gen. et sp. indet.
    - Erinaceinae indet.
  - Family Heterosoricidae
    - *Dinosorex sansaniensis* (Lartet, 1851)
  - Family Dimylidae
    - *Plesiodimylus chantrei* Gaillard, 1897
- Order CHIROPTERA
    - Chiroptera gen. et sp. indet.
- Order LAGOMORPHA
  - Family Ochotonidae
    - *Prolagus oeningensis* (König, 1825)
    - *Eurolagus fontannesi* (Depéret, 1887)
- Order RODENTIA
  - Family Paracricetodontidae
    - *Eumyarion leemani* (Hartenberger, 1965)
  - Family Cricetodontidae
    - *Hispanomys decedens* (Schaub, 1925)
    - *Hispanomys daamsi* Agustí et al., 2005
    - *Hispanomys* sp. (BCV1)
    - *Democricetodon brevis brevis* (Schaub, 1925)

Democricetodon brevis nemoralis Agustí, 1981
Democricetodon larteti (Schaub, 1925)
Democricetodon crusafonti (Agustí, 1978)
Megacricetodon gersii Aguilar, 1980
Megacricetodon minor minor (Lartet, 1851)
Megacricetodon minor debruijni Freudenthal, 1968
Megacricetodon cf. *crusafonti* (Freudenthal, 1963)
Megacricetodon ibericus (Schaub, 1944)
Family Anomalomyidae
Anomalomys gaudryi Gaillard, 1900
Family Eomyidae
Keramidomys carpathicus (Schaub & Zapfe, 1953)
Eomyops cf. *oppligeri* Engesser, 1990
Family Gliridae
Glirudinus undosus Mayr, 1979
Muscardinus sansaniensis (Lartet, 1851)
Muscardinus hispanicus De Bruijn, 1966
Microdyromys complicatus De Bruijn, 1966
Paraglirulus werenfelsi Engesser, 1972
Bransatoglis astaracensis (Baudelot, 1970)
Family Sciuridae
Albanensia albanensis albanensis (Major, 1893)
Miopetaurista neogrivensis (Mein, 1970)
Miopetaurista cf. *crusafonti* (Mein, 1970)
? *Blackia* sp.
Spermophilinus bredai (Von Meyer, 1848)
Heteroxerus sp.
Family Castoridae
Chalicomys sp. nov.
Order PROBOSCIDEA
Family Deinotheriidae
Deinotherium giganteum Kaup, 1829
Family Gomphotheriidae
Gomphotherium angustidens (Cuvier, 1817)
cf. *Tetralophodon longirostris* (Kaup, 1832)
Order PERISSODACTYLA
Family Chalicotheriidae
Chalicotherium grande Blainville, 1849
Family Equidae
Anchitherium sp.
Family Rhinocerotidae
Alicornops simorrensis (Lartet, 1851)
cf. *Hoploaceratherium tetradactylum* (Lartet, 1851)
Order ARTIODACTYLA
Family Suidae
Listriodon splendens Meyer, 1846
Conohyus steinheimensis (Fraas, 1870)
Korynochoerus palaeochoerus (Kaup, 1833)
Albanohyus pygmaeus (Depéret, 1892)
Family Palaeochoeridae (=Tayasuidae s.l.)
cf. *Taucanamo* sp.
Family Tragulidae
Dorcatherium naui Kaup, 1834
Family Bovidae
Miotragocerus cf. *monacensis* Strömer, 1928
cf. *Eotragus* sp.
Family Moschidae
Micromeryx flourensianus Lartet, 1851
Family Cervidae
Euprox furcatus (Hensel, 1859)
Order CARNIVORA
Family Mustelidae
Martes munki Roger, 1900

    - *Ischyrictis mustelinus* (Viret, 1933)
    - *Trocharion albanense* Major, 1903
  - Family Nimravidae
    - *Sansanosmilus jourdani* (Filhol, 1883)
  - Family Viverridae
    - *Leptoplesictis* cf. *aurelianensis* (Schösser, 1888)
  - Family Felidae
    - *Pseudaelurus* sp.
  - Family Hyaenidae
    - *Thalassictis montadai* (Villalta & Crusafont, 1943)
    - *Protictitherium crassum* (Depéret, 1892)
- Order PRIMATES
  - Family Pliopithecidae s. l.
    - Pliopithecidae Gen. et sp. indet.
  - Family Hominidae
    - *Pierolapithecus catalaunicus* Moyà-Solà *et al.*, 2004
    - *Dryopithecus* sp.
    - Gen. et sp. nov.

Chapter 3

A new beaver species from Abocador de Can Mata (Vallès-Penedès Basin, Catalonia, Spain) and a discussion on the taxonomy and paleobiology of the genus *Chalicomys* Kaup, 1832

3.1. Introduction

Unlike many other rodents, castorids are relatively scarce in most sites (Aldana Carrasco, 1992), this being probably related to taphonomic biases as well as particular ecological requirements. In this chapter, the first castorid remains from the Abocador de Can Mata series (ACM, els Hostalets de Pierola) are described. These fossil remains, including some dentognathic specimens and a single postcranial bone, are very rare among the ACM fauna. They represent less than 0.05 % of the total recovered vertebrate remains at ACM, which contrasts with the higher abundance that they present in certain Late Aragonian sites of the Vallès area: close to 4 % in Sant Quirze (Crusafont, 1956; see chapter 6) and more than 50 % in Castell de Barberà (see chapter 6). In fact, fossil beavers had never been found before in the Penedès/Anoia area of the Vallès-Penedès Basin, and this negative evidence had been employed to infer somewhat less humid conditions than in other areas of the same basin (Crusafont, 1950).

Bataller (1918) published the first citation of castorids from the Catalan Neogene, but the first reference to those from Vallès-Penedès Basin is not found until Bataller (1924), on the basis of dental material from Trinxera del Ferrocarril in Sant Quirze (MN 7+8). Bataller (1928) first attributed these remains to *Steneofiber sansaniensis*, but later on, Bataller (1938) attributed the smaller remains to *Steneofiber minutus*, and the larger ones to *Steneofiber minutus* raça [sic] *catalaunica*. This attribution was followed by Villalta & Crusafont (1941), who further reported the occurrence of *Steneofiber Jaegeri* [sic] from Viladecavalls (MN 10). A few years later, Crusafont & Truyols (1947) reported the presence of *Monosaulax minutus* at Can Ponsic (MN 9), and slightly later, in their revision of fossil beavers from Spain, Crusafont *et al.* (1948) added the presence of *Steneofiber depereti* at this site. Crusafont *et al.* (1948) further synonymized with the latter species the large castorid from Sant Quirze. Additional castorid findings at the Vallès-Penedès Basin were reported for Can Llobateres (MN 9) (Crusafont & Truyols, 1960; Crusafont, 1964), as well as Castell de Barberà and Can Feliu (MN 7+8) (Crusafont-Pairó & Golpe, 1972).

More recently, Aldana Carrasco (1991) reviewed the sciuromorph rodents from the Catalan Neogene in his doctoral thesis, further publishing the part devoted to castorids in Aldana Carrasco (1992). This investigator does not significantly depart from previous taxonomic schemes, by recognizing the presence at the Vallès-Penedès of the previously cited taxa (*Chalicomys* or *Palaeomys depereti*, *C. jaegeri* or *P. castoroides*, and *Monosaulax minutus*), plus a new genus and species, *Schreuderia adroveri*, from Torrent de Febulines (MN 10). After Hugueney's (1999) revision of European Miocene Castoridae, *Steneofiber* and *Chalicomys* are no longer considered synonyms, the small castorid from Sant Quirze is transferred to *Trogontherium (Euroxenomys) minutus*, and the large taxon from Sant Quirze is recognized as a distinct species ?*Eucastor (Schreuderia) catalaunicus*. Finally, Korth (2001) considers that *Euroxenomys* and *Schreuderia* should be ranked at the genus level, further transferring the latter to the Castorinae. In this paper, the castorid remains from ACM are attributed to a new species of the genus *Chalicomys*, whereas the material of the large species from Sant Quirze is further referred to this genus.

3.2. Systematic paleontology

Order **Rodentia** Bowdich, 1821

Suborder **Sciuromorpha** Brandt, 1855

Infraorder **Castorimorpha** Wood, 1955

Family **Castoridae** Hemprich, 1820

Subfamily **Castorinae** Hemprich, 1820

Genus *Chalicomys* Kaup, 1832 (= *Palaeomys* Kaup, 1832; *Chelodus* Kaup, 1832)

Type species: *Chalicomys jaegeri* Kaup, 1832.

Emended diagnosis: Medium- to large-sized Castorinae, with a tetralophodont occlusal pattern, with the synclines/-ids parallel to one another. Anteriorly flattened incisors, with subtriangular occlusal contour. Strong degree of hypsodonty. Rooted cheek teeth with cement (usually abundant) on the synclines/-ids. Hypostria/-iid moderately to very long. Para-, meso- and metastria/-iid long but ending far from the crown base. In molars, mesostria/-iid longer than the other striae; in premolars, parastria/-iid longer than metastria/-iid. Premolar longer than molars. 8-shaped lower premolar, not clearly pyramidal. Long mesoflexus, directed backwards until nearly reaching the posterior margin of the tooth. Hypoflexus facing the paraflexus. End of mesoflexid anterior to hypoflexid.

Differential diagnosis: Differs from *Steneofiber* Geoffroy-Saint-Hilaire, 1833 by the tetralophodont (instead of pentalophodont) occlusal pattern, the markedly more hypsodont cheek teeth, the greater abundance of cement, and the somewhat longer mesostria. Differs from *Castor* Linnaeus, 1758, by the rooted and less hypsodont cheek teeth, the less abundant cement, the slightly shorter hypostria/-iid, the longer third molars, the longer and 8-shaped P_4, and the shorter and stouter mandible. Differs from *Schreuderia* Aldana Carrasco, 1992 by the non-reduced M^3 and the lack of tendency towards an S-pattern.

Included species: *Chalicomys jaegeri* Kaup, 1832 (=*Palaeomys castoroides* Kaup, 1832; *Chelodus typus* Kaup, 1832); *Chalicomys subpyrenaicus* (Lartet, 1851); *Chalicomys catalaunicus* (Bataller, 1938) comb. nov.; ? *Chalicomys plassi* (Storch in Franzen & Storch, 1975); *Chalicomys* sp. nov.

Chalicomys n. sp.

(Figs. 3.1.-3.3.)

Holotype: Right hemimandible with complete definitive dentition (I_2 and P_4-M_3) and some associated bone fragments (IPS 41694, field number ACM13992) (Figs. 3.1. A-C and 3.2. A-C), housed at the collections of the Institut de Paleontologia M. Crusafont in Sabadell (Catalonia, Spain).

Paratypes: Left maxillary fragment with M^2-M^3 (IPS 41695a, field number ACM13976) (Figs. 3.1. D–F and 3.3. A-C), plus associated isolated left P^4 (IPS 41695c)

(Figs. 3.1. G–I and 3.3. D-F) and isolated right $M^{1/2}$ (IPS 41695b) (Figs. 3.1. J–L and 3.3. G-I); right maxillary fragment with P^4 (IPS 41696, field number ACM16213) (Figs. 3.1. M–O and 3.3. J-L). These remains are housed at the collections of the Institut de Paleontologia M. Crusafont in Sabadell (Catalonia, Spain). The paratypes were found at the type locality, not only at the same stratigraphic level than the holotype, but very close to it (at a distance of about 40 cm in the case of IPS 41695, and about 65 cm in the case of IPS 41696), which suggests that they probably belong to the same individual.

Type locality: ACM/C4-C2, i.e. Abocador de Can Mata locality C4-C2.

Age: Middle Miocene (Late Aragonian, MN 7+8 biozone).

Diagnosis: Lower incisor with subtriangular occlusal contour and flattened anterior surface. Rooted cheek teeth with a marked degree of hypsodonty. Tetralophodont occlusal pattern, with abundant cement on the flexi/-ids and fossettes/-ids. All these valleys parallel to one another, and somewhat oblique relative to the mesiodistal axis of the crown. Long hypostria/-iid on all cheek teeth, almost reaching the crown base. Premolars longer than molars. Third molars similar in length to other molars, but M_3 more similar to the P_4 in occlusal outline. Occlusal surface of the whole lower postcanine tooth row slightly concave. 8-shaped lower premolar, becoming only minimally larger towards the base, and with a very long mesostriid. Lower molars with shorter mesostriid than the premolar. Para- and metastriid on all lower cheek teeth shorter than the mesostriid. Many cheek teeth, specially lower ones and P^4, with pronounced secondary enamel folds (crenulations) resulting in complex patterns on certain fossetids. Mesoflexids end mesially from hypoflexids. Upper cheek teeth conspicuously curved. Mesostriae ending far from the base of the crown, and hypoflexus facing the paraflexus. Long mesoflexus curved backwards towards the distal margin of the crown. On P^4, parastria almost twice longer than mesostria; mesoflexus open at the distal margin; mesiobuccal cusp isolated from the rest of the first loph.

Differential diagnosis: Differs from other *Chalicomys* species by the common presence of pronounced secondary enamel folds, particularly on P_4, M_3 and P^4 (in *C. subpyrenaicus* only evaluable on P_4), and by the distally-open mesoflexus (only evaluable in *C. jaegeri* and *C. catalaunicus*). Further differs from *C. jaegeri* by the smaller size, the somewhat shorter hypostria/-iid, and the lower degree of hypsodonty. Further differs from *C. subpyrenaicus* by the lingually-open paraflexid, by the morphology and proportions of P_4 and by the longer mesostriid on this tooth. Further differs from *C. catalaunicus* by the larger size, the greater abundance of cement, the longer hypostria/-iid, and the longer mesostriid on the lower premolar. Further differs from ?*C. plassi* by the larger size and the greater degree of hypsodonty, among others.

Measurements:

Mandible

Description of the measurement	IPS 41694
Length of postcanine series at the occlusal level	28.10
Length of postcanine series at the alveolar level	31.40
Symphysis height	32.80
Height of mandibular body at the lingual side (perpendicular to the alveolar level), at the level of P_4	22.70
Height of mandibular body at the lingual side (perpendicular to the alveolar level), at the level of M_1	22.00
Height of mandibular body at the lingual side (perpendicular to the alveolar level), at the level of M_2	19.80
Height of mandibular body at the lingual side (perpendicular to the alveolar level), at the level of M_3	18.80
Breadth of mandibular body (perpendicular to mandibular height), at the level of P_4	14.40
Breadth of mandibular body (perpendicular to mandibular height), at the level of M_1	16.10
Breadth of mandibular body (perpendicular to mandibular height), at the level of M_2	17.40
Breadth of mandibular body (perpendicular to mandibular height), at the level of M_3	18.80

Lower incisor

Description of the measurement	IPS 41694
anterior width at occlusal level	(7.20)
posterior width at occlusal level	(5.30)
wear facet anteroposterior length	8.60

Cheek teeth

	Lower cheek teeth						Upper cheek teeth				
	WS	L	W	H	HH		WS	L	W	H	HH
P_4	2-3	9.00	6.20	-	-	P^4	2	7.70	(6.60)	21.50	9.60
							2	8.00	(6.80)	>17.90	>3.30
M_1	3	7.00	6.50	-	-	$M^{1/2}$	3	6.00	6.00	17.20	8.30
M_2	3	6.10	6.30	-	-	M^2	3	5.90	5.90	-	-
M_3	3	6.60	5.80	-	-	M^3	3	5.60	(5.50)	-	-

Hypodigm: A left femur (IPS 41693) (Fig. 3.4. C–D) from ACM locality C3-Ak is also tentatively attributed to this taxon.

3.2.1. Description of the holotype and paratypes

The holotype of *Chalicomys* sp. nov. (IPS 41694) includes an almost complete right hemimandible with associated bone fragments (including the left mandibular articular apophysis), whereas the paratypes include a right maxillary fragment with P^4 (IPS 41696), and a left maxillary fragment with M^{2-3} (IPS 41695a) with two associated teeth: a left P^4 (IPS 41695c) and a right $M^{1/2}$ (which is very close in size and morphology to the left M^2) (IPS 41695a). Below, we first described the mandible and the lower dentition (on the basis of the holotype), and then we described the preserved portion of the maxilla and the upper dentition (on the basis of the paratypes).

Mandible: It preserves the mandibular corpus and most of the mandibular ramus, except for the upper part of the coronoid apophysis and the angular apophysis almost entirely. Furthermore, the incisor and premolar alveoli are slightly damaged. The mandibular symphysis is preserved throughout its length. All the definitive dentition is present, including the single incisor and the whole postcanine series (from P_4 to M_3), and displays a moderately advanced degree of wear, indicating that these remains belonged to an adult individual.

Overall, the mandible is stout and relatively short, and the mandibular symphysis is quite deep as compared to the mandibular body. The symphysis is also considerably steep and almost straight (only slightly convex) in lateral view, with a well-developed digastric eminence. The occlusal surface of the postcanine series is not completely flattened, but slightly concave, with the premolar and the last molar further being slightly more elevated than the other teeth. Crown dimensions for the whole series are slightly greater at the alveolar than at the occlusal level. When the mandible is oriented horizontally on the basis of the alveolar plane, the tip of the incisor lies somewhat below the postcanine occlusal plane. The incisor is separated from the postcanine tooth row by a moderately deep and short diastema, which is somewhat asymmetrical (its lowermost point is placed slightly backwards). The mandibular corpus is robust and deep; it is widest at the level of M_2, and highest at the level of P_4, just behind the diastema, progressively decreasing until M_3. Albeit damaged, the mandibular ramus is complete enough as to see that it is quite steeply inclined (at about 60º from the alveolar plane). The anterior margin of the ramus originates from the level of M_1/M_2, and in buccal view it overlaps partially with M_2 and completely with M_3. In posterior view, the articular condyle and the angular process are directed medially, whereas the coronoid process, apparently more protruding that the mandibular condyle, is situated on the same plane than the rest of the ramus.

The mental foramen is elliptical, being situated below the diastema at about the middle height of the corpus. A well-developed upper masseteric ridge extends obliquely from the anterior margin of the ramus until a somewhat swollen region at about the middle height of the corpus at the level of M_1; the lower masseteric ridge is not well defined. A large, deep and rather U-shaped masseteric fossa occupies a large portion of the ramus until approximately the alveolar level. A small circular foramen lies just anterior to it. In lingual view, at the anterior portion of the ramus, there is a U-shaped insertion scar for the temporal muscle that almost reaches the alveolar plane. The mandibular foramen, which is large and elliptical, is placed more posteriorly. A similarly-shaped, but more ill-defined, insertion for the external pterygoid muscle is present below the mandibular condyle on the inner side of the ramus. The insertion area

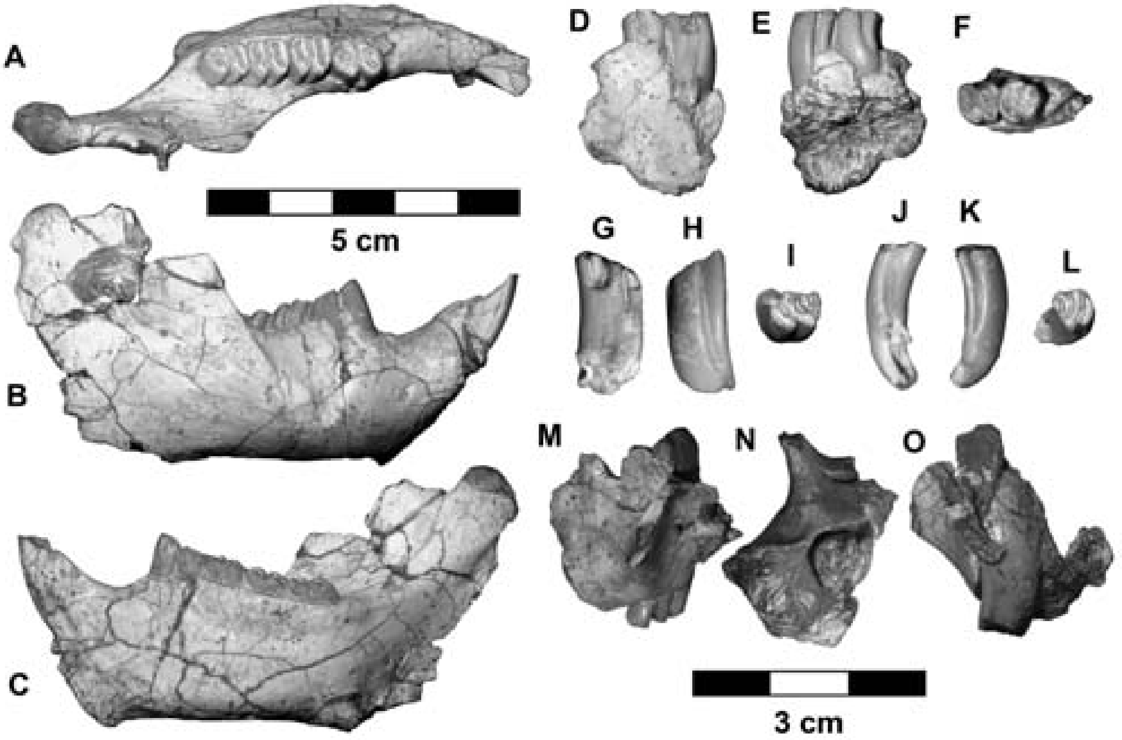

Figure 3.1. Holotype and paratypes of *Chalicomys* n. sp. from Abocador de Can Mata locality C4-C2. A, B, C, right hemimandible IPS 41694 (holotype), A, occlusal; B, buccal; C, lingual; D, E, F, left maxillary fragment with M^{2-3} IPS 41695a (paratype), D, buccal; E, lingual; F, occlusal; G, H, I, left P^4 IPS 41695c (paratype), G, buccal; H, lingual; I, occlusal; J, K, L, right $M^{1/2}$ IPS 41695b (paratype), J, buccal; K, lingual; L, occlusal; M, N, O, right maxillary fragment with P^4 IPS 41696 (paratype), M, buccal; N, occlusal; O, anterior.

for the mylohyoid muscle is well defined and extends throughout the lingual side of the corpus from M_3 to the diastema. At the lingual side of the angular apophysis, there is a relatively shallow fossa, at the area of insertion of the internal pterygoid. Finally, a small circular depression is present at the anteriormost part of the corpus, on the lingual side just next to the symphysis.

I_2: The lower incisor, albeit complete, is longitudinally broken into two blocks that are slightly displaced from one another. Distortion is however minimal, so that the morphology of the tooth can be adequately asserted. It is a robust and markedly curved incisor, with subtriangular outline on the occlusal surface, and with a flattened anterior side. The enamel is smooth and thin, and although enamel thickness is slightly greater at the external than at the symphyseal side, it does not even reach a third of crown's width.

P_4: Although the distolingual corner is damaged, with the enamel having partially collapsed into the metafossetid, this tooth is otherwise well preserved. It is a 8-shaped premolar, with two main parallel pillars, which are separated from one another by the mesostriid and the hypostriid. It is a rather cylindrical tooth, so that it does not become much narrower towards the occlusal surface. It is not completely vertically inserted into the mandible with respect to the alveolar plane, and the mesial lobe is higher than the distal one. The wear surface is rather flat, being moderately worn (stages 2-3 of Aldana, 1991), with the paraflexid and the metaflexid having almost become fossetids. There is a very long hypostriid, which enters into the alveolus. At the lingual side, only two striids are present: the parastriid and the mesostriid. The former is extremely short, unlike the mesostriid, which is much longer (similarly to the hypostriid). All the flexids and fossetids display abundant cement. Secondary enamel folds are specially common on the metafossetid. The tooth can be structured into four main lophids. The paraflexid is almost closed by the metaconid and by a well-developed mesostylid, which are situated very close to one another. This flexid, which is very long, is mesiobuccally directed, particularly on its buccal portion, almost reaching the mesiobuccal corner of the crown. On the contrary, the lingual portion of the paraflexid is less oblique, being parallel to the mesoflexid. The buccal end of the latter is placed mesially with respect to the hypoflexid, and extends beyond the buccolingual midline of the crown. On its extreme, the mesoflexid displays two spurs that originate in opposite directions. The distal valley displays a very complex structure, being open at the distalmost edge, although at the present level of wear this communication has been almost entirely lost. This valley is divided into two moieties by a prominent stylid-like fold originating from the third lophid, which almost contacts with the fourth one. In a somewhat more lingual position, also arising from the third lophid, there is another important fold parallel to the first one. The fourth lophid is interrupted before reaching the entoconid.

M$_1$: The first molar is quadrangular in outline, being inserted somewhat obliquely backwards into the mandible relative to the alveolar plane. The wear surface is flat, with a tetralophodont occlusal pattern. The mesoflexid is not closed, but only an extremely short lingual striid (the mesostriid) can be observed. The hypoflexid is continued by a hypostriid that passes the alveolar plane inside to the alveolus. The flexids and fossetids display abundant cement. These elements are parallel to one another, and slightly oblique with respect to the mesiodistal axis of the crown. The occlusal surface displays a moderate degree of wear (stage 3 of Aldana Carrasco, 1991), given the fact that two fossetids, the parafossetid and the metafossetid, can be recognized. The parafossetid is very long, almost extending from the lingual to the buccal sides of the crown. The mesoflexid is placed mesially relative to the end of the hypoflexid. The metafossetid is divided into two portions, a lingual and a buccal one. The lingual portion of the metafossetid displays a triangular contour, with the lingual end being more acute and mesiolingually directed, whereas the buccal portion is rather transversely aligned.

M$_2$: The second molar displays most of the already described characteristics of the first one, being similar in shape, although with a somewhat squarer outline. The degree of wear is quite similar to the M$_1$, with a somewhat longer but still quite short mesostriid. The parafossetid is also quite long, but with a more sinuous course. At this wear stage, the metaflexid has just become a metafossetid; it is wide and rather transversely aligned, displaying an isolated rounded stylid at the middle. A small secondary fold originating from the third lophid is situated mesially with respect to the latter stylid.

M$_3$: The last molar is similar to the premolar, but with the distal pillar being narrower than the mesial one. The wear surface is flat and the occlusal pattern is tetralophodont. All the flexids and fossetids, which display abundant cement, are parallel to one another, and oblique with respect to the mesiodistal axis of the crown. At the lingual wall of the crown there is only a short mesostriid, whereas at the buccal one the hypostriid penetrates into the alveolus. The degree of wear is moderate (stage 3 of Aldana, 1991); two fossetids can be appreciated: the parafossetid and the metafossetid. The parafossetid and the metafossetid display considerable crenulations. The parafossetid, which is very elongated like in the other lower cheek teeth, is divided into two portions by a secondary enamel fold arising from the first lophid and situated quite

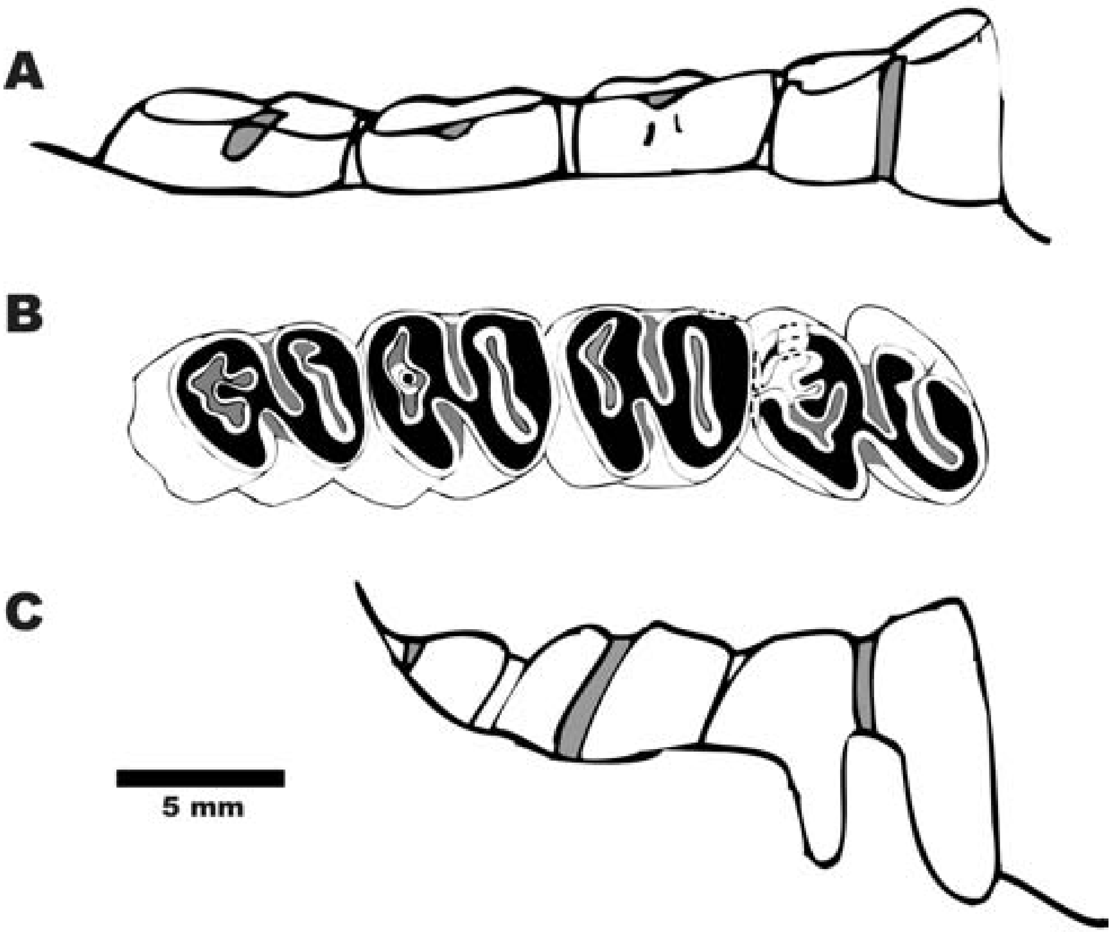

Figure 3.2. Schematic depiction of holotype of *Chalicomys* n. sp. from Abocador de Can Mata locality C4-C2: right P_4-M_3 IPS41694. **A**, lingual (reversed); **B**, occlusal; **C**, buccal. Cement is depicted in gray.

lingually. The buccal part of the parafossetid is relatively long and narrow, being somewhat transversely aligned; while the lingual one consists in a small elliptical fossetid weakly joined to the latter. The mesoflexid is long, somewhat curved and obliquely aligned, being placed mesially with respect to the hypoflexid. The metafossetid is also divided into two portions by a well-developed plicature originating from the third lophid. The lingual one is comma-shaped, being quite transversely aligned backwards. The buccal portion, on the contrary, is more elliptical, being united to the lingual one by a curved bridge. There is also a small, rounded submesofossetid placed somewhat lingually relative to the midline of the crown. This submesofossetid is connected to the lingual portion of the metafossetid through a constricted bridge.

Maxilla: The left maxillary fragment IPS 41695a partially preserves the alveoli of M^2 and M^3. The alveolus of M^2 is broken at the mesial and buccal sides, although crown base is only partially exposed at the mesiobuccal corner of the tooth. The alveolus of M^3 is partially broken at the lingual side. The right maxillary fragment IPS 41696 is slightly more informative. It is complete at the buccal side of P^4, but broken at the mesiolingual side, so that the whole length of the crown is exposed. This tooth is implanted quite obliquely with respect to the alveolar plane. Although still partially covered by bone, the whole length of the hypostria can be appreciated. The alveolus of M^1, albeit largely preserved, is filled with sediment. On the buccal side, the lowermost part of the zygomatic root is preserved, originating from about 5 mm above the alveolar plane, at the level of the distal lobe of P^4. In lateral view, the zygomatic root is markedly oblique with respect to the alveolar plane. On the inner side of the zygomatic root, the posterior opening of the infraorbital foramen is preserved.

P^4: The upper premolars are markedly curved and clearly mesiodistally longer than buccolingually wide. The crown is slightly shorter and narrower apically than towards the base of the crown, but the tooth is not pyramidal in shape. The basal part of the crown of IPS41695c is broken, and IPS41696 is still into the alveolus to a large extent, but it appears that a single lingual root (and presumably two buccal roots) were present. The wear surface is flat and the occlusal morphological pattern is tetralophodont. The degree of wear is moderate in both specimens (stage 2 of Aldana, 1991, at least in IPS41696, where a metafossette is present). The buccal side is damaged in IPS41695c, but it is completely preserved in IPS41696, showing that only two well-developed striae are present: the marked but relatively short mesostria, and the narrower parastria, which is more than twice longer than the mesostria. This specimen is slightly damaged at the mesiolingual wall of the crown, but this part is completely preserved in IPS41695c. Both specimens show that, at the lingual side, the hypoflexus originates a long hypostria, which occupies almost two thirds of crown height. The several flexi are parallel to one another, and obliquely oriented relative to the mesiodistal axis of the crown. All these flexi display plenty of cement. Enamel crenulations can also be observed at the mesoflexus and the paraflexus, although they are much less marked than in the lower molars. The hypoflexus and the paraflexus are obliquely aligned and face each other, being only separated by a very narrow bridge. The hypoflexus is much shorter than the paraflexus. A well-developed style-like secondary fold originates a large and rounded cusp at the mesiobuccal corner of the crown, being isolated from the rest of the first loph by a groove, which can be also appreciated at the mesial wall of the crown. In IPS41695c, there is a small circular subparafossette at the second loph, close to the mesostyle. This fossette is not completely closed in IPS41695c, opening to the mesoflexus. The mesoflexus is very long, curving distally until opening at the distal margin of the crown. At this point, in IPS41695c there is a rounded style-like secondary fold next to the hypocone, but separated from it by a very short groove. In IPS41696, this portion of the crown is somewhat more worn, and as a result the above-mentioned fold merges the hypocone. IPS41696 shows that the third loph is constricted just before the metacone, and further indicates that a subrectangular metafossette is present very close to the distobuccal margin of the crown.

M$^{1/2}$: Both the left M^2 and the right M$^{1/2}$ are virtually identical, so they will be described together; they are only minimally damaged at the buccal side. They both display a subquadrangular occlusal outline, and the crown is distally curved towards the base. The dimensions of the crown do not vary substantially from apex to base. There are three roots: a very wide mesiolingual one (that can be appreciated in IPS 41695b), and two reduced buccal ones (that can be appreciated in both IPS 41695b and IPS 41695a). All the flexi are filled with abundant cement. The occlusal surface is flat, with an advanced degree of wear (stage 3 of Aldana Carrasco, 1991). In IPS 41695b there are two fossettes (the parafossette and the metafossette), whereas in IPS 41695a the metaflexus is still open. The flexi and fossettes are roughly parallel to one another, and oblique relative to the mesiodistal axis of the crown. The hypostria is long, almost reaching the base of the crown, whereas at the buccal side, only an extremely short mesostria can be recognized. The hypoflexus is obliquely directed towards the

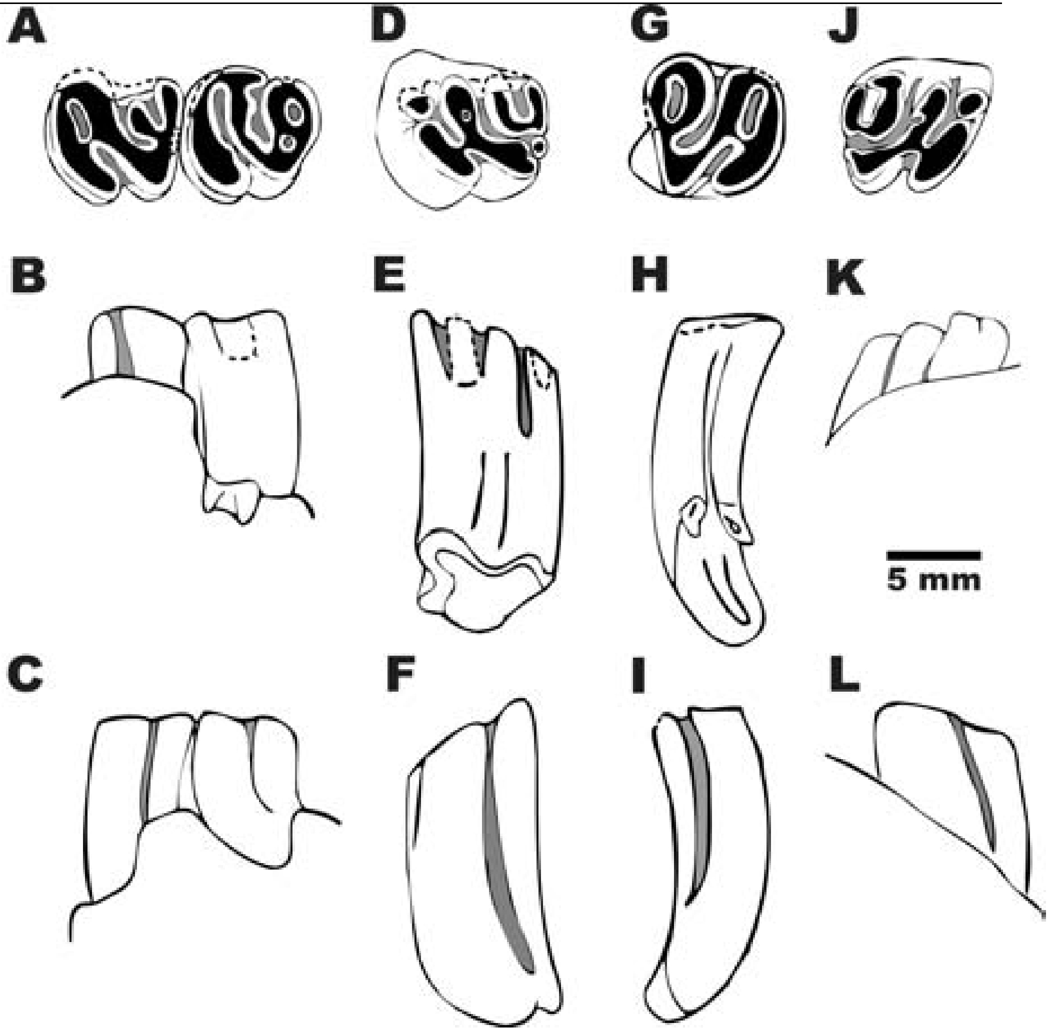

Figure 3.3. Schematic depiction of paratypes of *Chalicomys* n. sp. from Abocador de Can Mata locality C4-C2. **A**, **B**, **C**, left M^2-M^3 IPS41695a (paratype), **A**, occlusal; **B**, buccal; **C**, lingual; **D**, **E**, **F**, left P^4 IPS41695c (paratype), **D**, occlusal; **E**, buccal; **F**, lingual; **G**, **H**, **I**, right $M^{1/2}$ IPS41695b (paratype), **G**, occlusal; **H**, buccal; **I**, lingual; **J**, **K**, **L**, right P^4 IPS41696 (paratype), **J**, occlusal; **K**, buccal; **L**, lingual. Cement is depicted in grey.

parafossette, being separated from it by a narrow bridge. The parafossette is rather straight, and somewhat wider at the lingual than at the buccal end, especially on the left molar. The mesoflexus, very long, distally curves along its course, until almost reaching the distal margin of the crown. The metafossette is somewhat smaller than the parafossette.

M^3: The shape and occlusal pattern of this tooth closely resemble the other upper molars, although it is more markedly curved towards its base and more oval in shape (with the distal moiety of the crown slightly narrower than the mesial one). The occlusal surface is flat, with a moderate degree of wear (stage 3 of Aldana, 1991). The parafossette is not completely closed at the lingual end. It joins the hypoflexus, defining a very long syncline that almost reaches the mesiobuccal corner of the crown. All the flexi and fossettes are filled with cement; they are parallel to one another, being directed backwards on its lingual end. There is a long hypostria that enters into the alveolus, and a similarly long but narrower mesostria that also extends into the maxilla. The mesoflexus, which is slightly directed backwards, is partially obliterated by a secondary enamel fold arising from the second loph, and further displays a minor fold situated somewhat more lingually. The metafossette, reduced and elliptical in shape, is placed at the buccal moiety of the crown. There is also a small and rounded submesofossette, which is more lingually situated.

3.2.2. Postcranial material

Measurements and description

On the basis of postcranial material, castorids are only recorded from ACM by a left femur (IPS 41693) from locality C3-Ak, which is only about 10 m higher in stratigraphic series than the type locality of *Chalicomys* n. sp. On the basis of size, the IPS 41693 femur can be attributed to the same species than the dentognathic material from C4-C2. However, given the lack of associated dental material from C3-Ak, only tentative attribution of the femur to *Chalicomys* cf. n. sp. is warranted.

Measurements:

Description of the measurement	IPS 41693
Length (maximum, parallel to the long axis of the diaphysis)[20]	(90-92)
Diameter of the diaphysis below the lesser trochanter	ML (14.5); AP 10.2
Diameter of the diaphysis at distal epiphysis (maximum)	ML 28.7; AP ≥15.6
Diameter of the femoral head	AP 11.7; DV 11.8
Diameter of the femoral neck	AP 7.1; DV 8.6

Description: IPS 41693 is a fairly complete left femur (Fig. 3.4 C-D) preserving the femoral head, most of the diaphysis, and a great portion of the distal epiphysis, but lacking the major trochanter almost entirely (except for its base and the trochanteric fossa), as well as the externalmost portion of the third trochanter, the posterior and part of the anterior portions of the medial condyle, and a small fragment of the lesser trochanter. Furthermore, the diaphysis displays several transverse fractures; two of them involve some loss of bone, although the maximum length of the bone can be reasonably estimated by assuming a projection of the third trochanter similar to other castorids.

Overall, the femur has a markedly flattened appearance. In fact, the proximal end of the diaphysis, at the level of the lesser trochanter and at the base of the major trochanter, is approximately as wide anteroposteriorly than mediolaterally. However, the anteroposterior diameter of the diaphysis progressively decreases distally. At the same time, the diaphysis broadens mediolaterally, this being accentuated by the marked development of the very protruding, albeit thin, ledge of bone that extends throughout the whole the lateral margin of the diaphysis. The mediolateral width of the femur is greatest at the level of the third trochanter, which is broken, but was placed just above midshaft. Nevertheless, at about midshaft, just below the level of the third trochanter, the mediolateral diameter of the femoral shaft is about twice the anteroposterior one.

The distal portion of the diaphysis and the distal epiphysis are also markedly broader mediolaterally than anteroposteriorly, although bone damage precludes quantification. Both the lateral and the medial condyles protrude beyond the mediolateral margins of the diaphysis. This is particularly accentuated in the case of the medial condyle, especially at the level of the stout medial epicondyle, although the distal portion of the diaphysis just proximal to it is not so flattened and medially

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[20] Given that the greater trochanter is almost entirely missing, there remains some degree of uncertainty, so that we provide an interval instead of a single estimate.

protruding as in *Castor*. This results in a relatively straight contour of the shaft on the medial side, contrasting with the somewhat more concave profile in *Castor*. At the lateral condyle, the pit for insertion of the collateral ligament is more concave and extensive than at the medial one. Even though the medial condyle is damaged at both the anterior and posterior sides, it is clearly more voluminous than the lateral one, extending further distally. This results in a distal asymmetric profile of the epiphysis, at least as markedly asymmetric as in *Castor*. The patellar trochlea, albeit partially damaged, is also distally concave, although apparently somewhat narrower mediolaterally (especially at its proximal part). In posterior view, the intercondylar notch is somewhat narrower than in *Castor*. Above the patellar surface, in frontal view, there is only a shallow fossa, surrounded by two short and ill-defined crests that do not joint at the middle.

With regard to the proximal region of the femur, the lesser trochanter is partially missing, but it resembles extant *Castor*, being situated just below the base of the femoral neck. The greater trochanter, as judged from its base, appears to have been parallel and close to the main axis of the bone, rather than somewhat laterally deviated as in *Castor*. In posterior view, the greater and lesser trochanters are united by an ill-defined and semi-circular muscular insertion scar. The trochanteric fossa appears to have been more restricted and shallower than in *Castor*. Unlike the greater trochanter, the femoral head and the femoral neck are completely preserved. The neck is higher dorsoventrally than anteroposteriorly thick, and inclined at about 45º from the main axis of the bone, as in *Castor*. The femoral head is subspherical, with a rounded circular outline in lateral view (approximately equal anteroposterior and dorsoventral diameters); a relatively large and deep fovea capitis is present on the center of the head.

Morphological comparisons

For comparison with extant genus *Castor*, we examined postcranial material from *C. canadensis* housed at the Museu de Ciències Naturals – Museu de Zoologia de Barcelona. With regard to fossil material, to our knowledge, only a single femur of *Chalicomys*, attributed to *C. jaegeri*, from the Austrian locality of Mataschen (MN 7+8), has been reported (Daxner-Höck, 2004). Unfortunately, the published figure corresponds to a posterior view of the only partially prepared specimen (Daxner-Höck, 2004, her Plate 1a) and only a brief description is provided. The greater and third trochanters of this specimen are more completely preserved than in the Can Mata one, whereas, on the contrary, the lesser trochanter is almost entirely missing. At the collections of the Institut de Paleontologia M. Crusafont in Sabadell, there is also an unpublished partial left femur with associated right femoral head IPS 31008 (Fig. 3.4. A–B) from the locality Sant Quirze, from the Late Aragonian (MN 7+8) of the Vallès-Penedès Basin. Two different castorid species have been recorded at this locality: *Euroxenomys minutus* and *Chalicomys catalaunicus*; however, given the obvious size differences between both taxa (cheek teeth about twice larger in the latter taxon), the above-mentioned femur can be unambiguously attributed to *Chalicomys*. This femur from Sant Quirze is more incompletely preserved, because the distal epiphysis is completely missing, further lacking the greater trochanter. The lesser trochanter is however preserved (unlike in the C3-Ak specimen), and the third trochanter is only minimally damaged.

Amongst the three *Chalicomys* species, the femur of *C. jaegeri* most closely resembles extant *Castor* in size; the femur of *C. catalaunicus* is markedly smaller, whereas that of *C.* cf. n. sp. is intermediate in size. Morphologically, as far as it can be ascertained (due to the incomplete preservation of the three specimens), the femora of the two *Chalicomys* species from the Vallès-Penedès Basin, as well as the *Chalicomys* femur from Austria (Daxner-Höck, 2004), resemble the femur of *Castor* in several respects. These include the generally flattened (i. e., anteroposteriorly compressed) appearance of the diaphysis, as well as the shape and position of the lesser trochanter, the placement of the third trochanter approximately at midshaft, and the development of a shelf-like bone ridge along all the lateral margin of the diaphysis. In the Sant Quirze femur, the diaphysis at about midshaft is nearly as flattened as in the ACM specimen, and the same appears to be in the Austrian specimen, although this cannot be evaluated for certainty because the specimen figured is not completely prepared. The position of the third trochanter is also the same in the three *Chalicomys* specimens, which further display a considerable development of the lateral ridge along the diaphysis. In the Sant Quirze specimen, the lateral ridge of the diaphysis is less developed, and it can be only qualified as a crest distally from the third trochanter. In the ACM specimen, the lateral ridge is well developed, particularly proximal from the third trochanter, being even greater than in *Castor* (perhaps compensating for the less mediolaterally expanded diaphysis sensu stricto at this region).

Regarding the above-mentioned features, the femora of *Chalicomys* resemble extant beavers more closely than the femora of both *Trogontherium* (Mol *et al*., 1998) and *Steneofiber* (Filhol, 1879) do. In particular, despite its similarly flattened diaphysis, the femur of the castoroidine *Trogontherium cuvieri* does not display a marked bone ledge distally from the third trochanter, which moreover is very proximally situated, just below the greater trochanter, instead of at midshaft (Mol *et al*., 1998). In the case of the primitive castorine *Steneofiber eseri*, from the Early Miocene (MN 2) of Saint-Gérand-le-Puy (France), Filhol (1879) notes a considerable degree of inter-individual variation regarding diaphyseal flattening and development of the third trochanter. The femur figured by Filhol (1879, Plate 6), in any case, is more reminiscent of a terrestrial quadruped than the femora of *Castor* and *Chalicomys*, differing by the less compressed diaphysis, the lack of a lateral diaphyseal bone ridge, and the more proximally-placed third trochanter (at about the first third of the diaphysis, rather than at midshaft).

Only some minor differences relative to extant beavers can be discerned in the femora of *Chalicomys*. These differences are mainly related to the proximal femur, with *Chalicomys* displaying a more vertically oriented greater trochanter, a more restricted and shallower trochanteric fossa, and a less pronounced ridge connecting the lesser trochanter with the base and greater trochanter. The distal portion of the *Chalicomys* femur, especially on the basis of the ACM specimen, closely resembles *Castor* by the laterally deviated distal epiphysis and the very developed medial condyle and epicondyle, although the distal diaphysis is not so medially broadened. The shape of the distal epiphysis cannot be evaluated in the Sant Quirze specimen, although the distal

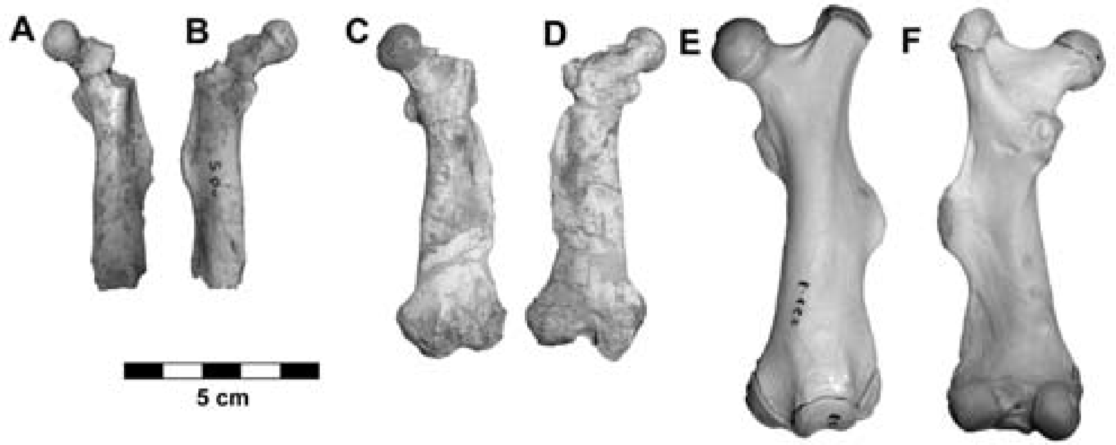

Figure 3.4. Femora of *Chalicomys* from the Vallès-Penedès Basin as compared to extant *Castor*. A, B, partial femur IPS 31008 of *C. catalaunicus* (Bataller, 1838) from Sant Quirze, A, anterior; B, posterior; C, D, partial femur IPS 41693 of *C.* cf. n. sp. from ACM/C3-Ak, C, anterior, D, posterior; E, F, femur 94-0641 of extant *Castor canadensis* Kuhl, 1820, E, anterior; F, posterior.

portion of the diaphysis is less broadened and displays a less extensively developed ridge.

3.3. Discussion

3.3.1. Taxonomy

Many authors (e.g., Aldana, 1991, 1992) have employed a broad definition of the genus, by including in it species that are currently attributed to the genus *Steneofiber*. *Chalicomys* and *Steneofiber* are no longer considered synonymous (Hugueney, 1999; Korth, 2001), but as a result, previous diagnoses of *Chalicomys* (=*Palaeomys*), such as Aldana's (1991, 1992), cannot be employed, because they simultaneously refer to the genus *Steneofiber*. The emended diagnosis provided in this paper clarifies the criteria on which the generic attribution of the newly erected species from ACM is based.

Regarding the species included in the genus *Chalicomys* we consider *C. subpyrenaicus*, from the French localities of Villafranche-d'Astarac and Simorre (MN7+8) as a valid species. Because of the scarcity of the available material, this species is usually synonymized with *C. jaegeri*. The P_4 morphology and the presence of a thin cement layer in the valleys indicate similarities with *C. jaegeri*, but the size of the cheek teeth is noticeably smaller and the P_4 does not display a lingually open paraflexid (Hugueney, 1999). *Chalicomys* n. sp. is only slightly larger (length of P_4-M_2 at the occlusal level: 22,1 mm) than *C. subpyrenaicus* (length of P_4-M_2 at the occlusal level: 20 mm). However, the P_4 is relatively more elongated with respect to the following first and second molars in *Chalicomys* n. sp.. This tooth is more 8-shaped in *Chalicomys* n. sp., further displaying a lingually-open paraflexid as in *C. jaegeri*. The mesostriid of P_4 is longer in the Can Mata specimen than in *C. subpyrenaicus*. Nevertheless, the differences between both species do not appear to be very great, and with the recovery of additional material they might finally prove to be best distinguished at the subspecies level. The presence of abundant enamel crenulations, particularly on the metafossetid of P_4 and M_3, in *Chalicomys* n. sp. clearly performs diagnostic character distinguishing it from the remaining *Chalicomys* species. Nevertheless, the diagnostic value of enamel secondary folds (crenulations) has been recently questioned in the case of the genus *Castor* (Hugueney, 2004; Barisone et al., 2006). Western-Central Europe Villafranchian beaver remains were assigned to *Castor plicidens* by some authors because of the presence of complex enamel crenulations (Friant, 1960-1962, 1964), while other authors have classified them as *C. fiber* on the basis of other morphological patterns (Hugueney, 2004; Barisone et al., 2006). On the basis of morphometric analyses of the occlusal surface pattern Barisone et al. (2006) regarded *C. plicidens* as an exclusively Italian subspecies of *C. fiber* in which crenulations tend to be more abundant. The Western-Central Europe remains are attributed to *C. fiber fiber* by these authors. Similar pronounced secondary folding has not been reported in the case of *Chalicomys*, although minor crenulations and granulations may be present in *C. jaegeri* (see for example Van de Weerd, 1976, his plate 15 figure 4b). The taxonomic value of secondary enamel folding in *Chalicomys* is currently unknown. Given the fact that only a single individual is currently available for the ACM species, the intraspecific variability of this trait cannot be evaluated until further material is recovered. Therefore the validity of secondary enamel folding as a diagnostic character may be compromised if the recovery of more material reveals that this is a variable trait.

The species ?*C. plassi*, is based only on two isolated teeth from the German locality of Dorn-Dürkheim (MN11). This taxon is much smaller and less hypsodont than other *Chalicomys* species, and in our opinion, the attribution to this genus is doubtful. On the contrary, an additional *Chalicomys* species, *C. catalaunicus* (Bataller, 1938) comb. nov., can be further distinguished at the Catalan locality of Sant Quirze. This taxon was classified as *Steneofiber depereti* Mayet, 1908 by Crusafont *et al.* (1948) and Aldana (1991, 1992). The latter author, in fact, synonymized *Steneofiber* with *Chalicomys/Palaeomys* partly as a result of his erroneous attribution of the *Chalicomys* material from Sant Quirze to *"Chalicomys/Palaeomys" depereti*. Xu (1994) attributed the material from this locality to *Steneofiber hesperus* Douglass, 1901, but as noted by Hugueney (1999), this attribution is also erroneous. This taxon, unlike that from Sant Quirze, is not very hypsodont and lacks cement. Hugueney (1999) further emphasized the presence of interrupted longitudinal crests in some of the specimens figured by Crusafont et al. (1948), thus defining a pre-S-pattern. This led her to refer to tentatively refer this material to ?*Eucastor (Schreuderia) catalaunicus* Bataller, 1938. However, as noted by Korth (2001), *Schreuderia* is in fact a castorine that might be even regarded a subgenus of *Chalicomys*. Both genera display in common a tetralophodont occlusal pattern with parallel synclines/-ids, a high degree of hypsodonty, and relatively to very abundant cement. However, we maintain a separation at the genus level because *Schreuderia* differs from *Chalicomys* by a few apomorphic traits.

The species *C. jaegeri* spread across Europe during MN9 (Hugueney, 1999), although dentognathic material tentatively attributed to this species (albeit somewhat smaller in size) has been recovered from MN7+8 levels of Turkey (Ünay, 1976). For Hugueney (1999), this Turkish material would reinforce the contention that *C. jaegeri* is not an offspring of *Steneofiber depereti*, but could be rather an immigrant of Asian origin. The discovery of additional *Chalicomys* material from MN7+8 levels in the Vallès-Penedès Basin leaves open other possibilities, with the two Catalan species being more derived than *Steneofiber*, but apparently more primitive than the later *C. jaegeri*.

3.3.2. Nomenclatural issues

Through the years, several investigators (e.g., Stirton, 1935; Crusafont *et al.*, 1948; Hugueney, 1999; Korth, 2001) have referred to the nomenclatural difficulties arising from the initial simultaneous description by Kaup (1832) of three genus and species: *Palaeomys castoroides*, from Weisenau; and *Chalicomys jaegeri* and *Chelodus typus*, from Main in Eppelsheim. Von Meyer (1838) considered the former two taxa to be synonymous, whereas Stirton (1935) considered that all the three genera originally described by Kaup (1932) merely reflected different wear stages of the same taxon. This opinion was followed by most subsequent workers (e.g., Hünermann, 1966). The issue was further complicated by the proposal that *Chalicomys* and/or *Palaeomys* were synonyms of *Steneofiber* (e.g., Bataller, 1938; Crusafont *et al.*, 1948), leading to the use of the binomen *Steneofiber jaegeri*. In fact, taxonomic disagreements aside, the genus *Steneofiber* was erected later in time than both *Chalicomys* and *Palaeomys*, and accordingly, if *Steneofiber* is to be synonymized with either (or both) of them, then it must be considered a junior synonym (e.g. Aldana Carrasco, 1991, 1992).

The current taxonomic agreement (Hugueney, 1999; Korth, 2001) that *Chalicomys* and *Palaeomys* are not only distinct from *Steneofiber*, but synonyms with one another, has not yet resulted in nomenclatural stability. In a recent revision of castorid systematics, Korth (2001) stressed that *Chalicomys* and *Palaeomys* are to be considered synonymous, but refrained from judging which should be given priority over the other. In spite of the fact that Stirton (1935) selected the nomen *Palaeomys castoroides* on the basis that this “is the first specimen mentioned by Kaup” (Stirton, 1935: 426), he already recognized that Von Meyer (1838:414), almost a hundred years before, had already “considered *Palaeomys castoroides* as nothing other than *Chalicomys jaegeri*” (Stirton, 1935:427). Later on, Hünermann (1966) retained the nomen *Chalicomys* due to the better preservation of the holotype, an opinion that was followed by Aldana Carrasco (1991) in this doctoral dissertation, but not by Aldana Carrasco (1992) in the published paper that followed. Both Aldana Carrasco (1992) and Stefen (1997) explicitly returned to Stirton’s (1935) argument, according to which the nomen *Palaeomys* should be retained on the basis of page priority. However, as noted by Hugueney (1999), priority in this particular case must be decided on the basis of the Principle of the First Reviser. In the current Fourth Edition of the International Code of Zoological Nomenclature (ICZN, 1999), the Principle of the First Reviser (Article 24.2.1) clearly states that when the precedence between names cannot be objectively determined (as in Kaup’s original publication), it is fixed “by the action of the first author citing in a published work those names”, which is termed the “First Reviser”. As argued by Hugueney (1999), Von Meyer (1838) must be considered the First Reviser in this particular case; and given the fact that the latter author selected the nomen *Chalicomys jaegeri*, *Palaeomys* must be considered a synonym of *Chalicomys*, instead of the reverse. Although Kaup (1832) did not explicitly designate a type species for either genera, both were originally intended to include a single species, so that according to the International Code of Zoological Nomenclature (ICZN, 1999), the type species must be determined by monotypy (Article 68.3). Consequently, the type species of the genus *Chalicomys* must be *C. jaegeri* Kaup, 1832 (contra Aldana Carrasco, 1991).

Finally, some nomenclatural considerations must be added regarding the nomen *Chalicomys catalaunicus* (Bataller, 1938). Bataller (1938) referred to this taxon as *Steneofiber minutus* raça *catalaunica*. According to the International Code of Zoological Nomenclature (ICZN, 1999), a species-group name, following a binomen, that was originally proposed to denote an infrasubspecific entity (as it is the case), must have been published before 1961 expressly for a “‘variety” or “form” in order to be available from its original publication (Articles 10.2, 45.5 and 45.6). Although Bataller (1938) employed the term "raça" (Catalan word for 'race') in the first citation of the nomen and in all figure legends, he also used the term "varietat" ('variety') in the text (Bataller, 1938: 37). Accordingly, the nomen *catalaunica* is available from its original publication, as already admitted by Hugueney (1999).

3.4. Paleobiology

3.4.1. Body mass estimation

We employed the estimated length of the IPS 41693 femur (FL) to infer the body mass (BM) of *C.* cf. n. sp.. We used the least-square equations derived by Reynolds (2002), on the basis of an ontogenetic series of 26 *C. canadensis* specimens (ranging in body mass from 5 to 35 kg; log BM = 2.607 log FL - 4.115), as well as on the basis of mean adult values for 19 extant rodent species (log BM = 3.436 log FL - 6.071). On the basis of ontogenetic allometry, a BM estimate between 9.5 and 10 kg was obtained. This contrasts with the estimate of 4.4–4.7 kg that was obtained on the basis of interspecific allometry. In other words, the allometric equation based on an ontogenetic series of extant beavers yields a body mass estimate more than twice the estimate based on a broad sample of living rodents.

In order to investigate which estimate might be more accurate, we extracted from the Figure 2 of Reynolds (2002) the original data on femoral length and body mass of the ontogenetic series employed to derive the allometric equation. When the data on femoral length were employed to estimate body mass with the other allometric equation, and estimated body mass was compared with actual body mass, an average degree of 48% body mass underestimation (from 20% to 63%) was obtained. In other words, the interspecific allometric equation understimates to a significant degree body mass in extant beavers, and therefore does not seen advisable for estimating body mass in extinct ones. This is probably to result from the highly specialized locomotor repertoire of extant (and probably extinct) castorids, and in any case indicates that the body mass estimate of about 9.5-10 kg for *C.* cf. n. sp. is the most reliable one. This is approximately between 1/2 and 2/3 the body mass of a extant beaver, given that an extant *C. canadensis* generally weights between 15-20 kg, and may exceed 30 kg (Reynolds, 2002).

3.4.2. Mode of locomotion

The two *Chalicomys* femora reported in this paper permit to make some paleobiological inferences regarding the locomotor repertoire of these extinct beavers. Extant *Castor fiber* and *C. canadensis* are usually considered semi-aquatic mammals, in the sense that they are facultative, non-obligated swimmers, which usually live partly on the water and partly on the ground (Müller-Schwarze & Sun, 2003; Lavender & Chen, 2007a). Living castorids employ a drag-based propulsion system (as opposed to the more efficient, lift-based propulsion systems), which is based on bipedal pelvic paddling (Fish, 1996, 2001). Accordingly, whereas the forelimbs reflect an anatomical compromise between the different functions they serve (manipulation, fur grooming, burrowing, terrestrial locomotion), the hind limbs are more committed to locomotion. The latter are specifically adapted to aquatic locomotion; thus, whereas the small and unwebbed front feet are merely held tight against the body during swimming, the larger and webbed hind feed provide the primary propulsive force by rapidly paddling in the water (Young, 1937; Jenkins & Busher, 1979; Lavender & Chen, 2007a,b,c). The beaver's tail further contributes to aquatic locomotion by functioning as an efficient rudder, but also serve many other functions, such as fat storage, head exchange, emission of warning signals by slapping against water, etc. (Lavender & Chen, 2007a,b). Like in the giant river otter (*Pteroneura brasiliensis*), the dorsoventral movements of the flattened tail could further produce additional propulsive force in particular instances (Fish, 2001).

Due to its specialization to aquatic locomotion, the hind limb in extant beavers displays multiple anatomical features that are functionally linked with aquatic locomotion. Propulsion during swimming mainly results from rapid, alternative plantar- and dorsiflexion at the ankle joint (Lavender & Chen, 2007c,d, after Young, 1937), with the large and webbed foot of the beaver functioning as a paddle. This is reflected in the great development of dorsal leg muscles (for plantarflexion) as well as intrinsic foot muscles (for abducting the digits, thus spreading the webbed foot). On the contrary, the thigh and proximal leg are tightly bound by muscles and connective tissue to the pelvic and gluteal regions, whereas the knee is permanently flexed, so that very restricted flexion/extension is possible at the knee and hip joints (Lavender & Chen, 2007c,d, after Young, 1937). In order to limit the mobility at the hip joint, extant beavers therefore possess powerful adductor muscles, with their various attachments extending throughout all the length of the mediolaterally broadened diaphysis femur. The femur is somewhat exorotated, in comparison to a terrestrial quadruped, resulting in increased adductor capabilities. In order to separate the legs from the body during swimming, flexing them along the parasagittal plane, some morphological reorganization of the leg and the knee joint are required. On the tibia, this is reflected in a very marked lateral curvature of the shaft, with the distal portion being further torsioned, so that the plantar surface the feet while swimming is laterally deviated (pers. obs.). On the knee joint, this is further reflected by the asymmetric distal contour of the femoral condyles and the obliquely inclined trochlea patellaris (pers. obs.). All these features impose severe restrictions on the efficiency of terrestrial quadrupedalism, resulting in a relatively slow and short gait (Lavender & Chen, 2007c), and must hence reflect a considerable degree of commitment to aquatic locomotion.

In the case of the three *Chalicomys* genera, a similarly specialized locomotor repertoire can be inferred on the basis of their flattened diaphysis and mediolaterally broadened distal epiphysis, from the position of the third trochanter at about midshaft, and from the marked development of certain muscular insertion areas. A considerable development of adductor muscles, similar to that of *Castor*, can be inferred for *Chalicomys* (especially in the ACM specimen), given the extensive development of the lateral ridge that extends across the lateral side of the diaphysis. This would be consistent with *Chalicomys* displaying a high capability of thigh adduction, which would be further reinforced by the position of the third trochanter. Two adductor muscles of the thigh (the obturator externus and the adductor magnus, which originate from the pubis) do insert onto the third trochanter of the femur (Young, 1937; Lavender & Chen, 2007c), and accordingly, the distal position of the third trochanter in both *Castor* and *Chalicomys*, as compared to *Trogontherium*, would have provided an increased lever arm for the above-mentioned adductor muscles.

The considerable development of the medial femoral condyle and epicondyle in *Chalicomys* (unknown in the Sant Quirze specimen) would further provide large insertion areas for several of the adductor muscles of the thigh (the adductor brevis, the adductor magnus, the adductor longus, and the larger portion of the pectineus) (Young, 1937; Lavender & Chen, 2007c), resulting in a high capability of thigh adduction, as in *Castor*. These adductor muscles, and especially the adductor longus, contribute to a large extent in maintaining the distal femur and the proximal leg tightly bound to the caudal portion of the body. According to this, restriction of mobility at the hip joint would have been more pronounced in the ACM specimen than in the other *Chalicomys* femora, thus more closely resembling the condition of extant beavers. The asymmetrical distal profile of the distal epiphysis of the femur in *Chalicomys* (unknown in the Sant Quirze specimen) and *Castor* implies a permanent lateral deviation of the tibia with respect to the main axis of the femur. As explained above, this is likely to be an adaptation to maintain the tibia near to the parasagittal plane, given the markedly adducted and somewhat exorotated position of the femur.

With regard to the proximal femur, it should be taken into account that the trochanteric fossa serves for insertion of the obturator internus and of the tendon of the anterior and posterior gemellus muscles, which abduct (the former) or abduct and laterally rotate (the latter) the thigh, with the medial portion of the greater trochanter further serving as the insertion area of the gluteus medius, which is an extensor and abductor of the thigh (Lavender & Chen, 2007c). Accordingly, the more extensive trochanteric fossa of *Castor* would imply the presence of larger insertion areas for the muscles that abduct and exorotate the thigh. However, given the fact that extant beavers display very restricted abductor capabilities at the hip joint, it seems more likely that this represents a refinement for maintaining the femur permanently not only adducted, but also somewhat laterally rotated.

To sum up, the morphology of the *Chalicomys* femora permits to infer a locomotor repertoire more similar to that of extant beavers than in the case of other extinct castorid genera. This includes the castoroidine *Trogontherium*, which despite some adaptations to swimming (such as diaphyseal flattening), displays a less pronounced commitment to aquatic locomotion (at least judging from the position of the third trochanter), and would have been much more agile when moving on the ground (Hugueney, 2004). It also includes the early castorine *Steneofiber*, which is likely to reflect the primitive condition from which *Chalicomys* evolved, whith a less anteroposterior femoral diaphysis and distal epiphysis, and a less asymmetric distal profile, among others. The phalangeal material of *Steneofiber* from the Early Miocene (MN 2) of Mointagu-le-Blin (France) indicates the presence of adaptations for grooming the fur, and permits to infer the presence of a non-wettable fur in this taxon (Hugueney & Escuillié, 1995). In semi-aquatic mammals, the presence of non-wettable fur increases buoyancy, thus permitting to maintain a horizontal orientation of the body during swimming without the intervention of the forelimbs for generating lift (Fish, 1993, 1996, 2001). It is generally assumed that primitive aquatic mammals would have first swum by alternate quadrupedal paddling (like most terrestrial mammals do), with bipedal paddling evolving as a possible secondary step, in order to avoid the mechanical and hydrodynamic interference between the fore- and the hind limbs (Fish, 1996, 2001).

Given the presence of non-wettable fur in *Steneofiber* (Hugueney & Escuillié, 1995), it is likely that this taxon already displayed a preponderance of hind limb propulsion during swimming. Although this is reflected in its postcranial morphology, these aquatic adaptations are less developed than in *Castor*. Thus, the lumbar vertebrae of *Steneofiber* lack the wing-like transverse processes displayed by *Castor*, indicating that this extinct beaver still possessed an essentially cylindrical tail (Hugueney & Escuillié, 1995), which would have implied a decreased maneuverability and perhaps even some decreased propulsive force in this taxon. The tibia is also less curved and less distally torsioned than in *Castor*, whereas the femur displays a less flattened femoral diaphysis and a only slightly asymmetrical distal epiphysis, as in most quadrupedal mammals. This suggests a lesser development of adductor musculature on the hind limbs in *Steneofiber*, whereas *Chalicomys*, on the contrary, displays a more derived condition, most similar to that of *Castor*. Neither tail shape nor tibial morphology can be evaluated in *Chalicomys* for the moment being. Femoral anatomy, however, permits to conclude that this Middle to Late Miocene taxon already displayed a type of aquatic locomotion, based on bipedal paddling, much more similar to that of *Castor* than in the case of other fossil castorids. This further suggests that *Chalicomys* might closely reflect the ancestral condition from which the extant genus *Castor* evolved, which is consistent with the dental evidence (e.g., Korth, 2001:291). The prospects to find further postcranial castorid remains amongst the abundant postcranial material from C3-Ak, C4-C2, and other ACM localities might permit to test this hypothesis in the future.

3.5. Paleoecological implications

The presence of a castorid species with swimming adaptations in Abocador de Can Mata allows us to infer the presence of permanent water streams or water masses. In the past, the absence of castorid remains in the area of Hostalets was contrasted with the presence of abundant castorid remains in other, similarly-aged localities from the Vallès area, such as Sant Quirze (Crusafont, 1950, 1952; Crusafont & Truyols, 1954b). However, it should be taken into account that the fauna from Lower Hostalets and the fauna from ACM localities do not necessarily represent the same time span (see chapter 2). Moreover, castorids do represent a very rare element of the ACM fauna. They have been thus far recorded only at two localities, which are stratigraphically very close. This indicates that, for the moment being, the above-mentioned paleoenvironmental conditions can only be inferred for a small portion of the ACM stratigraphic series.

The ACM series mainly consists of alternating reddish to yellowish/ochre lutite layers, with bluish to grayish colorations occurring only rarely. Differences in coloration are basically attributable to water table oscillations and changes in reducing/oxidizing conditions: reddish tones indicate oxidation due to subaerial exposure, whereas lighter colorations indicate more reducing conditions in water-saturated sediments. Particular sedimentological conditions can be inferred for two horizons that are situated only some meters below the castorid localities: a bluish lutite layer and a grayish sandstone layer, which respectively suggest the presence of more developed wet areas than elsewhere in the series. To sum up, both the paleontological and sedimentological evidence permit to infer a short-lasting time interval with more humid conditions than usual, owing to climatic fluctuations and/or changes in the dynamics of the alluvial system.

3.6. Conclusions

The first castorid remains from the area of els Hostalets de Pierola (Vallès-Penedès Basin, Catalonia, Spain) are reported. A new species, *Chalicomys* n. sp., is described on the basis of a complete hemimandible and some associated dentognathic material from Abocador de Can Mata locality C4-C2 (Middle Miocene, Late Aragonian, MN 7+8). The previously recognized large castorid from the late Aragonian locality of Sant Quirze (Vallès-Penedès Basin, Catalonia, Spain) is transferred to the genus *Chalicomys*, as *C. catalaunicus* comb. nov. Albeit simultaneously described, and despite page priority, *Palaeomys* is recognized as a junior synonym of *Chalicomys*, on the basis of the Principle of the First Reviser and an emended diagnosis of the genus is provided.

Two castorid femora are reported: a relatively complete one from Abocador de Can Mata locality C3-Ak (chronologically very close to C4-C2), which is attributed to *Chalicomys* cf. n. sp.; and a second one from Sant Quirze, which is attributed to *C.*

catalaunicus. These femora are compared with those of other castorid species. They indicate that *Chalicomys* was highly committed to aquatic locomotion, presumably already swimming by bipedal hind feet paddling, thus being more derived than *Steneofiber* and most closely resembling extant beavers with regard to femoral anatomy.

The record of a semi-aquatic castorid in the area of els Hostalets de Pierola indicates the presence of permanent water streams and/or water masses, suggesting a much more humid environment than previously inferred. Given the rarity of these taxa in the series of Abocador de Can Mata, however, these particular conditions might have been quite restricted in time.

Chapter 4

The rodents from the Late Aragonian (Middle Miocene) of Barranc de Can Vila 1 (Vallès-Penedès Basin, Catalonia, Spain)

4.1. Introduction

In May 1941, Crusafont found a left mandibular fragment with M_2-M_3 at a locality called Can Vila near Els Hostalets de Pierola, from which only the isolated molars remain today (see Golpe-Posse, 1982, 1993). This finding was initially attributed to *Dryopithecus fontani* Lartet, 1856 by Villalta & Crusafont (1941a), although soon afterwards Villalta & Crusafont (1944a) employed the specimen to erect a new species, *Sivapithecus occidentalis*. Much later, Crusafont & Hürzeler (1961) attributed the Can Vila remains to *Hispanopithecus laietanus* Villalta & Crusafont, 1944. Szalay & Delson (1979) synonimized the two taxa erected by Villalta & Crusafont (1944a) with *Dryopithecus (Dryopithecus) brancoi* (Schlosser, 1901), but during the last two decades or so, the distinct status of *D. laietanus*, with *"S." occidentalis* being considered a junior synonym, has been recognized by most authors (e.g. Moyà-Solà *et al.*, 1989-1990; Golpe-Posse, 1993; Andrews *et al.*, 1996). The inclusion of both holotypes in the same hypodigm is however far from clear, since the remains from Can Vila are too fragmentary to permit a secure taxonomic assignment.

From the 1950s to the 1970s, many hominoid discoveries were done in the Vallès-Penedès Basin by Crusafont and co-workers. But most of the new material discovered, however, came from localities in the Vallès area, such as Can Ponsic, Polinyà and Can Llobateres. From the Hostalets area, only an isolated canine from Can Mata I was reported (Crusafont & Golpe-Posse, 1973), and attention was progressively driven towards localities near Sabadell, culminating in the spectacular discoveries of *D. laietanus* at Can Llobateres during the 1990s (Moyà-Solà & Köhler, 1993, 1995, 1996).

Simultaneously, the area between the farm-houses of Can Mata de la Garriga and Can Vila at Els Hostalets de Pierola was used as a clandestine rubbish dump, which was conditioned and legalized by the 1980s. In fall of 2002 an extension of it began with the supervision of the excavation works by paleontologists in order to recover all the fossil material that may appear as a result of these works (see chapter 2). A month after the excavations began, the works marginally affected a ravine situated near Can Vila (the so-called Barranc de Can Vila), next to the road that leads from Can Mata to Can Vila. An upper premolar of *Deinotherium*, together with some postcranial remains that would ultimately prove to belong to a fossil great ape, were unearthed by an excavator machine. The next day, during the cleaning of the recently discovered site, further postcranial remains, together with the splanchnocranium of a fossil great ape, were recovered under the debris. Systematic paleontological excavations at the Barranc de Can Vila 1 site (BCV1) were finally undertaken during May-June 2003, providing as much as 83 bones or identifiable bone fragments from a single, adult male individual (IPS21350) of a new fossil great ape: *Pierolapithecus catalaunicus*. Unfortunately, no further remains were recovered during the next, June-July 2004 campaign.

The postcranial morphology shows *Pierolapithecus* to be a crown hominoid, while the cranial morphology further indicates that this taxon is a stem hominid, i.e. an early member of the great ape and human clade, which must have branched off after the hylobatid-hominid split, but before the pongine-hominine divergence (Moyà-Solà *et al.*, 2004). As such, *Pierolapithecus* best fits the ancestral great ape and human morphotype and, at least for the moment being, it cannot be attributed to any of the two extant subfamilies, being best considered a plesion within the Hominidae. *Pierolapithecus* provides the oldest unambiguous evidence of an orthograde bodyplan in the hominoid fossil record (Moyà-Solà *et al.*, 2004, 2005), otherwise not being well documented until the younger *D. laietanus* (Moyà-Solà & Köhler, 1996). Interestingly, although the orthograde design of *Pierolapithecus* indicates a higher commitment to vertical climbing, the retention of primitive features associated to palmigrady (Moyà-Solà *et al.*, 2004, 2005) and the lack of adaptations to below-branch suspension (Moyà-Solà *et al.*, 2004, 2005; contra Begun & Ward, 2005) simultaneously indicate that *Pierolapithecus* displayed a positional repertoire more primitive than that of *Dryopithecus*. This combination is most interesting, indicating that orthogrady was probably present in the last common ancestor of crown hominoids, but further suggesting that not all the traditionally-recognized hominoid postcranial synapomorphies, shared by extant members of this clade, were present in their last common ancestor, with suspensory adaptations having probably evolved independently at least between hylobatids and hominids. A better understanding of these and other phylogenetic and paleobiological questions requires an accurate contextualization of the *Pierolapithecus* remains from BCV1.

4.2. The mammal fauna from Barranc de Can Vila 1

In addition to *P. catalaunicus*, BCV1 has delivered remains of eight species of macromammals besides an abundant sample of micromammal cheek teeth distributed amongst 19 species. A provisional faunal list, which was based in unprepared material and only included part of the micromammal sample (less than 100 cheek teeth), was given in Moyà-Solà *et al.* (2004)[21]. The recovered remains include a few shell fragments of middle-sized turtles and some dentognathic fragments of minute reptiles. The macromammal fauna (apart from *P. catalaunicus*) includes proboscideans (*Deinotherium giganteum*); suids (*Listriodon splendens*); moschids (*Micromeryx flourensianus*); cervids (*Euprox furcatus*); besides three carnivores (*Thalasictis montadai*, *Leptoplesictis* cf. *aurelianensis* and Mustelidae indet.).

Most of the sediment removed during the systematic excavation of BCV1 was screen-washed in order to search for small bone fragments and micromammals. An abundant micromammal sample, including more than 400 isolated cheek teeth, was recovered. The majority of the sample is defined by rodent remains (more than 300 cheek teeth), although insectivores are also common (123 isolated teeth). The lagomorphs are extremely rare. All the lagomorph remains found at BCV1 can be ascribed to the ochotonid species *Prolagus oeningensis*. The available material is quite scanty (3 dental fragments and a mandibular fragment with P_3-M_1), a quite uncommon situation, since-*Prolagus* remains are usually very abundant in Neogene European fossil sites (López Martínez, 2001) and also in the Vallès-Penedès localities (data in López Martínez, 1989). *P. oeningensis* specimens from BCV1 are quite large and show a

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[21] The faunal list reads as follows: *Democricetodon larteti*, *Democricetodon gaillardi*, *Eumyarion* aff. *leemani*, *Megacricetodon minor debruijni*, *Cricetodon* sp., *Microdyromys complicatus*, *Paraglirulus werenfelsi*, *Glirudinus undosus*, *Muscardinus sansaniensis*, *Bransatoglis* sp., *Spermophilinus bredai*, *Albanensia albanensis*, Soricidae indet., Erinaceidae indet., *Deinotherium giganteum*, *Euprox furcatus*, *Dorcatherium* sp., *Listriodon splendens*, Carnivora indet.

number of morphologic features that are forerunners of *P. crusafonti*, which, in all probability, is a descendant of *P. oeningensis*.

Up to five insectivore families have been recognized in BCV1. The heterosoricids are represented by *Dinosorex sansaniensis*, which makes up about the third part (33 %) of the total insectivore assemblage. According to the data compiled by Van den Hoek Ostende & Furió (2005) the presence of this species in Spain is temporally restricted to the MN 7+8 and MN 9, and geographically confined to north-eastern basins. The true shrews (family Soricidae) are only represented by two I^1 and one P^4. Although this material is certainly scarce, two different morphologies on the incisors indicate that at least two different species are present. One of them shows a strong curvature on its dorsal side, which added to its rather small size and no fissidenty, suggests that it belongs to a Crocidosoricinae (sensu Reumer, 1987). The talpids are represented by two different species: *Talpa minuta*, which in Spain has only been reported from the Vallès-Penedès Basin, and cf. *Proscapanus* sp. The erinaceids include two species: *Parasorex socialis* (representing a 28 % of the total insectivore remains) and a second unidentified form. The dimylids are represented by *P. chantrei* (17 %). Like in the case of the heterosoricid *Dinosorex*, the occurrences of *Plesiodimylus* in Spain are restricted to Late Aragonian and Vallesian sites from north-eastern basins.

As already stated, rodent remains define most of the recovered micromammal assemblage, including more than 300 teeth distributed amongst eleven species and three families. In this chapter this rodent fauna is described and a refinement on the chronology of BCV1 is provided.

4.3. Systematic paleontology

Order **Rodentia** Bowdich, 1821

Suborder **Sciuromorpha** Brandt, 1855

Infraorder **Sciurida** Carus, 1868

Family **Sciuridae** Fischer de Waldheim, 1817

Subfamily **Sciurinae** Fischer de Waldheim, 1817

Tribe **Marmotini** Pocock, 1923

Subtribe **Spermophilina** Moore, 1959

Genus *Spermophilinus* De Bruijn & Mein, 1968

***Spermophilinus bredai* (Von Meyer, 1848)**

(fig. 4.1.3-9)

Material: 3 DP^4 (IPS 23357, IPS 23359, CV BCV1 309), 5 P^4 (IPS 23182, IPS 23183, IPS 23356, IPS 23358, IPS 23361), 11 M^{1,2} (IPS 23184, IPS 23360, IPS 23362 – IPS 23370), 3 M^3 (IPS 23185, IPS 23371, IPS 23372), 3 P$_4$ (IPS 23180, IPS 23373, IPS 23374), 7 M$_{1,2}$ (IPS 23181, IPS 23375 – IPS 23380), 3 M$_3$ (IPS 23381 – IPS 23383).

Measurements:

	L	W

	N	min.	mean	max.	s. d.	N	min.	mean	max.	s. d.
P^4	5	1.53	1.58	1.62	0.05	4	1.70	1.82	1.97	0.12
$M^{1/2}$	11	1.60	1.76	2.06	0.14	11	1.64	2.07	2.30	0.19
$M_{1/2}$	5	1.74	1.94	2.21	0.17	5	1.71	1.90	2.16	0.18

Lower cheek teeth			Upper cheek teeth		
	L	W		L	W
P_4	1.75	1.19	dP^4	1.52	1.54
	1.74	1.35		1.62	1.63
	1.58	1.37			
M_3	2.24	2.00	M^3	2.21	1.92
	2.28	-		1.96	1.98
	2.12	-		2.18	2.06

Description:

Upper cheek teeth: The premolars (both deciduous and definitive) and all the molars except the M^3 exhibit a similar pattern in cusp and ridge arrangement. The tooth surface is crossed by four transverse ridges: anteroloph, protoloph, metaloph and posteroloph. The anteroloph and the posteroloph are lower than the remaining ridges. The anteroloph and the protoloph are transverse, while the metaloph points forwards. The posteroloph always closes the posterior valley. There are two prominent buccal cusps, paracone and metacone, while the lingual cusps cannot be distinguished from the endoloph. The central valley is shallow. The enamel is smooth. The dP^4 is triangular shapped, while the P^4 and the $M^{1/2}$ are rectangular, being significantly wider than longer. The P^4 and the $M^{1/2}$ present a robust and flattened lingual root and two smaller and cylindrical buccal ones. The M^3 is longer than the premolar and the molars and it is tongue-shaped. This tooth is three-rooted, presenting two mesial roots and a robust and backwards-directed distal one.

dP^4 (fig. 4.1.3.): A small anteroconule fused to the base of the endoloph is present in two teeth (IPS 23359 fig. 4.1.3., CV BCV1 309[22]). In the remaining one the anterior valley is open both buccally and lingually. The central valley is closed by a low ridge departing from the distal wall of the paracone that does not reach the metacone. IPS 23359 (fig. 4.1.3.) shows a well-developed metaconule which is situated next to the metacone. A similar conule is weakly joined to the endoloph. The metaloph is interrupted between both cusps in this premolar.

P^4 (fig. 4.1.4.): The first valley is open both buccally and lingually. The central valley is always closed by a prominent mesostyl which is fused to the posterior wall of the paracone. The metaloph, which is very wide, is constricted before reaching the endoloph, being separated from this crest by a shallow groove in two teeth (IPS 23183, IPS 23361). In IPS 23361 (see fig. 4.1.4.) a second groove separates this loph from the metacone.

$M^{1/2}$ (fig. 4.1.5.): The anterior valley is closed by the anteroloph both buccally and lingually in all teeth but one (IPS 23360). A small anteroconule fussed to the base of the endoloph is present in many slightly worn individuals (IPS 23184, IPS 23362, IPS 23367, IPS 23368 fig. 4.1.5.). In IPS 23368 there is also a similarly-developed parastyl

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[22] This premolar was overlooked when the BCV1 collection was prepared and it was re-discovered during the taphonomical study of the site (see chapter 5). A final collection number (IPS) has not been assigned to this tooth yet, and here the provisional number is given.

obtruding the buccal end of the anterior valley. The metalophule is constricted before reaching the endoloph (see fig. 4.1.5.). The central valley is open in all teeth but one, in which it is closed by a poorly-developed mesostyl (IPS 23368 fig. 4.1.5.).

M^3 (fig. 4.1.6.): Only two cusps can be distinguished, paracone and protocone, the buccal one being more prominent than the lingual one. There is a narrow anterior valley which is closed by the anteroloph and the protoloph. Both lophs are transverse and the anteroloph is lower than the protoloph. A continuous and very low crest defines the margin of the tooth from the protocone until the paracone. This crest quickly disappears with slight wear.

Lower cheek teeth: The lower cheek teeth are wedge-shaped, with markedly curved lingual and distal margins and more straight mesial and labial ones. The P_4 and $M_{1/2}$ are narrower mesially than distally, while in the case of the M_3 the opposite is true. The M_3 is larger and more elongated than the $M_{1/2}$. In this molar the distal margin is much narrower than the mesial one. There are three main cusps: protoconid, metaconid and hypoconid. A vestigial entoconid can be appreciated in a few specimens. The metaconid is always the most prominent cusp and it faces the protoconid, being placed just slightly more mesially. The protoconid and the hypoconid are joined by a low ectolophid that presents a well-developed mesoconid at the midpoint. The posterolophid is robust and it continues in a lower ridge that runs through the lingual margin of the tooth until the metaconid. This ridge delimitates a deep valley that covers most of the surface of the tooth.

P_4 (fig. 4.1.7.): This tooth presents a mesial and a distal root markedly oblique. A deep groove isolates the metaconid from the protoconid. In one specimen (IPS 23180) a large and prominent anteroconulid is present at the mesial margin of the tooth, between the metaconid and the protoconid. A vestigial entoconid can be distinguished in two teeth (IPS 23374 fig. 4.1.7., IPS 23180). The ridge that runs through the lingual margin is separated from the metaconid by a deep groove.

$M_{1/2}$ (fig. 4.1.8.): These molars present four roots: two lingual ones and two buccal ones. There is a poorly developed anterolophid pointing obliquely forward, which in one tooth (IPS 23181) joins the metaconid to the protoconid. In some slightly worn specimens the anterolophid is separated from the metaconid by a weak groove (IPS 23375 fig. 4.1.8., IPS 23377, IPS 23378, IPS 23380). There is a residual metalophid departing from the metaconid though not reaching the protoconid. The sinusid is transverse. A vestigial entoconid can be appreciated in three teeth (IPS 23375 fig. 4.1.8., IPS 23376, IPS 23377), being separated from the lingual crest by a weak groove anterior to this cusp. A similar groove separates the lingual crest from the metaconid in a few teeth.

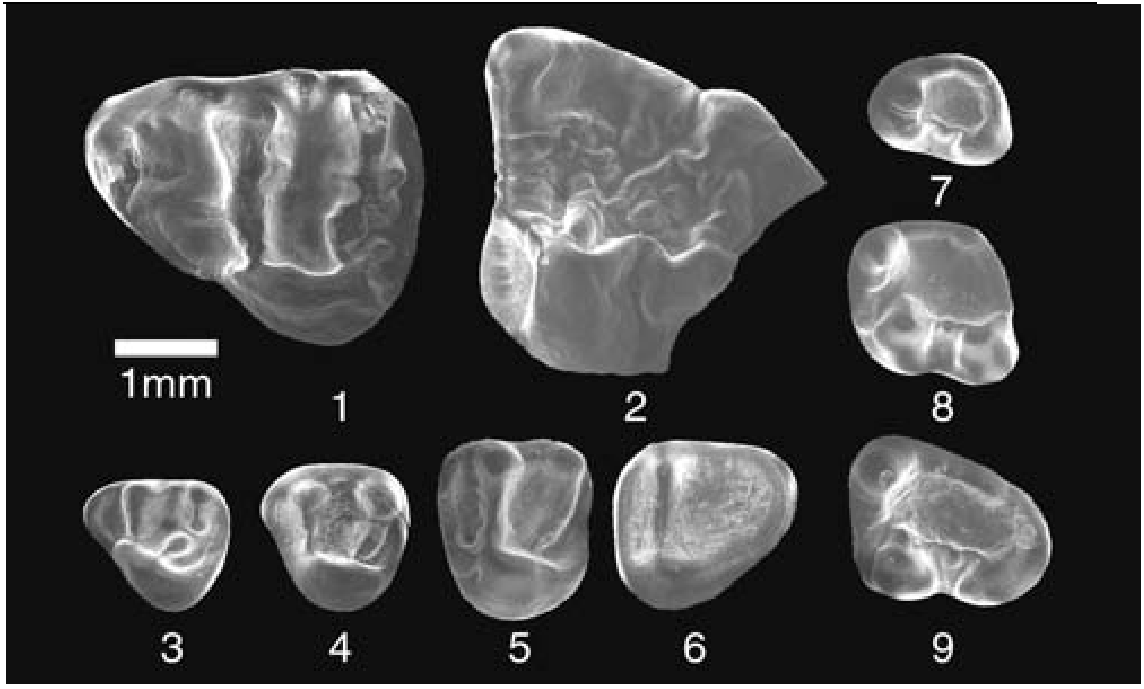

Figure 4.1. SEM micrographs of selected cheek teeth of the Sciuridae from BCV1. *Miopetaurista* cf. *crusafonti*. Figs. 1-2. 1. Left P^4, IPS 23354. 2. Left $M_{1/2}$, IPS 23355. *Spermophilinus bredai*. Figs. 3-9. 3. Right dP^4 (reversed), IPS 23359. 4. Left P^4, IPS 23361. 5. Left $M^{1/2}$, IPS 23368. 6. Right M^3 (reversed), IPS 23371. 7. Right P_4 (reversed), IPS 23374. 8. Left $M_{1/2}$, IPS 23375. 9. Left M_3, IPS 23381.

M_3 (fig. 4.1.9.): This molar presents two small messial roots besides a more robust distal one which points obliquely backwards. The anterior part of the tooth has only been preserved in one specimen (IPS 23381, fig. 4.1.9.). The anterolophid departs from the metaconid and it is separated from the protoconid by a weak groove. There is no trace of the entoconid.

Subfamily **Pteromyinae** Brandt, 1855

Genus *Miopetaurista* Kretzoi, 1962

***Miopetaurista* cf. *crusafonti* (Mein, 1970)**

(fig. 4.1.1-2)

Synonymy: *Albanensia albanensis* in Moyà-Solà *et al.* (2004).

Material: A right mandible fragment with M_3 (IPS 23186), 1 P^4 (IPS 23354), 1 broken $M_{1/2}$ (IPS 23355).

Measurements:

Lower cheek teeth			Upper cheek teeth		
	L	**W**		**L**	**W**
	4.03	-	**P^4**	3.59	3.23
M_3	4.34	3.63			

Description:

Mandible: The mandible fragment is very damaged and only part of the corpus below M_3 and the base of the ramus have been preserved. Apparently the ramus is not very vertical, so the M_3 is perfectly visible from the buccal side.

Upper cheek teeth (fig. 4.1.1.)**:** Just a single P^4 has been recovered (IPS 23354). The premolar has a subtriangular outline, with the lingual side conspicuously narrower than the buccal one. It is clearly longer than wider. The buccal margin is straight, while the lingual one is more curved. The bases of two cylindrical buccal roots, besides a more robust, flattened lingual one can be observed. The enamel of the valleys and cusps shows crenulations. There are three buccal cusps: parastyl, paracone and metacone. The parastyl is lower than the main cusps. The protocone and the hypocone are integrated into the endoloph, so they cannot be distinguished. The anteroloph joins the parastyl to the base of the endolph, closing the lingual end of the anterior valley. A small styl between the paracone and the parastyl obtrudes the buccal end. The protoloph and the metaloph are transverse and parallel to each other, reaching the endoloph separately. These lophs are robust and much higher than the anteroloph and the posteroloph. The central valley is narrow and shallow. This valley is closed by a rounded and prominent mesostyl. A well-developed metaconule is clearly distinguished within the metaloph. Between the metaconule and the metacone there are two short spurs that point distally although they do not reach the posteroloph. A similar, though even shorter, postero-buccally directed spur is also present at the point where the metaloph joins the endoloph. The posterior valley is closed by the posteroloph.

Lower cheek teeth: One M_2, broken at its postero-buccal corner (IPS 23355 fig. 4.1.2.), and a very badly preserved M_3 have been recovered. The molars are wedge-shaped, and clearly longer than wider. The buccal and mesial margins are straight, while the lingual and distal ones are more curved. The teeth are conspicuously wider on their mesial half than on their distal one. The enamel in the cusps and valleys shows abundant well-developed crenulations. The metaconid is placed slightly more mesially than the protoconid and is the most prominent cusp. The mesial cusps are higher than the distal ones. The ectolophid is M-shaped and presents a well-defined mesoconid. The central valley is closed by a crest departing from the posterior wall of the metaconid which is interrupted just before reaching the entoconid.

M_2 (fig. 4.1.2.): Four main cusps surround a subtriangular valley: metaconid, protoconid, entoconid and mesoconid (the hypoconid is broken). A robust anterolophid departs from the metaconid and joins the protoconid. There is a lower anterior cingulum that closes the anterosinusid. A low and transverse metalophid departs from the protoconid, althought it does not reach the metaconid. The entoconid is separated from the posterolophid by a deep groove. There seems to be a low and sinuous entolophid fused to the base of the entoconid.

M_3: The teeth has tree roots: two mesial ones and a very robust distal one. Six cusps can be distinguished: protoconid, metaconid, entoconid, hypoconid, mesoconid and hypoconulid. The protoconid is crescent-shaped and it fusses to a robust anterolophid that joins the metaconid. Similarly, the hypocone, which is also crescent-shaped fuses to the posterolophid. The hypoconulid is very small and it is placed rather lingually. This cusp joins the entoconid by the means of a short and weak ridge.

Comments and comparisons:

Villalta (1950) described a new subspecies of flying squirrel, *Albanensia albanensis quiricensis* (*Sciuropterus albanensis quiricensis* in the original paper), from the Sant Quirze site in the Vallès Occidental area. The type specimen, a lower mandible with the complete definitive series, which mainly differs of *A. albanensis albanensis* by its larger size and by its slightly hypsodont cheek teeth. Villalta (1950) further reported this subspecies from Can Vila on the basis of a toothless mandible found by Bataller that had already been lost by this time. The presence of a set of characters indicate that the material described from BCV1 does not belong to *Albanensia*: metaloph and protoloph parallel and not converging towards the protocone on the P^4 besides the absence of a well delimited protocone in the same tooth; or the presence of an anterolingual cingulum on M_2 and a subcomplete entolophid in the same molar. The morphology of the parastyl and the metaloph (with its backwards-directed spurs) on the P^4 are very similar to those of *Miopetaurista crusafonti*. The morphology of the lower molars is also very similar to those species. The size of the specimens is clearly smaller than *M. neogrivensis*, and also somewhat smaller than *M. crusafonti*. In the view of the fragmentary remains recovered the adscription should stay as *M.* cf. *crusafonti*.

Suborder **Glirimorpha** Thaler, 1966

Family **Gliridae** Muirhead, 1819

Subfamily **Glirinae** Muirhead, 1819

Tribe **Muscardini** Palmer, 1899

Genus *Glirudinus* De Bruijn, 1966

***Glirudinus undosus* Mayr, 1979**

(fig. 4.2.1-3)

Material: 1 M^1 (IPS 23348), 1 M_1 (IPS 23176), 5 M_2 (IPS 23343, IPS 23344, IPS 23175, IPS 23177, IPS 23345), 2 M_3 (IPS 23346, IPS 23347).

Measurements:

	L					W				
	N	**min.**	**mean**	**max**	**s. d.**	**N**	**min.**	**mean**	**max**	**s. d.**
M_2	5	0.98	1.02	1.09	0.05	5	0.89	0.95	1.02	0.05

Lower cheek teeth			Upper cheek teeth		
	L	**W**		**L**	**W**
M_1	0.91	0.90	**M^1**	1.00	1.13
M_3	0.92	0.88			
	1.05	1.04			

Description:

Upper cheek teeth (fig. 4.2.3.)**:** Just a single molar has been recovered (IPS 23348). This an extremely low-crowned molar. The wear surface is slightly concave. The messial margin is conspicuously narrower than the distal one, suggesting that it is an M^1 rather than an M^2, which would present a similar mesial and distal width. There is a single well-developed and flattened lingual root besides two smaller cylindrical buccal ones. The occlusal pattern is defined by numerous transverse thin ridges that define an angle close to 45 ° with the mesiodistal axis of the molar. The main cusps cannot be distinguished. There are seven complete ridges that merge a continuous endoloph and six long secondary ridges, in a number of one between each complete one. The three first complete ridges are also joined to a buccal ridge which is interrupted just after the third one. The four distal complete ridges join a similar buccal ridge. The secondary ridges are very long. The first one merges the endoloph, while the second one joins the third complete ridge at its buccal end. The third secondary ridge is slightly shorter and it is isolated. A small and isolated rounded cusp is present at the buccal end of the third secondary ridge. The last secondary ridge is slightly shorter than the others.

Lower cheek teeth: The recovered molars exhibit an extremely low crown and a slightly concave wear surface. The roots have been preserved only in two M_2. There are two cylindrical mesial roots which are straight, besides a flattened distal root. Certain main cusps are distinguished, while others are not. The dimensions of the three molars are very similar. The M_1 and M_2 are rather square and can only be distinguished because the mesial margin of the M_1 is slightly concave, while in the case of the M_2 it is straight. The M_3 is clearly distinguished by its rounded distal end. The occlusal pattern is similar to that of the upper molars, although the ridges are not so oblique to the mesiodistal axis of the teeth. The main ridges are wider than the secondary ones, particularly at their buccal end. There are five main, complete ridges besides seven to eight secondary ones. The secondary ridges usually do not reach the buccal margin. The main ridges merge an almost continuous endolophid (usually being briefly interrupted after the metaconid in M_1 and M_2) at the lingual side. On the contrary, the ridges end free at the buccal side, so the valleys are bucally open.

M_1 (fig. 4.2.1.): The first syncline includes up to three secondary ridges, the second one being longer than the others. This second secondary ridge merges the endolophid and reaches the buccal margin. The other two ridges are isolated. A thin and short ridge, presumably an anterior centrolophid, departs from the metaconid. After this ridge the endolophid is interrupted. There is a better-developed, longer ridge (almost reaching the buccal margin) departing from the entoconid, that presumably corresponds to the posterior centrolophid. This ridge is weakly joined to the mesolophid at its buccal end. Up to three secondary ridges can be recognized between the mesolophid and the posterolophid. The second is nearly as developed as the main ones, while the remaining two are much shorter and thinner. These three ridges are isolated.

M_2 (fig. 4.2.2.): The endolophid is completely continuous in one specimen (IPS 23343), while in the others is interrupted after the metaconid as usual. There are three to four secondary ridges between the two main ones (anterolophid and metalophid). Three specimens show four secondary ridges (IPS 23176, IPS 23177 fig. 4.2.2., IPS 23244), and in those cases the second one is very reduced. This ridge is just outlined in a third specimen, which shows two small elongated enamel folds coinciding with its position (IPS 23345). The two secondary ridges that are more distally situated merge the endolophid, while the first one is isolated in two individuals (IPS 23343, IPS 23244) and joins the endolophid in three more (IPS 23176, IPS 23177 fig. 4.2.2., IPS 23345). Three secondary ridges are present between the metalophid and the mesolophid. The central one, which may correspond to the centrolophid, merges the endolophid and is more developed than the others. In one specimen (IPS 23343) the first one of these ridges also joins the endolophid. A weak buccal contact between the mesolophid and the posterolophid is observed in three teeth (IPS 23344, IPS 23345, IPS 23177 fig. 4.2.2.). Between these two main ridges there are three secondary ridges more, the central one being clearly more developed than the others.

M_3: The recovered specimens are rather worn, therefore some morphological traits cannot be distinguished. Up to five secondary ridges can be distinguished between the anterolophid and the metalophid. The fourth one is more developed and merges the endolophid, while the remaining ones are isolated. The third and particularly the first secondary ridges are vestigial. There are three ridges more between the metalophid and the mesolophid. The central one, presumably corresponding to the centrolophid, is more developed and merges the endolophid, while the other two are isolated. Finally three ridges more can be recognized between the mesolophid and the posterolophid. As usual, the central one is more developed than the others, being comparable to the main ridges. The first one is very reduced. These three secondary ridges are isolated.

Comments and comparisons:

The stratigraphic range of *Glirudinus undosus* covers most of the Aragonian (MN 3 to MN 7+8). This genus is quite rare in Spain, although it has been reported from the Ramblian and the Early Aragonian of the Calatayud-Daroca area (Daams *et al*., 1988). In the Vallès-Penedès Basin this species has been reported from Can Martí Vell I and II (Agustí, 1983), which are attributed to the MN 4 (although an MN 5 age was not discarded by Agustí, 1983), and from the Late Aragonian (MN 7+8) of Castell de Barberà (Agustí *et al*., 1985). A few teeth of this species have also been recovered in Sant Quirze A and Abocador de Can Mata (ACM) C4-A4. The persistence, although in low numbers, of *G. undosus* in the Vallès-Penedès Basin during the Late Aragonian evidences the closer relationship of its faunas with northern ones as compared to other Spanish basins.

Genus *Muscardinus* Kaup, 1829

***Muscardinus sansaniensis* Lartet, 1851**[23]

(fig. 4.2.4-5)

Material: 2 broken M_1 (IPS 23349, IPS 23350), 1 M_3 (IPS 23351), 1 M^2 (IPS 23352), 1 M^3 (IPS 23178). One eroded lower molar, most probably an M_1 (IPS 23178), may also belong to this taxon.

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[23] *M. sansaniensis* is ascribed by certain authors to a the genus *Eomuscardinus* Hartenberger, 1966. Hartenberger (1966) proposed *Eomuscardinus* as a subgenus of *Muscardinus* and considered it the ancient stock of the genus. This new subgenus would have a relatively large P^4 compared to the more modern *Muscardinus* species and *Muscardinus thaleri* was not included in it. According to Daams (1999), as far as the complexity of the dental pattern is concerned no difference is observed between the Middle Miocene *M. thaleri* and *M. sansaniensis*. The relative size of the P^4 is not sufficient to warrant generic separation in the opinion of Daams (1999). We follow Daams (1999) in considering *Eomuscardinus* a junior synonym of *Muscardinus*.

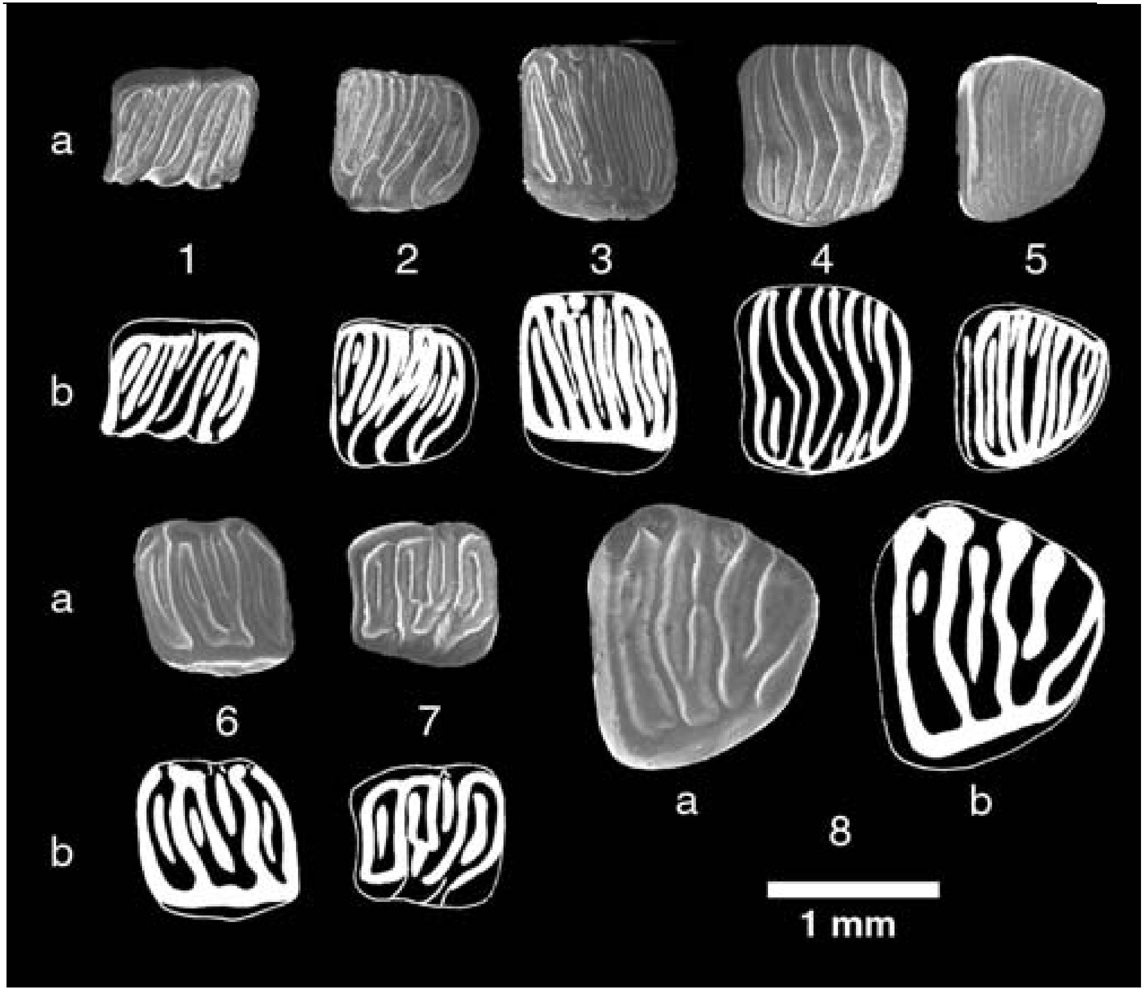

Figure 4.2. SEM micrographs of selected molars of the Gliridae from BCV1(a) and schematic drawing of the photographed specimens (b). *Glirudinus undosus*. Figs. 1-3. 1. Left M_1, IPS 23175. 2. Right M_2 (reversed), IPS 23177. 3. Right M^1 (reversed), IPS 23348. *Muscardinus sansaniensis*. Figs. 4-5. 4. Left M^2, IPS 23352. 5. Left M^3, IPS 23178. *Microdyromys complicatus*. Figs. 6-7. 6. Right $M^{1/2}$ (reversed), IPS 23341. 7. Left $M_{1/2}$, IPS 23340. *Bransatoglis* sp. Fig. 8. Right M^3 (reversed), IPS 23353.

Measurements:

Lower cheek teeth			Upper cheek teeth		
	L	**W**		**L**	**W**
			M^2	1.20	1.34
M_3	1.11	1.02	**M^3**	0.94	1.05

Description:

Upper cheek teeth: The crown is very low and the wear surface is flat. The roots have not been preserved in any of the recovered teeth. The occlusal surface is crossed by numerous transverse thin ridges. The width of the secondary ridges is similar to that of the main ones. The main cusps cannot be distinguished. The complete ridges usually merge a continuous endoloph. The valleys limited by these main ridges are buccally open.

M^2 (fig. 4.2.4.): This is a square-shaped molar, although the distal outline is somewhat more rounded than the mesial one. There are up to seven S-shaped complete ridges. All but the fifth ridge merge a continuous endoloph. The third and the fourth complete ridges fuse close to the lingual margin before joining the endoloph. Besides these main

ridges there are numerous secondary ones: a long lingual isolated ridge between the first and the second ones; and two minute ridges, labial and lingual, between the fourth and the fifth, and between the fifth and the sixth. In both cases the lingual secondary ridge is weakly united to the endoloph.

M^3 (fig. 4.2.5.): The distal margin, which is rounded, is conspicuously narrower than the mesial one, which is straight. There are up to nine main ridges which merge a continuous endoloph. All this ridges reach the buccal margin, except the second one which is somewhat shorter. The eighth ridge bifurcates before reaching the buccal margin. There is a vestigial ridge, lower than the remaining ones, situated at the mesiobuccal margin of the tooth, just in front of the first main ridges. There are two secondary ridges, one between the third and the fourth main ridges, and another one between the fourth and the fifth ones which is somewhat longer.

Lower cheek teeth: The lower molars are clearly longer than wider. The crown is very low and the wear surface is flat. The main cusps cannot be distinguished. The morphology of the teeth can only be adequately described in the case of the M_1, because the only M_3 recovered is eroded, so the main ridges are not clearly distinguished. However, the shape of this molar, with an slightly concave mesial margin and a narrower and more straight distal one, clearly indicates that this tooth is in fact an M_3. The roots have not been preserved in any of the recovered teeth. The secondary ridges are as wide as the main ones.

M_1: In two of the recovered specimens the anterior part is broken (IPS 23349, IPS 23350), while the third one is so eroded that its identification as an M_1 is entirely based on its size and the shape of its outline (IPS 23178). The molars are somewhat longer than wider, and the mesial margin is narrower than the distal one. There are up to five main ridges: anterolophid, metalophid, mesolophid, posterior secondary ridge and posterolophid. These ridges merge in a continuous endolophid which is interrupted just after a vestigial centrolophid. All these ridges display a mesially directed inflexion at the midpoint of their path. The posterior secondary ridge and the posterolophid are also joined at the buccal margin, therefore the last syncline, which in its turn is quite wide is completely closed.

Comments and comparisons:

This is the first time that *Muscardinus sansaniensis* is reported from the Vallès-Penedès Basin. Other *Muscardinus* species, such as *M. hispanicus* and *M. vallesiensis* have been reported from similarly-aged sites of the basin, such as Sant Quirze or Castell de Barberà (see Aguilar *et al.*, 1979; Agustí, 1981a; Agustí *et al.* 1985). The described material is clearly distinguished of both species by its clearly more complex dental pattern, which includes a greater number of secondary ridges. It is further distinguished from *M. hispanicus* by its larger size.

Subfamily **Leithiinae** Lydekker, 1896

Tribe **Leithiini** Lydekker, 1895

Genus *Microdyromys* De Bruijn, 1966

Microdyromys complicatus De Bruijn, 1966

(fig. 4.2.6-7)

Synonymy: *Paraglirulus werenfelsi* (pro parte) in Moyà-Solà *et al.* (2004).

Material: 2 $M^{1/2}$ (IPS 23341, IPS 23342), one of them broken, 3 $M_{1/2}$ (IPS 23174, IPS 23339, IPS 23340), one of them broken.

Measurements:

Lower cheek teeth			Upper cheek teeth		
	L	**W**		**L**	**W**
$M_{1/2}$	1.08	0.97	**$M^{1/2}$**	0.97	1.00
	0.98	0.87			

Description:

Upper cheek teeth (fig. 4.2.6.)**:** Just two $M^{1/2}$ have been recovered, though one of them is broken. These are square-shaped molars. The wear surface is strongly concave and the main cusps cannot be distinguished from the ridges. The development of main and secondary ridges is similar. There are up to five complete transverse ridges parallel to each other: anteroloph, protoloph, anterior centroloph, metaloph and posteroloph. All these ridges merge an endoloph, which is interrupted between the anterior centroloph and the metaloph. The lingual end of these ridges is slightly wider than the buccal one and is somewhat distally directed. The main valleys are occupied by secondary ridges. There is a well-developed ridge which divides the first syncline. The anteroloph is separated from the paracone by a deep groove. Between the protoloph and the anterior centroloph there is another short and isolated secondary ridge which is situated quite buccally. The posterior centroloph is shorter than the anterior one and it is separated from the metacone. Finally an isolated secondary ridge is present between the metaloph and the posteroloph. The posteroloph is separated from the metacone by a narrow groove.

Lower cheek teeth (fig. 4.2.7.)**:** Three $M_{1/2}$ have been recovered, although one of them is very broken. The molars are conspicuously longer than wider and the mesial margin is somewhat narrower than the distal ones. The buccal and the lingual margin are straight, while the mesial one may be straight or concave. Those molars which show a markedly concave mesial margin may be regarded as M_1 (such as IPS 23340 fig. 4.2.7.). The distal margin is somewhat curved. The crown is low and the wear surface is markedly concave. There are up to five main ridges parallel to each other: anterolophid, metalophid, centrolophid, mesolophid and posterolophid. The centrolophid is the only ridge that does not reach the buccal margin. All these ridges merge a continuous endolophid which is interrupted just after the centrolophid. These five main ridges delimitate four buccally open valleys which are occupied by secondary ridges. These secondary ridges are as wide as the main ones. The first and particularly the last secondary ridges are longer than the remaining ones. In one specimen (IPS 23340 fig. 4.2.7.) the secondary ridge between the metalophid and the centrolophid is weakly joined to a short buccal secondary ridge. This buccal ridge is also weakly joined to the tip of the centrolophid. In another specimen (IPS 23174) the mesolophid presents a short posterior spur at its buccal end which contacts with the posterolophid. Therefore, the last syncline is closed in this tooth.

Comments and comparisons:

Microdyromys complicatus is here reported from the Vallès-Penedès Basin for the first time. This species is present in other temporally close sites of the ACM series (such as C4-C1) and also from Sant Quirze A where it is very rare.

Genus *Bransatoglis* Hugueney, 1966

***Bransatoglis* sp.**

(fig. 4.2.8.)

Material: 1 M^3 (IPS 23353).

Measurements: L = 1.48 W = 1.74

Description (fig. 4.2.8.)**:** This molar its outstanding because of its size, clearly larger than the remaining Gliridae recovered, and distinct occlusal pattern. The molar is conspicuously wider than longer. The mesial margin is straight, while the distal one, which is narrower, is curved. The crown is low and the wear surface strongly concave. There are up to six transverse main ridges (anteroloph, protoloph, centroloph, metaloph, posterior secondary ridge and posteroloph) which are quite wide. The buccal cusps are rounded and prominent. Concerning the lingual ones only the protocone can hardly be distinguished. The main ridges merge into a continuous endoloph. However, the posterior secondary ridge joins the endoloph at a lower high. The centroloph is isolated and ends in a small buccal cusp. The metaloph is sinuous . There is a very short and low isolated buccal secondary ridge between the anteroloph and the protoloph.

Comments and comparisons:

During the Late Aragonian and the Vallesian the genus *Bransatoglis* is quite common in Central Europe, but in Spain it has only been reported from the sites of the Vallès-Penedès Basin (see Agustí *et al.*, 1985 and Agustí *et al.*, 1997 for a list of the sites). During this time interval this genus is represented by the species *B. astaraciensis* which can not be confidently identified on the basis of the material recovered at BCV1. The presence of this genus, together with of *Glirudinus undosus* indicates affinities with the rodent faunas of higher latitudes.

Suborder **Myomorpha** Brandt, 1855

Infraorder **Myodonta** Schaub, in Grassé & Dekeyser, 1955

Superfamily **Muroidea** Illiger, 1811

Family **Paracricetodontinae** Mein & Freudenthal, 1971

Subfamily**Eucricetodontinae** Mein & Freudenthal, 1971

Genus *Eumyarion* Thaler, 1966

Eumyarion leemani (Hartenberger, 1965)

(fig. 4.3.1-3, fig 4.4., fig. 4.5.)

Synonymy: *Eumyarion* aff. *leemani* in Moyà-Solà *et al.* (2004).

Material: two mandibles belonging to the same individual (IPS 20266), a left lower molar series with associate I_2 (IPS 20241), 26 M^1 (IPS 23120 – IPS 23139, IPS 23207 – IPS 23218, IPS 23287 – IPS 23290), 24 M^2 (IPS 23130 – IPS 23140, IPS 23219 – IPS 23228, IPS 23291 – IPS 23293), 21 M^3 (IPS 23141 – IPS 23149, IPS 23229 – IPS 23236, IPS 23294 – IPS 23297), 20 M_1 (IPS 23150 – IPS 23159, IPS 23187 – IPS 23196, IPS 23298, IPS 23299), 20 M_2 (IPS 23160 – IPS 23168, IPS 23197 –IPS 23202, IPS 23237, IPS 23238, IPS 23300 – IPS 23302), 12 M_3 (IPS 23169 – IPS 23173, IPS 23203 – IPS 23206, IPS 23303 – IPS 23305).

Measurements:

Mandibles

Description of the measurement	IPS 20266 (right)	IPS 20266 (left)
Length of postcanine series at the occlusal level	-	4.94
Length of postcanine series at the alveolar level	(5.10)	4.96
Symphysis height	(2.63)	
Height of mandibular body at the lingual side (perpendicular to the alveolar level), at the level of M_1	(3.49)	(4.08)
Height of mandibular body at the lingual side (perpendicular to the alveolar level), at the level of M_2	(3.51)	(3.61)
Height of mandibular body at the lingual side (perpendicular to the alveolar level), at the level of M_3	3.33	3.30
Breadth of mandibular body (perpendicular to mandibular height), at the level of M_1	(2.65)	(2.65)
Breadth of mandibular body (perpendicular to mandibular height), at the level of M_2	(2.32)	2.54
Breadth of mandibular body (perpendicular to mandibular height), at the level of M_3	(2.46)	2.59

Lower incisors

Description of the measurement	IPS 20266 (right)	IPS 20266 (left)	IPS 20241
anterior width at occlusal level	0.92	0.93	0.78
posterior width at occlusal level	0.51	0.47	0.53
wear facet anteroposterior length	2.86	2.80	2.49
whole length of the incisor	-	-	10.26

Cheek teeth

	L					W				
	N	min.	mean	max	s. d.	N	min.	mean	max	s. d.
M^1	21	1.91	2.06	2.24	0.12	23	1.29	1.52	1.70	0.09
M^2	20	1.40	1.60	1.75	0.09	24	1.34	1.52	1.67	0.08
M^3	21	0.90	1.20	1.35	0.13	21	1.06	1.28	1.45	0.12
M_1	19	1.73	1.98	2.15	0.11	20	1.09	1.26	1.38	0.06
M_2	18	1.56	1.69	1.80	0.06	19	1.31	1.37	1.44	0.04
M_3	12	1.41	1.61	1.80	0.11	11	1.11	1.26	1.37	0.08

Description:

Mandibles (fig. 4.3.1-3)**:** Both mandibles (IPS 20266) were recovered during the systematic macropaleontological excavation carried at BCV1. The mandibles appeared in the same block and very close to each other (the lower molar series IPS 20241 was also recovered during the excavation). Albeit the mandibular symphysis is somewhat damaged in the recovered mandibles, the left mandible perfectly fits with the right one. The degree of tooth wear is analogous in both mandibles, further evidencing that they belong to the same individual. The ramus is broken in both mandibles, while the corpus is well preserved and only minimally damaged at its ventral side, close to the symphysis. The M_1 and the M_2 are missing on the right mandible. Overall, the mandible is stout and relatively short. The incisor is rather curved and its tip is situated above the alveolar plane. The incisor extends along the ventral side of the mandible beyond the M_3 into the ramus. Apparently the digastric eminence did not exist or it was not marked. The molar series is separated of the lower incisor by a short, somewhat shallow and symmetrical diastema. The molar series is procumbent lingually and its wear surface is rather flat. The length of the molar series at the alveolar level is not significantly different from its length at the occlusal level. The roots of the molars are visible in buccal view and in lingual view as well. The mandibular corpus is robust and deep. The ramus originates near the mesial margin of the M_3, and obscures the distal part of this molar. The mental foramen is situated at the end of the diastema, just anterior to the mesial root of the M_1, and it is situated quite dorsally. This foramen is medium-sized and rounded. The masseteric fossa is V-shaped and is limited by the strong upper and lower masseteric ridges. The lower masseteric ridge is more marked than the upper one and apparently it extended into the angular apophysis. The upper masseteric ridge merges the lower one at the level of the anterior root of the M_1, at about the middle height of the corpus. The fusion of both ridges defines a pronounced “V” with a well developed inflation at its vertex (the masseteric tubercle). In lingual view of the corpus, the insertion area for the mylohyoid muscle can hardly be appreaciated. The symphysis

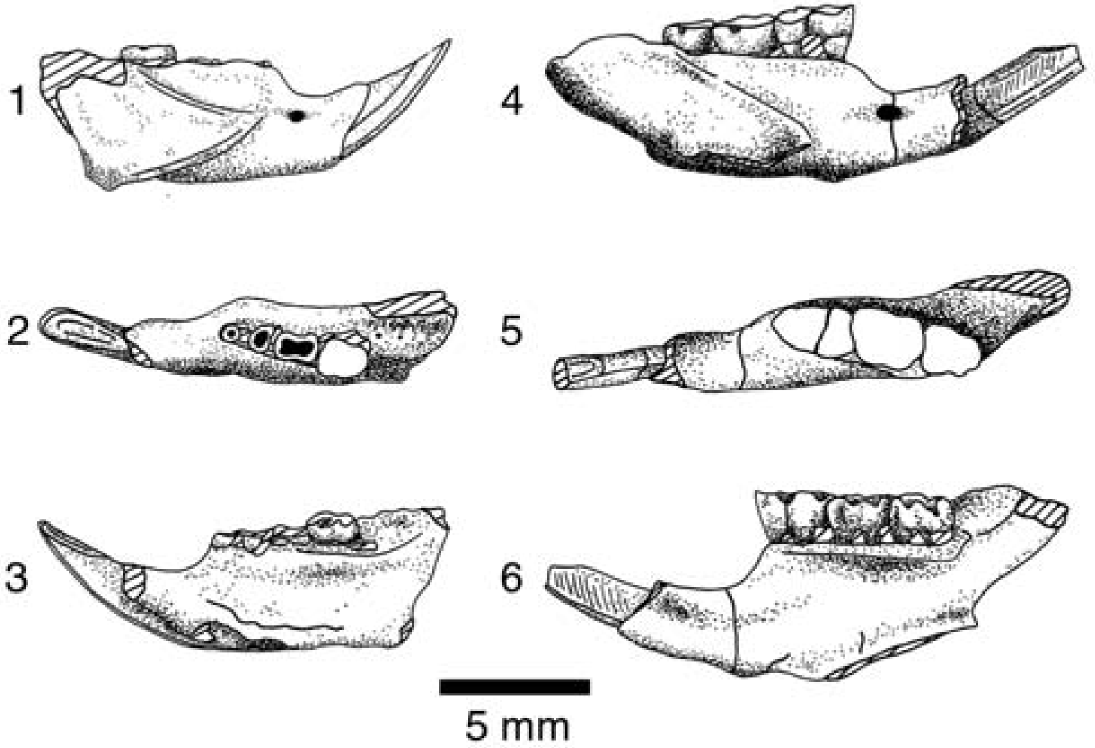

Figure 4.3. Light camera drawings of two “cricetid” mandibles from BCV1. *Eumyarion leemani*. Figs. 1-3. Right mandible of IPS 20266. 1. Buccal view. 2. Occlusal view. 3. Lingual view. *Hispanomys* sp. Figs. 4-6. Right mandible, IPS 20242. 4. Buccal view. 5. Occlusal view. 6. Lingual view.

is damaged. A well defined and wide insertion area (presumably for the temporal) is observed on the inner side of the preserved portion of the ramus, just posterior to the M_3. Two small foramina are present on the inner side of the ramus, near the alveolar plane and distally to M_3.

I_2: The incisor is not strongly curved. Its mesial and buccal margins are rounded. The enamel reaches the medium width of the crown in buccal view, while at the symphyseal side only a thin enamel line can be appreciated. The enamel presents two parallel longitudinal ridges. One of these ridges is situated somewhat dorsally, so it can be observed when the mandible lays on its lingual side. The wear surface is elongated and only slightly concave, forming a continuous curved line with the diastema. Several isolated lower incisors as well as incisor fragments (without an assigned collection number) may be attributed to *Eumyarion leemani* on the basis of their size and morphology.

Upper cheek teeth: Moderately hypsodont molars with the buccal cusps clearly higher than the lingual ones (terraced sensu Hershkovitz, 1967). The wear surface is flat at the lingual side and slightly concave at the buccal one. As wear progresses this wear surface becomes slightly concave, and in senile individuals it is completely flat (see fig. 4.4.). The M^3 are rather reduced and button-shaped. The occlusal pattern is very complex, presenting numerous extra connections between the main cusps and long transverse ridges as well. In unworn to slightly worn molars it can be appreciated that the main cusps, particularly the buccal ones, are integrated into the main ridges. These ridges are very high and well developed. The M^2 and M^3 present a narrow and bucolingually elongated anterosinus which is closed by the labial arm of the anteroloph, which in its turn is high and well-developed. These molars lack the protosinus and the lingual arm of the anteroloph. The lingual anteroloph is also missing in the M^1, although these molars show a reduced protosinus. There is a wide and relatively long posterior protolophule in the M^1 and M^2. The part of longitudinal ridge anterior to the protolophule curves lingually and joins the protocone. The mesoloph in the M^1 and M^2 is wide and middle-sized. This ridge is transverse, although its end may point towards the metacone. The mesosinus is closed by a cingulum merging the paracone to the metacone. Usually in the M^3 this cingulum is as high as the main ridges and merges the posteroloph. Therefore, a continuous cingulum running through the distal and buccal margin of the M^3 from the hypocone to the paracone is defined. In M^1 and M^2 the sinus is open and very proverse. The metalophule is long and transverse in the M^1 and M^2. The posterosinus is narrow and transversely elongated in the M^1 and M^2. This valley is limited by a well-developed posteroloph which becomes very low at its buccal end. However, this ridge merges the metacone, so the posterosinus is closed.

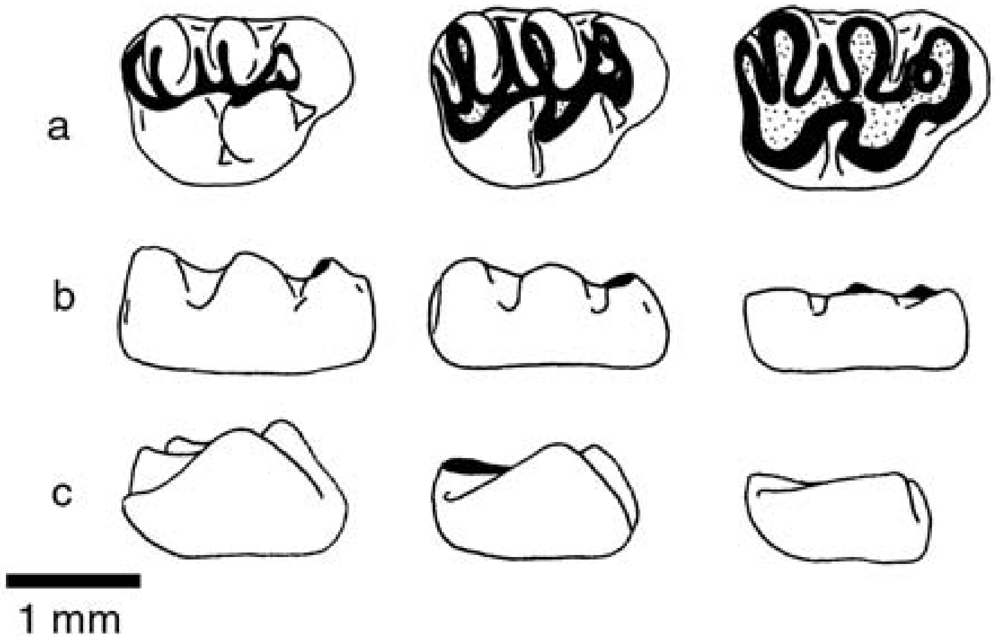

Figure 4.4. Light camera drawings of three M^1 of *Eumyarion leemani* from BCV1 at different stages of wear in occlusal (a), lingual (b, mesial side to the right) and distal view (c, buccal side to the left),. The specimen on the left (IPS 23126) shows minimum degree of wear with no dentine exposed. In the specimen placed in the middle (IPS 23212) the degree of wear is moderate and the dentine (dotted) is exposed on the main cusps. The distal view of the same specimen shows the development of a concave wear surface. The specimen on the right (IPS 23216) is highly worn, so dentine is exposed also on the main ridges. The distal view of this tooth shows the development of a flat wear surface.

M^1 (fig. 4.4., fig. 4.5.1): The prelobe is very developed. The unworn molars show a buccolingually elongated, ridge-like anterocone. This anterocone is slightly divided into two lobes. The buccal lobe is usually larger than the lingual one (see for example IPS 23124, fig. 4.5.1.). In a few cases this subdivision is accompanied by a groove at the mesial wall of the anterocone (such as IPS 23207), while in most of the molars this wall is smooth. 7 molars (out of 21) present a small styl situated at the mesial wall of the anterocone, just below its buccal lobe (see fore example IPS 23211, or IPS 23124 in fig. 4.5.1.). In a few cases this styl is rather cingular-like (see for example IPS 23126). The anterosinus, which is rather wide, is closed by a high cingulum. In nearly the 25 % of the teeth this cingulum presents a parastyl. The protocone is very close to the lingual cusp of the anterocone, and a short and high ridge (which may correspond to the lingual anteroloph) merges the two cusps. This fact implies the strong reduction of the protosinus. This valley may be closed by a weak cingulum. The labial lobe of the anterocone presents a well-developed and distolingually directed posterior spur which

joins a long and high anterior spur of the protocone, defining and oblique anterolophule. The point where both spurs meet resembles a small cusp in many molars. In more than 30 % of the molars the anterior spur of the protocone continues beyond the point it joins the posterior spur of the anterocone. Therefore a short and buccally-pointing spur is definded. This spur becomes immediately very low in most of the cases (see for example IPS 23124, fig. 4.5.1.). In a few molars the spur is better-developed and merges the base of the paracone. The ridge that joins the protocone and the lingual cusp of the anterocone also presents a short buccal spur, presumably the anteromesoloph. This anteromesoloph merges the anterolophule and closes a small subtriangular fossete. In one molar (IPS 23212) the anterior spur of the protocone does not reach the posterior spur of the anterocone and the anteromesoloph is longer and better developed. In three teeth (IPS 23127, IPS 23128, IPS 23213) there is an anterior spur departing from the base of the paracone which is directed towards the anterolophule. In 6 molars (out of 21) the paracone presents a short and low ectoloph which points towards the mesoloph. In three of them (such as IPS 23123) the ectoloph is fused to the mesoloph. In the same three teeth the buccal end of the mesoloph points strongly backwards and merges the base of the metacone.

M^2 (fig. 4.5.2.): The labial arm of the anteroloph is wide and high, and may develop a small cusp near its buccal end (see for example IPS 23130, fig. 4.5.2.). The anteroloph is very low at the buccal margin but still it closes the anterosinus. This anteroloph departs directly from the protocone, which is crescent shaped. The hypocone is also crescent shaped. About 30 % of the molars show a vestigial anterior protolophule which is very low and may merge the base of the anteroloph (see for example IPS 23225, IPS 23226). The mesosinus is closed by a high cingulum which may present a well-developed mesostyl (see for example IPS 23135 or IPS 23136). In one molar the mesoloph is longer than usual and merges this buccal cingulum (IPS 23131). In many cases the buccal end of the mesoloph joins two very low cingula departing from the base of the paracone and the metacone, respectively. One molar shows a small, mesially-directed spur departing from the metalophule.

M^3 (fig. 4.5.3.): The distal cusps are very reduced, and the metacone can hardly be distinguished. The protocone occupies most of the surface of the molar and is crescent shaped. The paracone is the most prominent cusp. The anteroloph departs directly from the protocone. This ridge is well developed and merges the anterior wall of the paracone, closing the anterosinus. There is a long and wide posterior protolophule. Three molars also present a weak anterior protolophule which is complete in one case (IPS 23145). In the remaining two teeth this anterior protolophule may be defined by two spurs, one departing from the paracone and another departing from the protocone, which are not fused (IPS 23146), or it may consist in a short anterior spur of the paracone (IPS 23236). The protocone is rotated and its distal wall is in contact with a short spur departing from the mesial wall of the hypocone, defining a neo-entoloph that closes the sinus. The longitudinal ridge (axioloph) originates from the protolophule and it is wide and arched. A medium-sized to long transverse mesoloph is also present. This ridge merges the buccal ridge that closes the mesosinus. In IPS 23141 the buccal end of the mesoloph is mesially directed and joins the posterior wall of the paracone. In a few molars the buccal ridge that closes the mesosinus may be interrupted before reaching the metacone. In IPS 23294 this buccal ridge does not exist and the mesosinus is obtruded by a well-developed mesostyl. The hypocone merges the vestigial metacone through a wide, long and transverse centroloph. In a few teeth this centroloph is divided into two vestigial metalophules before reaching the hypocone (for example IPS 23143, fig. 4.5.3., IPS 23144). The anterior metalophule is somewhat weaker than the posterior arm. A very small circular fossete is defined between both arms of the metalophule.

Two molars (IPS 23144, IPS 23145) present a third longitudinal ridge (besides the longitudinal ridge or axioloph, and the neo-entoloph) placed more buccally than the others. This ridge is defined by a posterior spur of the protolophule which merges the centroloph. This ridge is also present in two other teeth (IPS 23229, IPS 23294), although it is defined by a posterior spur of the protolophule and an anterior one of the centroloph which are not fused. In the cases that present a third longitudinal ridge the mesoloph is missing. In IPS 23236 the mesosinus is crossed by several oblique ridges. This molar presents a neo-entoloph and an axioloph as well. Besides these ridges the prolophule presents a long postero-buccally directed spur which merges a similarly developed anterior spur of the hypocone. Both ridges are also joined to a high cingulum that closes the mesosinus. A weak connection to the posterior wall of the paracone also exists. The anterior spur of the hypcone presents a short and low spur which points to a similarly developed one departing from the metalophule.

Lower cheek teeth: Moderately hypsodont molars (terraced sensu Hershkovitz, 1967) with the lingual cusps clearly higher than the buccal ones. The wear surface of the buccal cusps is flat, while in the lingual ones it is slightly concave. As wear progresses the whole wear surface becomes slightly concave, as already described in the case of the upper molars (see also fig. 4.4.). The M_3 is quite elongated, instead of reduced as the upper one. The occlusal pattern is very complex since numerous transverse ridges and extra connections between the main cusps exist. The main ridges are well-developed and very high. The mesial valleys are narrow and very reduced in the M_2 and the M_3. These valleys are closed by the two arms of the anterolophid, which merge the base of the protoconid and the metaconid. There is a relatively long and wide anterior metalophulid, as well as a posterior one. The posterior metalophulid does not reach the metaconid. This ridge is wide and very long, pointing obliquely backwards, although its buccal end is mesially directed and joins a posterior spur of the metaconid in most teeth. In the M_1 and M_2 the mesolophid, which is medium-sized and points forwards, usually merges the posterior metalophulid. Therefore, a small triangular depression is defined by both ridges. A well-defined mesoconid is present in most of the molars. The sinusid and the mesosinusid are wide. The sinusid is slightly retroverse and it is closed by a low cingulum departing from the posterior wall of the protoconid. There is always an anterior hypolophulid which is long, wide and transverse. There is also a posterior hypolophulid in the M_1 and the M_2 which joins the posterolophid enclosing a small and elongated depression. This tiny depression tends to disappear with moderate wear and the posterior hypolophulid fuses to the posterolophid (see for example IPS 23165, fig 4.5.5.). The posterolophid, which is long and high, closes a wide posterosinusid.

M_1 (fig. 4.5.5.): The anteroconid is situated very mesially. This is a rounded cusp which is unequally worn. The disto-buccal portion of the anteroconid is worn more rapidly than the lingual one. One molar (IPS 23299) presents a small cingulum situated at the base of the mesial wall of the anteroconid, somewhat displaced towards the lingual side.

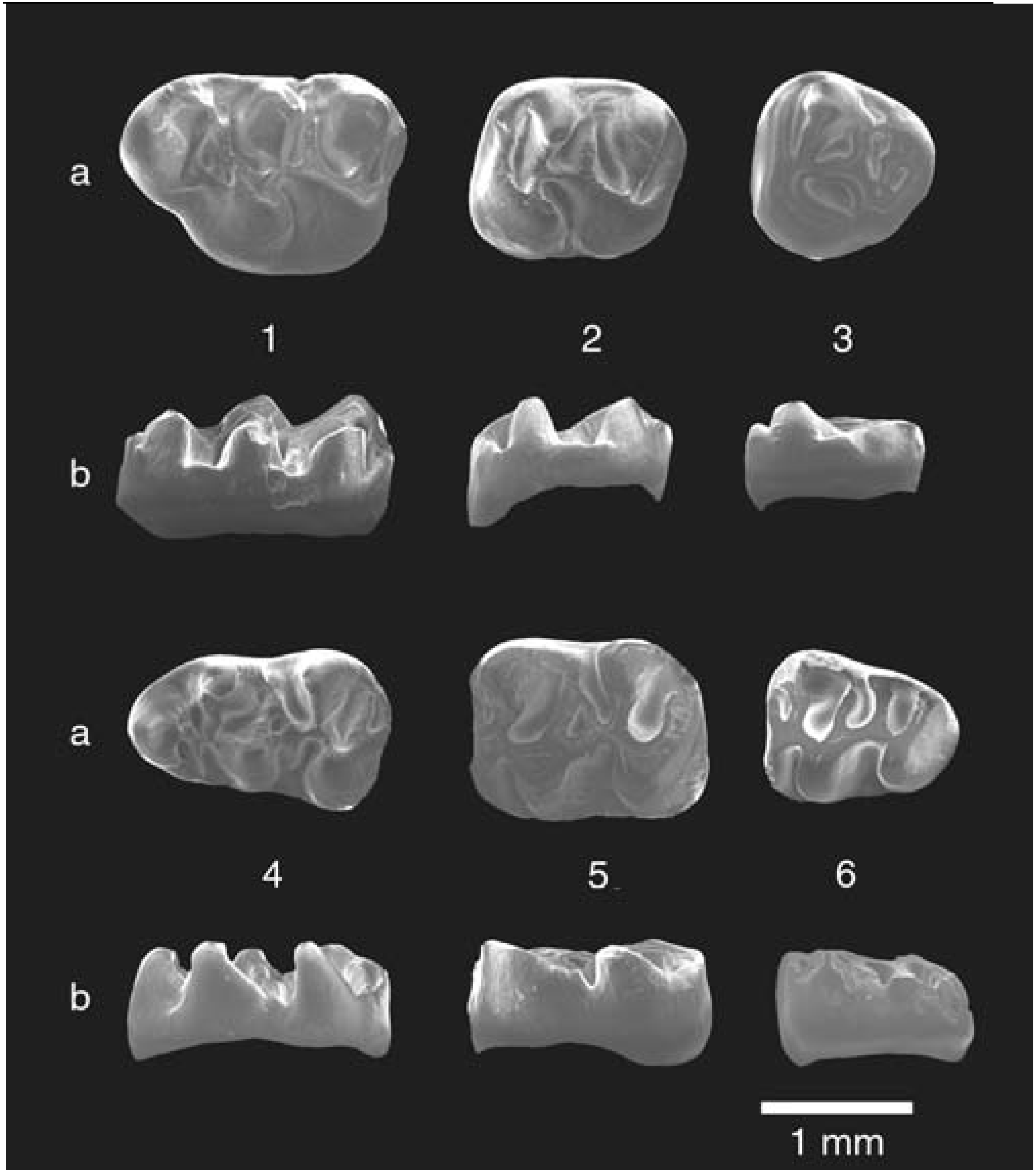

Figure 4.5. SEM micrographs of selected molars of *Eumyarion leemani* from BCV1 in oclusal view (a), labial view for upper molars (b) and lingual view for lower ones (b). The mesial side is always to the left in side view of the molars, accordingly all but the right ones are reversed in side view. 1. Left M^1, IPS 23124. 2. Left M^2, IPS 23130. 3. Left M^3, IPS 23143. 4. Left M_1, IPS 23152. 5. Right M_2 (reversed), IPS 23165. 6. Right M^3 (reversed), IPS 23171.

There is a labial anterolophid which joins the base of the protoconid and closes the protosinusid. In four teeth the anterolophid presents an inflation resembling a protostylid (see for example IPS 23152, fig. 4.5.4.). The metaconid is placed very mesially and it is joined to the anteroconid by a very high and short ridge, presumably the lingual anterolophid. This fact implies the reduction of the anterosinusid, which in most molars can be recognized as a slight concavity on the lingual wall. A few molars present a more developed anterosinusid which is closed by a low cingulum (see for example IPS 23155, IPS 23187 and IPS 23190). The protoconid presents an anterior spur which is fused to a posterior spur of the anteroconid, although at a very low high of the crown. Therefore, the ridge joining the protoconid to the anteroconid seems to be interrupted except in very worn specimens The posterior spur of the anteroconid is arched and points towards the buccal side, even merging the labial anterolophid in many molars. The anterior metalophulid is somewhat constricted at the point it joins the anterior spur of the protoconid (see for example IPS 23152, fig. 4.5.4.). In 25 % of the teeth this anterior metalophulid is interrupted before reaching this anterior spur (see for example IPS 23193). In two molars (IPS 23157, IPS 23158) the posterior spur of the anteroconid is straight and points towards the protoconid, instead of being directed towards the lingual side. This spur becomes increasingly lower distally and does not merge the protoconid. The buccal end of the posterior metalophulid curves towards the mesial side in 45 % of the molar and joins a long and low posterior spur of the metaconid (see for example IPS 23152, fig. 4.5.4.). The mesosinusid is partially closed by this posterior spur of the metaconid. In the remaining molars this ridge merges a low cingulum which closes the mesosinusid. In most of the molars (more than 85 %) there is a medium-sized mesolophid that points towards the posterior metalophulid, and it is fussed to this ridge in about 55 % (see for example IPS 23152, fig. 4.5.4.). Two teeth (IPS 23151, IPS 23156) present a long and progressively lower mesolophid which is fused to the base of the entoconid. Three molars present a small stylid obtruding the sinusid (IPS 23156, IPS 23189, IPS 23194). In three teeth (IPS 23153, IPS 23156, IPS 23158) the posterior hypolophulid is not fused to the posterolophid.

M_2 (fig. 4.5.5.): Both arms of the anterolophid depart from a cusp-like inflation situated at the medium width of the molar. The lingual arm of the anterolophid is shorter and higher than the labial one. This ridge joins the metaconid in all the molars but one (IPS 23237). A medium-sized, mesially-directed mesolophid merges the posterior metalophulid in 70 % of the molars. In the remaining teeth the mesolophid is interrupted just before reaching the posterior metalophulid. The buccal end of the posterior metalophulid merges the posterior spur of the metaconid as described in the case of the M_1. Therefore, the mesosinusid is partially closed by this posterior spur in most of the molars (see for example, IPS 23165, fig. 4.5.5.). However, in a 40 % of the teeth this spur continues beyond the point where it merges the posterior metalopulid until it reaches the base of the entoconid. In these cases the mesosinusid is completely closed by a well-developed ridge (see for example IPS 23301). In two teeth the posterior hypolophulid is interrupted before reaching the posterolophid (IPS 23166, IPS 23301).

M_3 (fig. 4.5.6.): The buccal cusps are better-developed than the lingual ones, which are integrated into the transverse ridges. The entoconid can hardly be distinguished in slightly worn molars. The protoconid is the largest cusp. The two arms of the anterolohid originate from a cusp-like inflation similar to that described in the case of the M_1. The lingual anterolophid is higher and shorter than the buccal one. The anterosinusid is very reduced and it is closed by the lingual anterolophid. The metalophulid consists in a wide anterior arm and a longer posterior arm which points obliquely backwards. This posterior metalophulid usually merges a posterior spur of the metaconid, partially closing the mesosinusid (see for example IPS 23171, fig. 4.5.6.). In 60 % of the molars this lingual ridge continues beyond the point it joins the posterior metalophulid and reaches the base of the entoconid. In two teeth (IPS 23170, IPS 23303) the posterior metalophulid is not fused to the posterior spur of the metaconid, and its lingual end points towards the hypolophulid, although without reaching it. Only two molars present a medium-sized mesolophid which merges the posterior metalophulid as described in the case of the M_1 and the M_2 (IPS 23304, IPS 23305). The mesolophid is missing in the remaining teeth. There is a transverse, wide and very long anterior hypolophulid. A vestigial posterior hypolophulid, which merges the posterolophid at its buccal end, is observed in one molar (IPS 23303).

Comments and comparisons:

In 1947 Schaub described a mandible fragment with an M_1 from Can Flaqué (= Can Flaquer) near Can Mata de la Garriga. Schaub (1947) ascribed the material to *Cricetodon helveticus*[24]. Unfortunately, this material was lost and further *Eumyarion* remains were not recovered in that area. Later on, Hartenberger (1965) described a new *Eumyarion* species from the Vallesian site of Can Llobateres 1: *Eumyarion leemani*. Aguilar *et al.* (1979) also identified this species in the Late Aragonian site of Castell de Barberà, although these authors pointed that the molars showed a lesser degree of hypsodonty and were more slender than those of the type locality. Agustí (1981a) described a few *Eumyarion* remains from Sant Quirze (including material already described by Schaub, 1947) that were ascribed to *E.* cf. *medium* (sic) on the basis of their weaker hypsodonty and larger size as compared to the material from Can Llobateres 1. This author also attributes the material from Can Flaquer to *E.* cf. *medium* (sic) on the basis of the description provided by Schaub (1947). Agustí (1981a) further suggested a phylogenetic relationship between *E. medius* and *E. leemani*. Both species would be the members of a lineage with a tendency to the reduction of tooth morphology coupled to the increase in hypsodonty. In later works the material from Castell de Barberà was attributed to *E. medius* (Agustí *et al.*, 1984; Agustí *et al.*, 1985).

The material recovered at BCV1 displays several plesiomorphic characters that have already been lost in other *Eumyarion* species such as *E. medius*. These include the presence of a posterior metalophulid joining the mesolophid or the presence of a posterior hypolophulid merging the posterolophid in the lower molars. The high of the crown in the BCV1, Sant Quirze and Castell de Barberà specimens is comparable to that of *Eumyarion medius* from Sansan (cf. our fig. 4.5.4.b to plate XIV, figure 7 of Baudelot, 1972). The hypsodonty is higher in many of the specimens of *Eumyarion leemani* from Can Llobateres 1 (cf. our figs. 4.4. and 4.5.1.b to figures 2a and 2b of Hartenberger, 1965). The molar morphology is not reduced in the material from Castell de Barberà and Sant Quirze. This, together with the presence of high transverse ridges joining the main cusps, indicates that it belongs to *Eumyarion leemani*. The morphology of the specimens from these Aragonian sites is very similar to that of the type locality, and only minor differences regarding the structure of the anterior protolophule are detected. There main differences concern the degree of hypsodonty as well as the size of the molars (see figs. 4.6. – 4.7.). The size of *E. leemani* from Can Llobateres and *E. medius* from Sansan shows a great degree of overlap, although the molars of *E. medius*, and particularly the M_1 tend to be more elongated. *E. leemani* from BCV1, Castell de Barberà and Sant Quirze show a wider range of size variation that extends beyond the upper limit of both *E. medius* and *E. leemani* from the type localities.

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[24] Fahlbusch (1964) considered the nomen *Cricetodon helveticus* Schaub, 1925 as a synonym of *Cricetodon medius* Lartet, 1851 and included both species into the North American genus *Cotimus* (= *Leidymys*). Engesser (1979) reviewed the European and American species attributed to *Leidymys* and proved that the European material belonged to a different genus, *Eumyarion*, which had been already defined by Thaler (1966).

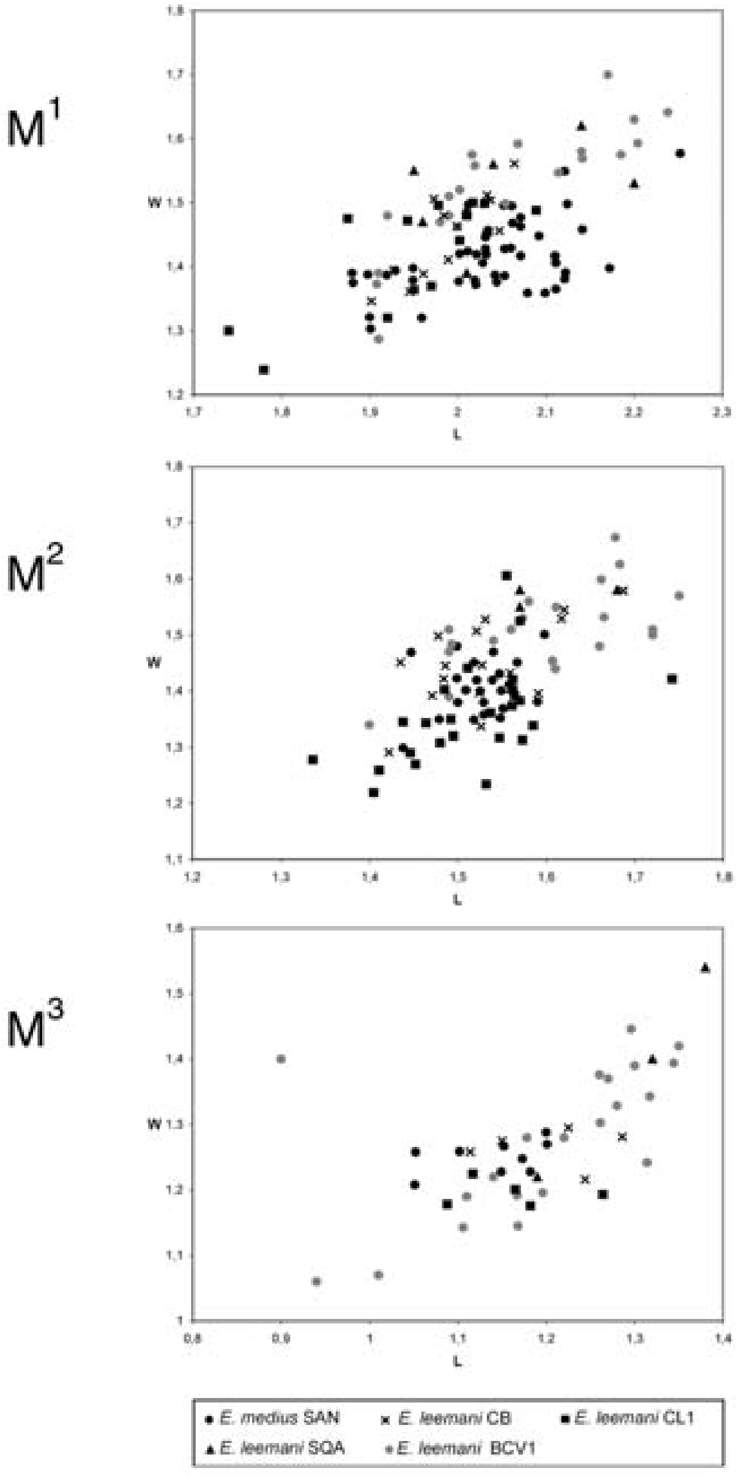

Figure 4.6. Scatter diagrams of the length and width values for the upper molars of different samples of *Eumyarion leemani* from the Vallès-Penedès sites and *Eumyarion medius* from the type locality. SAN = Sansan; CB = Castell de Barberà; CL1 = Can llobateres 1; SQA = Sant Quirze A; BCV1 = Barranc de Can Vila 1.

The hypothetical phylogenetic relationship between *E. medius* and *E. leemani* suggested by Agustí (1981a) is unlikely, since *E. medius* has already lost certain

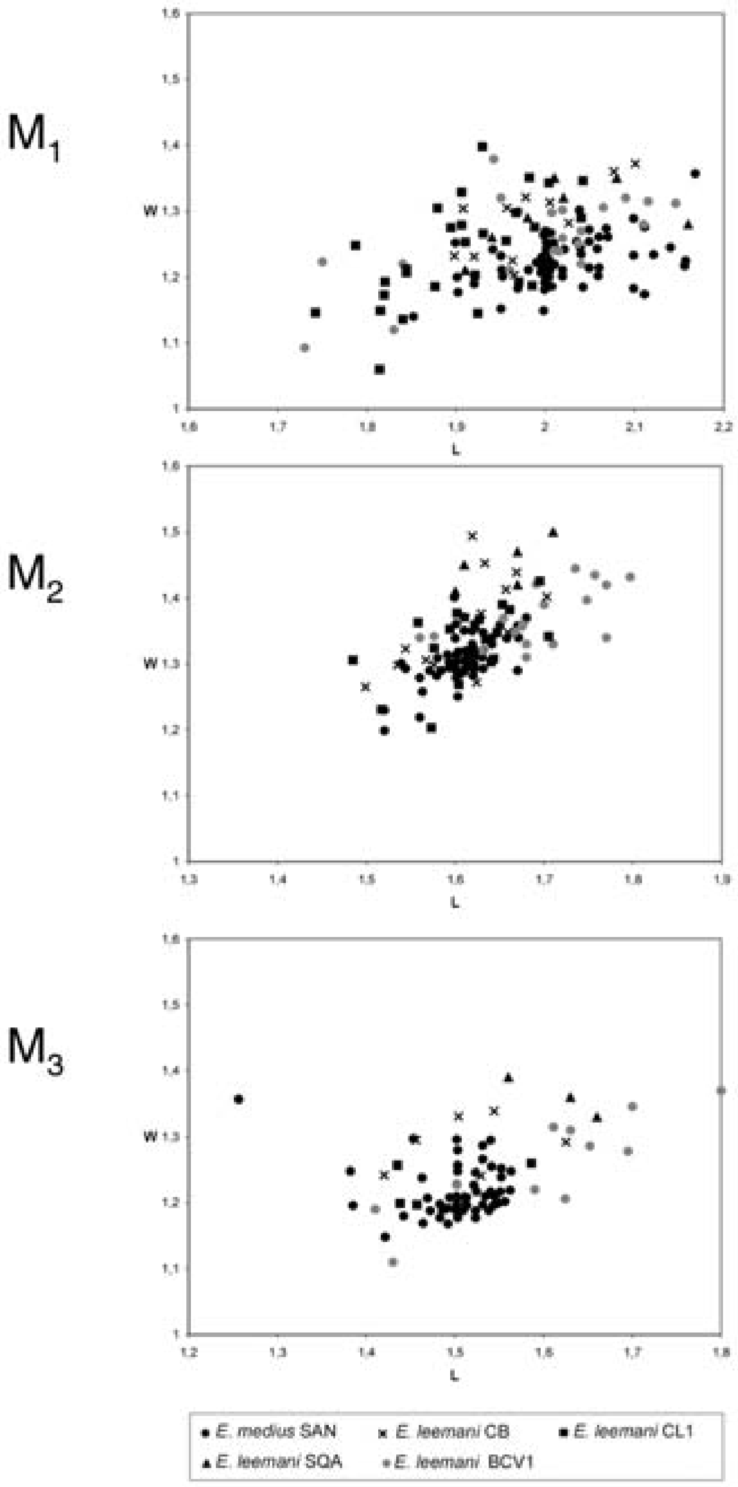

Figure 4.7. Scatter diagrams of the length and width values for the lower molars of different samples of *Eumyarion leemani* from the Vallès-Penedès sites and *Eumyarion medius* from the type locality. SAN = Sansan; CB = Castell de Barberà; CL1 = Can llobateres 1; SQA = Sant Quirze A; BCV1 = Barranc de Can Vila 1.

plesiomorphic traits of the genus *Eumyarion* that are still present in *E. leemani*. The development of moderately high-crowned molars in this species does not involve the reduction of tooth morphology, on the contrary the transverse ridges are retained and their height also increases. BCV1 represents the older site from which *E. leemani* is known.

Family **Cricetodontinae** Schaub, 1925

Subfamily **Megacricetodontinae** Mein & Freudenthal, 1971

Genus *Megacricetodon* Fahlbusch, 1964

Megacricetodon minor minor **(Lartet, 1851)**[25]

(fig. 4.8.6-11)

Synonymy: *Megacricetodon minor debruijni* in Moyà-Solà *et al.* (2004).

Material: 8 M^1 (IPS 23115, IPS 23282, IPS 23283, IPS 23326 – IPS 23330), 5 M^2 (IPS 23116, IPS 23284, IPS 23331 – IPS 23333), 5 M^3 (IPS 23117, IPS 23334 – IPS 23337), 12 M_1 (IPS 23105 – IPS 23111, IPS 23275 – IPS 23277, IPS 23322, IPS 23323), 5 M_2 (IPS 23112, IPS 23278 – IPS 23280, IPS 23324), 3 M_3 (IPS 23113, IPS 23114, IPS 23325). IPS 23326 and IPS 23331 arestill implanted to a left maxillary fragment.

Measurements:

	L					W				
	N	**min.**	**mean**	**max**	**s. d.**	**N**	**min.**	**mean**	**max**	**s. d.**
M^1	7	1.34	1.45	1.53	0.06	7	0.86	0.92	1.00	0.06
M^2	5	1.02	1.07	1.13	0.05	5	0.92	0.95	1.00	0.03
M^3	5	0.67	0.75	0.84	0.06	5	0.69	0.76	0.86	0.07
M_1	11	1.22	1.36	1.42	0.05	11	0.75	0.81	0.89	0.04
M_2	5	1.05	1.13	1.23	0.07	5	0.87	0.92	0.98	0.04

Lower cheek teeth		
	L	**W**
M_3	0.94	0.74
	0.84	0.69
	1.02	0.76

Description:

Maxillary fragment: Only a small portion of a left maxillary bone has been preserved. The M^1 and M^2 are still implanted into the alveoli. The distal margin of the foramen incisivum has also been preserved and it is placed more distally than the mesial root of the M^1.

Upper cheek teeth: The third molars are button-shaped and very reduced. Usually the mesial valleys are closed by the two arms of the anteroloph. The labial arm is higher than the buccal one. The mesial valleys are very reduced on M^2 and M^3. The protosinus has disappeared in all the M^3 and in one M^2 (IPS 23116). In the remaining M^2 there is a vestigial protosinus closed by a reduced lingual anteroloph. In M^1 and M^2 the mesoloph

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[25] We follow Agustí (1981a) who considers that the species *Megacricetodon minor*, *M. debruijni* and *M. primitivus* should be better regarded as different subspecies of *M. minor* since they only show minor differences regarding their size and the relative abundance of certain morphological features. Nevertheless, many authors (see for example Daams & Freudenthal, 1988b) consider them as different species.

may be medium-sized or, more frequently, long. When a long mesoloph is present it becomes increasingly low until it merges a well-developed cingulum that closes the mesosinus. In the molars that show a medium-sized mesoloph this buccal cingulum is lower. In the M^1 and the M^2 the sinus is straight and it is closed by a low cingulum departing from the hypocone. The posteroloph is robust and high. This ridge completely closes the posterosinus.

M^1 (fig. 4.8.6.): The prelobe is very developed and the morphology of the anterocone shows a high variability. The anterocone is slightly divided into two equal-sized cusps by a weak groove in three teeth (IPS 23115, IPS 23283 fig. 4.8.6., IPS 23330). This groove is better developed in two other molars, reaching the base of the crown (IPS 23327, IPS 23328). In another molar the anterocone is undivided and mesiobuccally elongated (IPS 23329). Finally, a last one shows a particular structure (IPS 23282) being well divided into two cusps, although the lingual one is much smaller and lower than the buccal one. These two cusps are joined through a high ridge situated mesially. Distally they join an isolated cuspule separately. In this particular teeth the anterosinus and the protosinus are open. In the molars that show a divided anterocone the anterolophule is forked and joins each cusp separately. The protolophule is double in three molars (IPS 23282, IPS 23327, IPS 23328), although the anterior arm is only well developed in IPS 23327. The remaining molars show only a posterior protolophule which is quite short (IPS 23283 fig. 4.8.6.). The mesoloph is long in one tooth (IPS 23330), while the remaining ones show a medium-sized mesoloph (such as IPS 23283 fig. 4.8.6.). The metalophule is short and joins the posteroloph behind the hypocone, implying a strong reduction of the posterosinus.

M^2 (fig. 4.8.7.): The protolophule is double and the posterior arm joins the longitudinal ridge near the mesoloph. The mesoloph is long and merges the ectoloph of the paracone, which is quite short and low. The metalophule is simple and straight in all the molars but one in which is somewhat mesially directed (IPS 23333).

M^3 (fig. 4.8.8.): Most of the recovered teeth are extremely worn, so many characters cannot be observed. The wear surface is slightly concave at the distal moiety of the molars. The distal cusps are very reduced and the metacone is undistinguishable from a high continuous ridge that runs through the labial and distal margin from the paracone to the hypocone. The labial anteroloph departs directly from the protocone and closes a narrow anterosinus. The protolophule is simple and straight. One molar (IPS 23337) presents an arched axioloph which merges the protolophule to the metalophule. A long, high and transverse mesoloph departs from the midpoint of this axioloph and joins a high cingulum that closes the mesosinus. The remaining molars also present a long mesoloph that merges this cingulum. The metalophule is transverse and short to medium-sized. The sinus is strongly reduced. This valley is transverse and open.

Lower cheek teeth: The labial anterolophid is longer than the lingual one and closes the protosinusid. In the M_2 and the M_3 the mesial valleys are very reduced. In these molars the metaconid joins the lingual anterolophid by the means of a very short

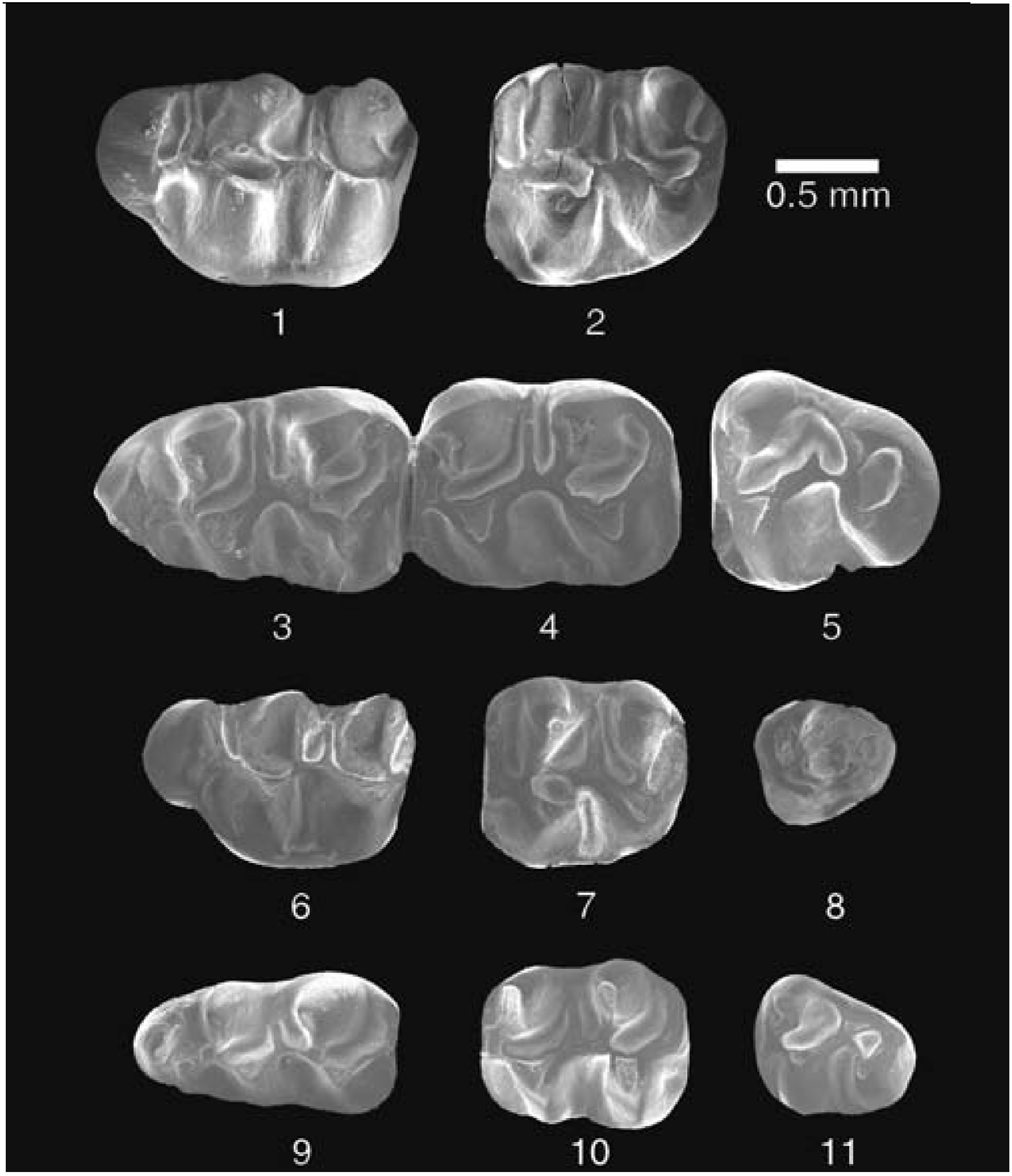

Figure 4.8. SEM micrographs of selected molars of *Democricetodon brevis brevis* and *Megacricetodon minor minor* from BCV1. *Democricetodon brevis brevis*. Figs. 1-5. 1. Right M^1 (reversed), IPS 23096. 2. Right M^2 (reversed), IPS 23273. 3. Left mandibular fragment with M_1 (IPS 23097) and M_2 (IPS 23100). 5. Left M_3, IPS 23103. *Megacricetodon minor minor*. Figs. 6-11. 6. Right M^1 (reversed), IPS 23283. 7. Right M^2 (reversed), IPS 23284. 8. Left M^3, IPS 23334. 9. Left M_1, IPS 23109. 10. Right M_2 (reversed), IPS 23279. 11. Left M_3, IPS 23114.

metalophulid, whereas the protoconid joins this anterolophid through a short anterolophulid. The hypolopulid is anterior and extremely short. The posterolophid, which is wide and high, merges the distal wall of the entoconid, so the posterosinusid is closed..

M_1 (fig. 4.8.9.): Very elongated molars molars, many of them subtriangular in shape. The anteroconid usually consists in a single and elliptical cusp (see for example IPS 23109 fig 4.8.9.). Two specimens present a weak groove that divides the anteroconid into two cusps. In one of these the lingual cusp is larger than the buccal one (IPS 23277), while in the other the opposite is true (IPS 23323). The anterosinusid is open in

three teeth (IPS 23275, IPS 23277, IPS 23323); closed by a metasylid in one (IPS 23275); and closed by the lingual anterolophid in the remaining eight molars (see for example IPS 23109 fig 4.8.9.). The metalophulid is short and anterior. In one tooth there is a double metalophulid, although defined by two arms that join the anterolophulid in front of the protoconid (IPS 23110). The mesolophid may be medium-sized (in five, see for example IPS 23109 fig 4.8.9.), short (in five more) or absent (in one molar). The sinusid is wide and slightly proverse. This valley is usually is closed by a low cingulum in all the molars but one, in which is obtruded by a prominent stylid (IPS 23275).

M_2 (fig. 4.8.10.): The labial anterolophid is always very long, while the development of the lingual one is highly variable. This ridge is long and closes the anterosinusid in one molar (IPS 23112); in two has a medium length (IPS 23279 fig. 4.8.10., IPS 23280); in another one is vestigial (IPS 23278); and in a last one there is neither lingual anterolophid nor anterosinusid (IPS 23324). In the remaining molars the anterosinusid is very narrow. The mesolophid is long to medium-sized in all teeth but one, in which it is vestigial (IPS 23112). This ridge never reaches the lingual margin. In all the molars except IPS 23278 the mesosinusid is closed by a low cingulum departing from the posterior wall of the metaconid. The sinusid is always straight being closed by a low cingulum in all molars but one, in which is open (IPS 23280). The cingulum that closes the sinusid may either depart from the base of the protoconid (IPS 23278, IPS 23279 fig 4.8.10.); from the base of the hypoconid (IPS 23112); or it may be completely isolated (IPS 23324). A prominent stylid is present near the base of the hypoconid in one molar (IPS 23279).

M_3 (fig. 4.8.11.): The distal cusps are more reduced than the mesial ones, and the entoconid cannot be distinguished from a high ridge that runs through the lingual and distal margin of the molar, from the metaconid to the hypoconid. A crescent-shaped protoconid occupies most of the molar surface. The lingual anterolophid is higher than the labial one, although it is shorter. The lingual anterolophid merges the metaconid, further closing a narrow anterosinusid. The mesolophid is absent. Nevertheless, the hypolophulid, which is situated quite mesially, is very wide, so it may correspond to the fusion of this ridge and the mesolophid. The sinusid points strongly backwards. In one molar this valley is closed by a low cingulum departing from the base of the protoconid (IPS 23114), while in the remaining ones the sinusid is open.

Comments and comparisons:

This subspecies has only been reported from another site of the Vallès-Penedès Basin: Sant Quirze (Trinxera) (Agustí, 1981a). *M. minor debruijni* is commonly present in the Late Aragonian (Castell de Barberà, Can Missert) and Early Vallesian sites of the same basin (Can Ponsic, Can Llobateres 1).

Subfamily **Copemyinae** Jacobs & Lindsay, 1964

Genus *Democricetodon* Fahlbusch, 1964

A few words on the taxonomic status of the genera *Democricetodon*, *Fahlbuschia*, *Pseudofahlbuschia* and *Renzimys*:

Recently the taxonomy of the genus *Democricetodon* has been profoundly shaked after the work by Van der Meulen *et al.* (2003). These authors have regarded the genera *Fahlbuschia*, *Pseudofahlbushia* and *Renzimys* as junior synonyms of *Democricetodon*, further synonymizing several species included within these genera (for example *D. darocensis* to *D. larteti* and *R. bilobatus* to *D. crusafonti*). Other authors had previously questioned the validity of the genera *Pseudofahlbuschia* and *Renzimys*, pointing out their great similarity to *Fahlbuschia* (see Kälin, 1999). However, the generic status of *Fahlbuschia* did not seem to offer doubts. The diagnosis of this genus (Mein & Freudenthal, 1971b) emphasizes the relative length of the foramen incisivum. According to Mein & Freudenthal (1971b) this character allows the distinction between Cricetodontinae and Cricetinae (sensu Mein & Freudenthal, 1971b). In *Fahlbuschia* the distal end of the foramen incisivum is situated behind the level of the anterior margin of the M^1, thus indicating that this genus belongs to the Cricetodontinae. In *Democricetodon*, the foramen ends mesially to the anterior margin of the M^1, so this genus may be regarded as a Cricetinae according to Mein & Freudenthal, 1971b. Van der Meulen *et al.* (2003) adequately point that the intraspecific variation of this character is not well known[26]. Concerning the diagnostic characters of molar morphology, these authors emphasize that these are highly variable and that they can not be recognized in earlier *Fahlbuschia* species. Finally, Van der Meulen *et al.*(2003) eluded any discussion about the diagnostic characters of the lower incisors with the following statement: "This difference has not been dealt with by Freudenthal & Daams (1988), and we have not studied it either (op. cit.: 395). Van der Meulen *et al.* (2003) synonymized *Fahlbuschia* to *Democricetodon* and further regarded the species formerly included within the genera *Pseudofahlbuschia* and *Renzimys* as "advanced" species of this genus. As a direct consequence these genera are also synonymized to *Democricetodon*. Quite surprisingly, these authors did not give an emended diagnosis of the genus *Democricetodon*, thus retaining the original diagnosis by Fahlbusch (1964) because "it allows the inclusion of *Fahlbuschia*, *Pseudofahlbuschia* and *Renzimys*" (Van der Meulen *et al.*, 2003: 429). As Freudenthal (2005) has noted, apparently the synonymy between these genera was an expected result of the work. Van der Meulen *et al.* (2003) also included an interpretation of the phylogenetic relations between the different *Democricetodon* species of the Calatayud-Daroca Basin. According to the cited authors only two different lineages would be present instead of the multiple phylogenetic lines proposed by Freudenthal & Daams (1988).

As it should have been expected this paper has incited a nearly instantaneous contrary response by certain palaeontologists. Freudenthal (2005)[27] has rejected almost all the conclusions of Van der Meulen *et al.* (2003). This author argues that the two lineages recognized by Van der Meulen and co-workers are based in an erroneous sequence of sites. Therefore, they are found to be incorrect. Freudenthal (2005) also stresses the diagnostic value of the M^3 morphology, as had already been pointed out by Freudenthal & Daams (1988). Nevertheless, the morphology of this tooth shows an

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[26] In fact, Engesser (1979) has questioned the diagnostic validity of this trait after observing that it is highly variable in recent *Peromyscus*.

[27] In a paper incorrectly subtitled "A reply to Van der Meulen *et al.* (2004)".

important intraspecific variability, which in our opinion precludes its use as a diagnostic character. Finally, Freudenthal (2005) rejects the synonymy of *Fahlbuschia* to *Democricetodon* (as well as the rest of synonymies proposed by Van der Meulen and co-workers), arguing that the diagnosis proposed by Fahlbusch (1964) would also include the North American genus *Copemys* (in fact Fahlbusch, 1967, had considered *Democricetodon* a subgenus of *Copemys*). Engesser (1979) has pointed that the molar morphology of certain species of *Democricetodon* and *Copemys* is so close that if both genera appeared together in a site their distinction would be very problematic. This author is unable to find any clear differential trait between the Eurasian and the North American genus. Nevertheless, he argues that synonymizing both genera would imply a very complicated biogeographic scenario of repeated migrations from Eurasia to North America and vice versa. Engesser (1979) concludes that more details on the cranial anatomy should be known in order to propose a differential diagnosis. Maybe in the case of *Democricetodon* and *Fahlbuschia* we face a similar problem. The molar morphology apparently is insufficient to discriminate between both genera, although details of the mandible and skull may confirm the validity of the genus *Fahlbuschia*. Since such study has not been performed yet we follow Van der Meulen *et al.* (2003) in considering that this genus is a junior synonym of *Democricetodon*.

Democricetodon brevis brevis **(Schaub, 1925)**[28]

(fig. 4.8.1-5)

Synonymy: *Democricetodon gaillardi* in Moyà-Solà *et al.* (2004).

Material: 2 M^1 (IPS 23095, IPS 23096), 2 M^2 (IPS 23273, IPS 23320) besides one fragment of M^2 (IPS 23321), 3 M_1 (IPS 23097 - IPS 23099), 3 M_2 (IPS 23100 – IPS 23102), 4 M_3 (IPS 23103, IPS 23104, IPS 23274, IPS 23281). IPS 23097 and IPS 23100 are still implanted to a very damaged left mandibular fragment.

Measurements:

Lower cheek teeth			**Upper cheek teeth**		
	L	**W**		**L**	**W**
M_1	1.66	1.26	**M^1**	1.52	1.17
	1.50	1.06		1.77	1.12
	1.62	1.15			
M_2	1.40	1.26	**M^2**	1.32	1.23
	1.47	1.14		1.42	1.27
	1.39	1.24		-	-
M_3	1.22	1.15			
	1.21	1.05			
	1.46	1.07			
	1.13	0.99			

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[28] Kälin (1999) considers the two subspecies of *D. brevis* as different species. Given the fact that only minor differences are observed between both taxa, we prefer to consider them as different subspecies as originally proposed by Agustí (1981b).

Description:

Upper cheek teeth: The mesial valleys are closed by the arms of the anteroloph. The labial anteroloph is higher than the buccal one. The protolophule is double, and the two arms show a similar development. The sinus is straight. The mesoloph is always very long becoming progressively lower until it reaches the margin of the mesosinus. This latter valley is usually closed by two low cingula departing from the paracone and the metacone respectively, although in some cases it may be closed by a single cingulum departing from the base of the metacone. These cingular formations merge the mesoloph or the mesostyl. The posteroloph closes a quite narrow posterosinus.

M^1 (fig. 4.8.1.): The molars are almond-shaped. The anterocone is simple, although in IPS 23096, which is only slightly wear, a weak groove is observed at the mesial wall of the anterocone (fig. 4.8.1.). The anterolophule, which is high and long, presents a very long labial spur which reaches the buccal margin in one molar (IPS 23096 fig. 4.8.1., this trait can not be observed in the other molar). This labial spur merges the labial anteroloph. A small parastyl is developed at the point where the two ridges meet. The sinus is open. The metalophule is posterior.

M^2 (fig. 4.8.2.): The mesial wall shows a concave contact facet. The mesial valleys are narrow. The anterolophule is wide and short. In one molar the posterior arm of the protolophule is very reduced (IPS 23320), while in the remaining ones it is as developed as the anterior one (see for example IPS 23273 fig. 4.8.2.). The sinus is closed by two low cingula, departing from the protocone and the hypocone respectively, in one tooth (IPS 23320). In the other molar in which this trait can be observed it is closed by only one cingulum departing from the anterior wall of the hypocone (IPS 23273 fig. 4.8.2.). The mesoloph joins the cingular ridges that close the mesosinus, and a prominent mesostyl is developed at the point of their union. Two molars present a double metalophule (IPS 23320, IPS 23321) with the posterior arm more developed than the anterior one in IPS 232321. In the remaining molar there is a vestigial anterior arm which does not reach the longitudinal ridge and a posterior one which merges the posteroloph (IPS 23273 fig. 4.8.2.).

Lower cheek teeth: The mesial valleys are reduced, particularly the anterosinusid which is very narrow in M_2 and M_3. The protosinusid points obliquely forward. These mesial valleys are closed by the two arms of the anterolophid. The lingual arm is higher than the labial one. The sinusid is transverse and it is frequently closed by one or two low cingula. The hypolophulid is defined by a very short and wide anterior arm. The mesolophid is well developed. The posterolophid is long and becomes increasingly low until it closes the protosinusid.

M_1 (fig. 4.8.3.): Elongated molars with the anteroconid situated very mesially. The anteroconid is simple and rounded. The anterolophulid is short. The metalophulid, which is also short, joins the anterolophulid. The sinusid is proverse in all molars but one, in which it is transverse (IPS 23098). This valley is closed by a low cingulum departing from the base of the protoconid in two molars (IPS 23097 fig. 4.8.3., IPS 23098), while in the third one it is closed by a similar cingulum departing from the hypoconid (IPS 23099). The mesolophid is very long and reaches the lingual margin, where it may merge a low cingulum that departs from the base of the metaconid.

M_2 (fig. 4.8.4.): The sinusid is very proverse in all the teeth but one, in which it is transverse (IPS 23101). This valley is closed by a low cingulum departing from the base of the protoconid in two molars (IPS 23100 fig. 4.8.4., IPS 23101), while in the third

one it is open (IPS 23102). The mesolophid is very long in one molar, reaching the lingual margin, where it ends in a prominent mesostylid (IPS 23100 fig. 4.8.4.). In the remaining teeth the mesolophid is somewhat shorter and becomes increasingly low as it approaches to the lingual margin of the tooth. In these situations the mesosinusid is closed by a low cingulum departing from the base of the metaconid which also presents a small mesostylid near the base of this cusp.

M_3 (fig. 4.8.5.): The entoconid can be hardly distinguished. The protoconid is crescent shaped and occupies an important part of the molar surface. The sinusid may either be transverse or point slightly backwards. This valley is always closed by a low cingulum departing from the distal wall of the protoconid. A very short mesolophid is present in one molar (IPS 23103 fig. 4.8.5.), while the remaining ones lack this ridge. The mesosinusid is closed by a high ridge which joins the metaconid to the entoconid. The hypolophulid is anterior and quite wide and long. The longitudinal ridge is interrupted just in front of the hypolophulid in one case (IPS 23104).

Comments and comparisons:

Agustí (1981b) defined a new subspecies of *Democricetodon brevis* from Castell de Barberà (MN 7+8): *D. brevis nemoralis*. This subspecies is characterized by its well-developed mesolophs/ids, the predominantly posterior protolophule on M^1, and the subdivision of the anteroconid on the M_1 in some individuals (Agustí, 1981a, 1981b). Nevertheless, these traits are not observed in the material from BCV1, which shows double protolophule on M^1 and M^2 besides an undivided anteroconid on M_1. Therefore, we ascribe the material to *D. brevis brevis*, which is here reported for the first time from the Vallès-Penedès Basin. *D. brevis nemoralis*, which has only been reported from this basin, may be in all probability a vicariant offshoot of earlier *D. brevis brevis* populations. This species is unknown from the inner Spanish basins, and further indicates affinities of the Vallès-Penedès Basin with northern areas.

***Democricetodon larteti* (Schaub, 1925)**

(fig. 4.9.)

Material: 18 M^1 (IPS 23070 – IPS 23076, IPS 23257 – IPS 23264, IPS 23306 – IPS 23308), 10 M^2 (IPS 23077 – IPS 23082, IPS 23265 – IPS 23267, IPS 23309), 8 M^3 (IPS 23083 – IPS 23085, IPS 23268 – IPS 23272, IPS 23319), 12 M_1 (IPS 23086 – IPS 23089, IPS 23239 – IPS 23244, IPS 23310, IPS23311), 14 M_2 (IPS 23090, IPS 23091, IPS 23245 – IPS 23251, IPS 23312 – IPS 23315), 10 M_3 (IPS 23092 – IPS 23094, IPS 23252 – IPS 23256, IPS 23316 – IPS 23318).

Measurements:

	L					W				
	N	**min.**	**mean**	**max**	**s. d.**	**N**	**min.**	**mean**	**max**	**s. d.**
$\mathbf{M^1}$	17	2.29	2.49	2.64	0.10	17	1.42	1.63	1.84	0.09
$\mathbf{M^2}$	9	1.88	1.95	2.04	0.06	9	1.54	1.60	1.66	0.04
$\mathbf{M^3}$	8	1.21	1.34	1.43	0.08	8	1.29	1.37	1.49	0.08
$\mathbf{M_1}$	7	2.10	2.24	2.31	0.07	11	1.26	1.37	1.45	0.06
$\mathbf{M_2}$	13	1.81	1.89	1.99	0.06	13	1.38	1.50	1.62	0.08
$\mathbf{M_3}$	10	1.49	1.60	1.66	0.05	10	1.24	1.37	1.46	0.06

Description:

Upper cheek teeth: The M^3 is button shaped and quite reduced. The main valleys on the M^1 and M^2 are quite wide, being usually transverse and closed, except the mesosinus which is more usually open. The mesial valleys are closed by the two arms of the anteroloph, which become progressively lower distally. The sinus may be closed either by a low cingulum departing from the base of the protocone or by two low ridges which originate from the base of the protocone and the hypocone, respectively. The mesoloph, when present, is short. The protolophule and the metalophule (when it exists) on the M^1 and the M^2 are posterior and very short. The posterosinus tends to be very reduced and it may be absent in many M^1 (see for example IPS 23308 fig. 4.9.3.) and M^2 (see for example IPS 23267 fig. 4.9.5.). In the cases that present posterosinus, it is completely closed by the posteroloph, which is quite low on its buccal end.

M^1 (figs. 4.9.1 and 4.9.3.): The molars are almond shaped. The anterocone is divided into two lobes by a weak groove that may also affect the mesial wall of this cusp. Usually the lingual lobe of the anterocone is slightly larger than the buccal one. This subdivision quickly disappears with moderate wear resulting in a broad and bean-shaped anterocone. The subdivision of the anterocone is always linked to a forked anterolophule, which presents two branches that reach the two lobes separately. This trait persists for a longer time, although it also disappears in heavily worn molars, resulting in an anterolophule presenting a very wide anterior half. A forked anterolophule is observed in 40 % of the teeth, so the presence of a subdivided anterocone is inferred by the same number of molars. Half of the molars present a stylform cingulum at the base of the mesial wall of the anterocone, somewhat lingually. There is a vestigial ectoloph of the paracone in two molars (IPS 23308 fig. 4.9.3., IPS 23261). The mesosinus is usually open, although it may also be closed; either by a low cingulum departing from the paracone which presents a mesostyle at its end; or by a two low cingula departing from the paracone and the metacone, respectively. A short mesoloph is present in 47 % of the teeth (see for example IPS 23260 fig. 4.9.1.), while the remaining molars lack this ridge (see for example IPS 23308 fig 4.9.3.). 23 % of the molars present a short posterior metalophule which joins the posteroloph at a very buccal position, implying the existence of a very reduced posterosinus which in its turn is closed by the posteroloph (see for example IPS 23260 fig. 4.9.1.). In the remaining molars the metalophule has disappeared and a robust posteroloph joins the metacone and the hypocone, implying the total absence of posterosinus (see for example IPS 23308 fig 4.9.3.).

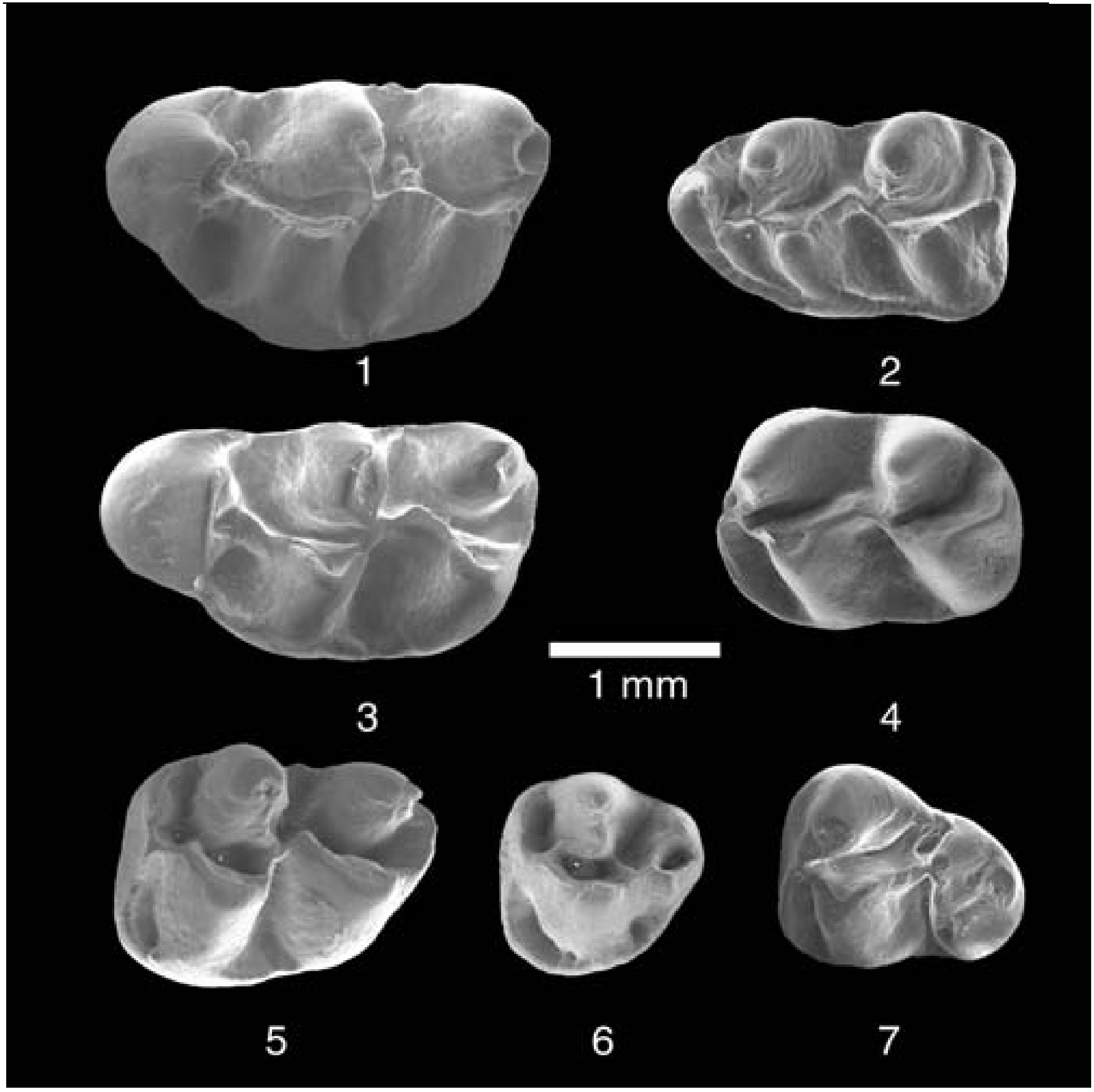


Figure 4.9. SEM micrographs of selected molars of *Democricetodon larteti* from BCV1. 1. Right M^1 (reversed), IPS 23260. 2. Left M_1, IPS 23240. 3. Right M^1 (reversed), IPS 23308. 4. Right M_2 (reversed), IPS 23250. 5. Right M^2 (reversed), IPS 23267. 6. Left M^3, IPS 23083. 7. Left M_3, IPS 23252.

M^2 (fig. 4.9.5.): The two arms of the anteroloph, which are very developed, depart from a cusp-like point. The mesial valleys are closed in all but two molars which present an open anterosinus (IPS 23079, IPS 23082). In 78 % of the molars the protolophule is double with a more developed posterior arm (see for example IPS 23267 fig. 4.9.5.). One molar shows a bizarre morphology of the protolophule (IPS 23079): an anterior protolophule and two posterior ones, with the more distal protolophule directly merging the posterior wall of the paracone. More than half of the molars present a short mesoloph (56 %; see for example IPS 23267 fig. 4.9.5.) while in the remaining ones this ridge does not exist although the longitudinal ridge appears somewhat inflated coinciding with its position. The mesoloph, when present, is situated quite distally and points the metacone, even reaching this cusp in two cases (IPS 23077, IPS 23080). In IPS 23080 the anterior arm of the metalopule points to the mesoloph but it does not reach this ridge. The mesosinus is usually open, although it may appear closed by a low cingulum (in two teeth: IPS 23077, IPS 23080) or by a mesostyl (in three molars: IPS 23078, IPS 23266, IPS 23267 fig. 4.9.5.)). The sinus points slightly backwards. This valley is usually closed by one or two cingula, except in one molar which presents a prominent entostyl (IPS 23080). A short posterior metalophule and a very reduced

posterosinus is present in 33 % of the molars, while the remaining ones lack the metalophule and the posterosinus.

M^3 (fig. 4.9.6.): The distal cusps of the molars are very reduced. The paracone and the protocone face each other. The mesial valleys are closed by the two arms of the anteroloph. The buccal arm is higher than the lingual one. In two molars (IPS 23083 fig. 4.9.6., IPS 23085) the lingual arm merges a low cingulum at the base of the protocone which closes the sinus and joins the base of the hypocone. The protolophule is highly variable, although commonly it is double, with the posterior arm more reduced than the anterior one (see for example IPS 23083 fig. 4.9.6.). In three teeth the posterior protolophule is wide and very developed and points backwards, thus defining and axioloph (IPS 23271). This axioloph joins the metalophule. In one molar the longitudinal ridge is interrupted just after the protocone (IPS 23270). The teeth lack the mesoloph. The sinus may point forwards or backwards. The mesosinus is open. The metalophule is wide and oblique, merging the longitudinal ridge or the axioloph. The metacone cannot be distinguished from the metalophule. In one tooth the metalophule is not continuous and is thinner than in the remaining ones (IPS 23319). The posteroloph, short and robust, encloses a small circular posterosinus.

Lower cheek teeth: The mesial valleys are narrow, particularly in the case of the anterosinusid which has even disappeared in many M_2 and M_3. The protosinusid is always closed by the labial arm of the anterolophid, which joins the base of the protoconid. The lingual anterolophid is not so well developed, and in some M_2 and M_3 which lack the anterosinusid this ridge is also missing. In these situations the labial arm of the anterolophid directly departs from the metaconid. The anterolophulid is very short in the case of M_2 and M_3. The metalophulid and the hypolophulid are defined by a single anterior arm which is very short. The entoconid joins the longitudinal ridge quite mesially. The sinusid and the mesosinusid are wide. Usually the M_1 and M_2 do not show mesolophid. The sinusid, that is usually transverse, is often closed by one or two low cingula. The posterolophid is long and becomes increasingly lower towards its lingual end. This ridge closes a narrow posterosinusid.

M_1 (fig. 4.9.2.): The anteroconid is usually rounded (see for example IPS 23240 fig 4.9.2.), but it may also be triangular. Half of the molars present a low lingual anterolophid which closes the anterosinusid (see for example IPS 23240 fig 4.9.2.). In one case there is a small metastylid obtruding this valley (IPS 23242). The anterolophulid is short and low. There is never a mesolophid. The sinusid is open in all molars but two. In IPS 23240 (fig 4.9.2.) and IPS 23241 this valley is closed by a cingulum departing from the base of the protoconid.

M_2 (fig. 4.9.4.): The molars lack the anterosinusid, but a vestigal lingual anterolophid merged to the anterior wall of the metaconid can be distinguished in 4 out of 13 molars (IPS 23245, IPS 23246, IPS 23249, IPS 23250 fig. 4.9.4.). Only two molars present a vestigial mesolophid which may point towards the entoconid (IPS 23090, IPS 23250 fig. 4.9.4.), while this ridge is completely lacking in the others. In most molars the mesosinusid is open, but in two teeth this valley is closed by a very low cingulum which joins the base of the metaconid to the entoconid (IPS 23246, IPS 23249). The sinusid is usually closed by a low cingulum departing from the protoconid.

M_3 (fig. 4.9.7.): The distal cusps, and particularly the entoconid, are reduced. Most of the teeth lack the anterosinusid and the lingual anterolophid. A vestigial lingual anterolophid similar to that described in the case of the M_2 is present in two molars (IPS 23316, IPS 23318). Three out of ten molars present a long, although very low,

mesolophid which reaches the lingual margin, ending in a prominent mesostylid. The mesosinusid is frequently closed by a high ridge which merges the entoconid to the distal wall of the metaconid. The sinusid may be partially or totally closed by a low cingulum departing from the posterior wall of the protoconid. This valley is open in two specimens (IPS 23255, IPS 23316).

Comments and comparisons:

Schaub (1944, 1947) identified two "forms" very similar to *Cricetodon larteti* from La Grive in the Vallès-Penedès sites. One of these forms, recovered at Sant Quirze (Trinxera), was clearly distinguished from the French species by its larger size, the absence of mesolophid and the less reduced third molars. Schaub (1944, 1947) did not create any specific name for this "form". This author further assigned a mandible with an M_2 from the Lower Hostalets de Pierola to this "form", while another mandible with M_2-M_3, also recovered at the Lower Hostalets de Pierola, was assigned to *Cricetodon larteti*. Agustí (1978a) erected a new species on the basis of the material from Sant Quirze: *Fahlbuschia crusafonti*. This author further assigned all the material from Hostalets de Pierola (recovered at the lower and upper levels) to this species. Therefore, the presence of *Democricetodon larteti* in the Vallès-Penedès Basin is here reported for the first time.

Van der Meulen *et al.* (2003) proposed new diagnosis and differential diagnosis for the species of the genus *Democricetodon* included in their review. According to these authors *D. crusafonti* differs from *D. larteti* by its larger size. The diagnostic value of the absolute size of the molars may be evaluated using two different approaches. The first one is a graphical approach based on scatter plots (figs. 4.10. – 4.11.). In the catter plots of figures 4.10 – 4.11. we have also included *D. koenigswaldi*, which according to Van der Meulen *et al.* (2003) is part of the *D. franconicus – D. crusafonti* lineage and the direct ancestor of *D. larteti*. There is little overlap between the populations of the three species, therefore size appears as a valuable diagnostic character. However, continuous data are only available for a few populations of the Calatayud-Daroca area, so it may be argued that there would be some (or a great) overlap if all the populations were plotted. Our second approach may partly solve this problem. This involves the use of Principal Components Analysis (PCA) on the mean length and width for all upper and lower molars of several *Democricetodon* populations belonging to the three different species (*D. koenigswaldi*, *D. larteti* and *D. crusafonti*). PCA is preferred instead of Discriminant Analysis for data exploration because no assumptions on the existence of different groups are made prior carrying the calculations. The mean values for the molars were compiled from the literature (Agustí, 1978a; Freudenthal & Mein, 1989; Van der Meulen *et al.*, 2003) (see appendix 4.1. for the sites included, their datings and the mean length and width values for all the populations). The scores for the different populations on the two principal components are shown in figure 4.12a. The first principal component (PC1) explains about 94 % of variance, while the second principal component (PC2) accounts for less than 3 %. The fact that PC1 captures most of the variance suggests that this component–represents the overall size of the

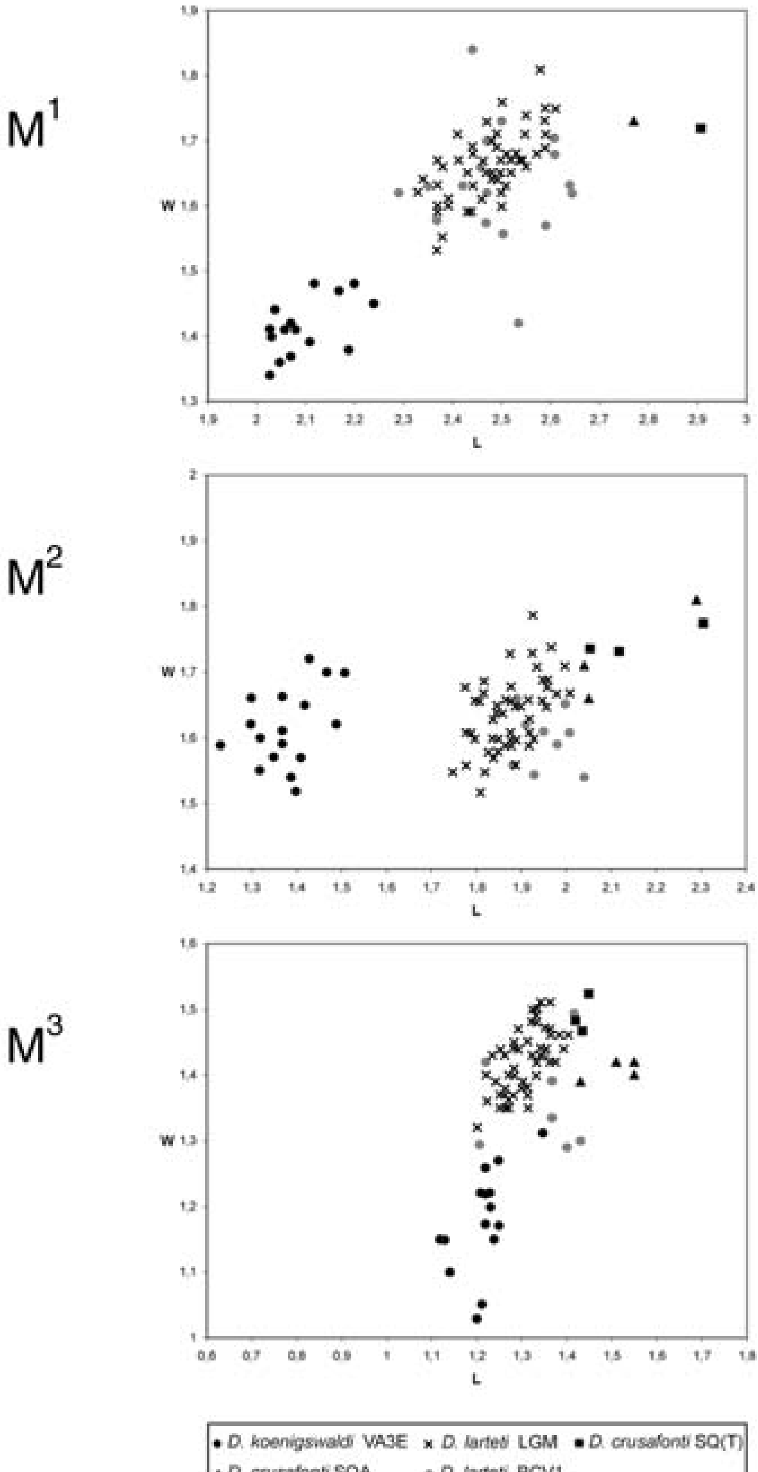


Figure 4.10. Scatter diagrams of the length and width values for the upper molars of different samples of medium-sized *Democricetodon species* (*D. koenigswaldi*, *D. larteti* and *D. crusafonti*). SQ (T) = Sant Quirze (Trinxera); SQA = Sant Quirze A; LGLM = La Grive M; BCV1 = Barranc de Can Vila 1; VA3E = Valalto 3E.

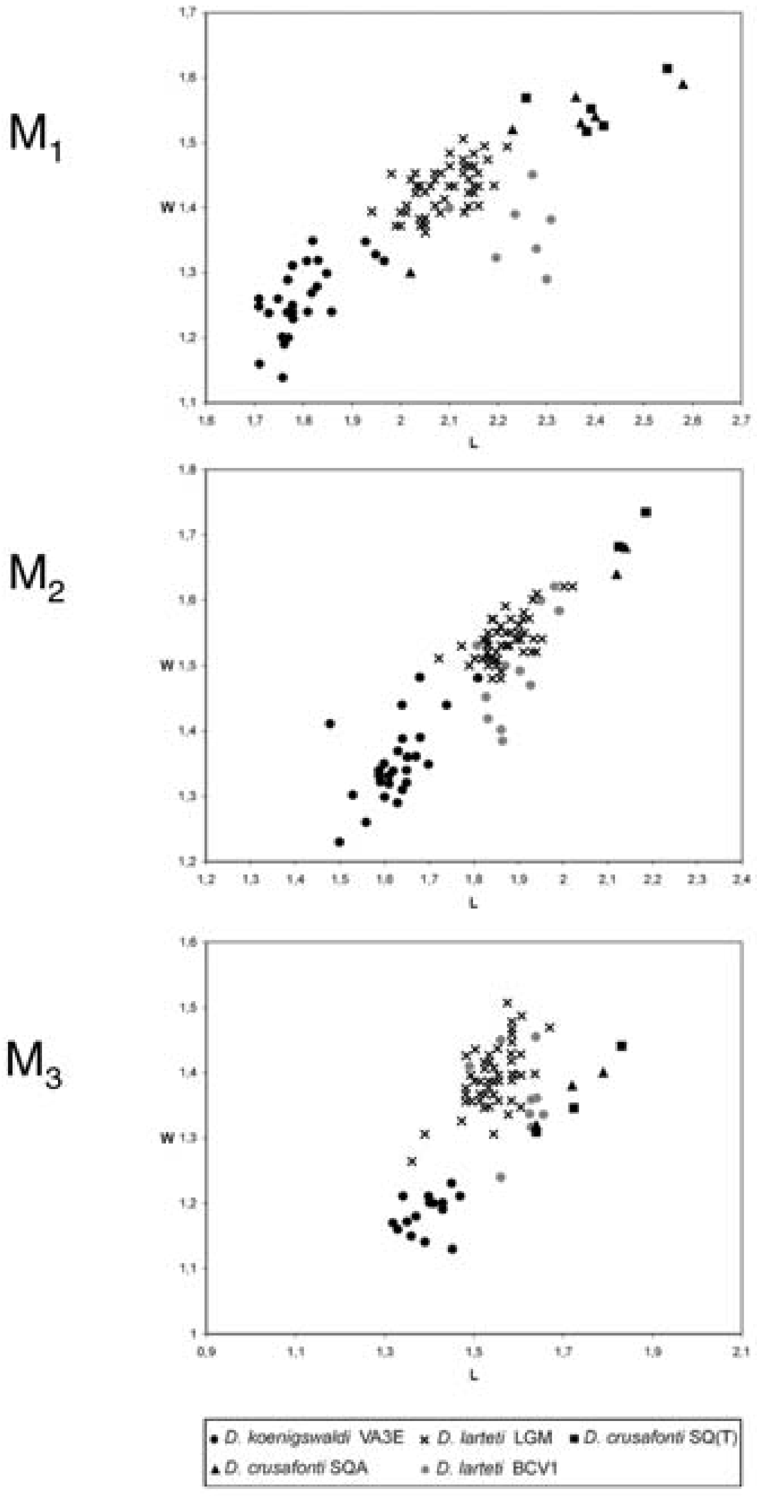


Figure 4.11. Scatter diagrams of the length and width values for the lower molars of different samples of medium-sized *Democricetodon species* (*D. koenigswaldi*, *D. larteti* and *D. crusafonti*). SQ (T) = Sant Quirze (Trinxera); SQA = Sant Quirze A; LGLM = La Grive M; BCV1 = Barranc de Can Vila 1; VA3E = Valalto 3E.

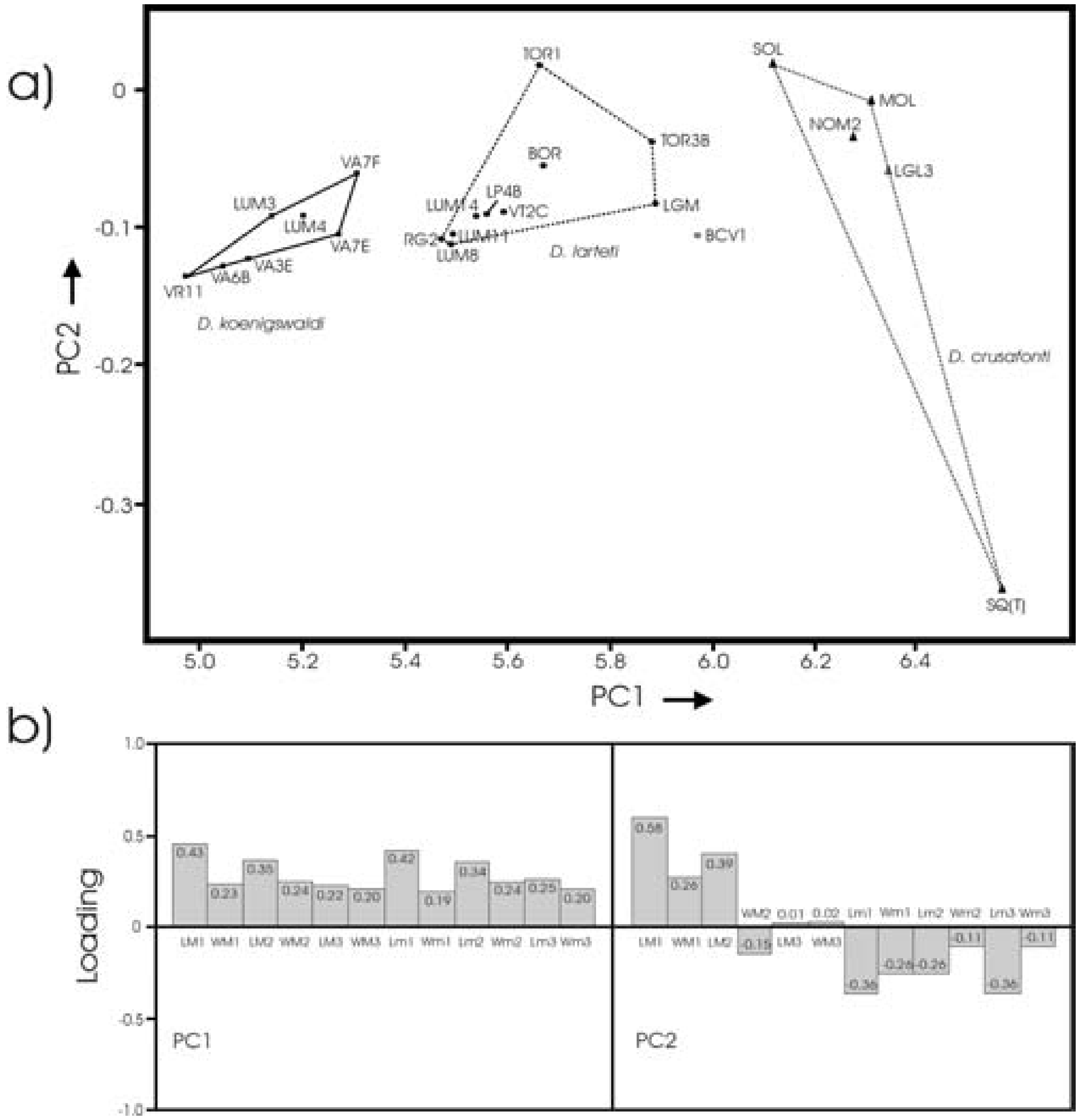
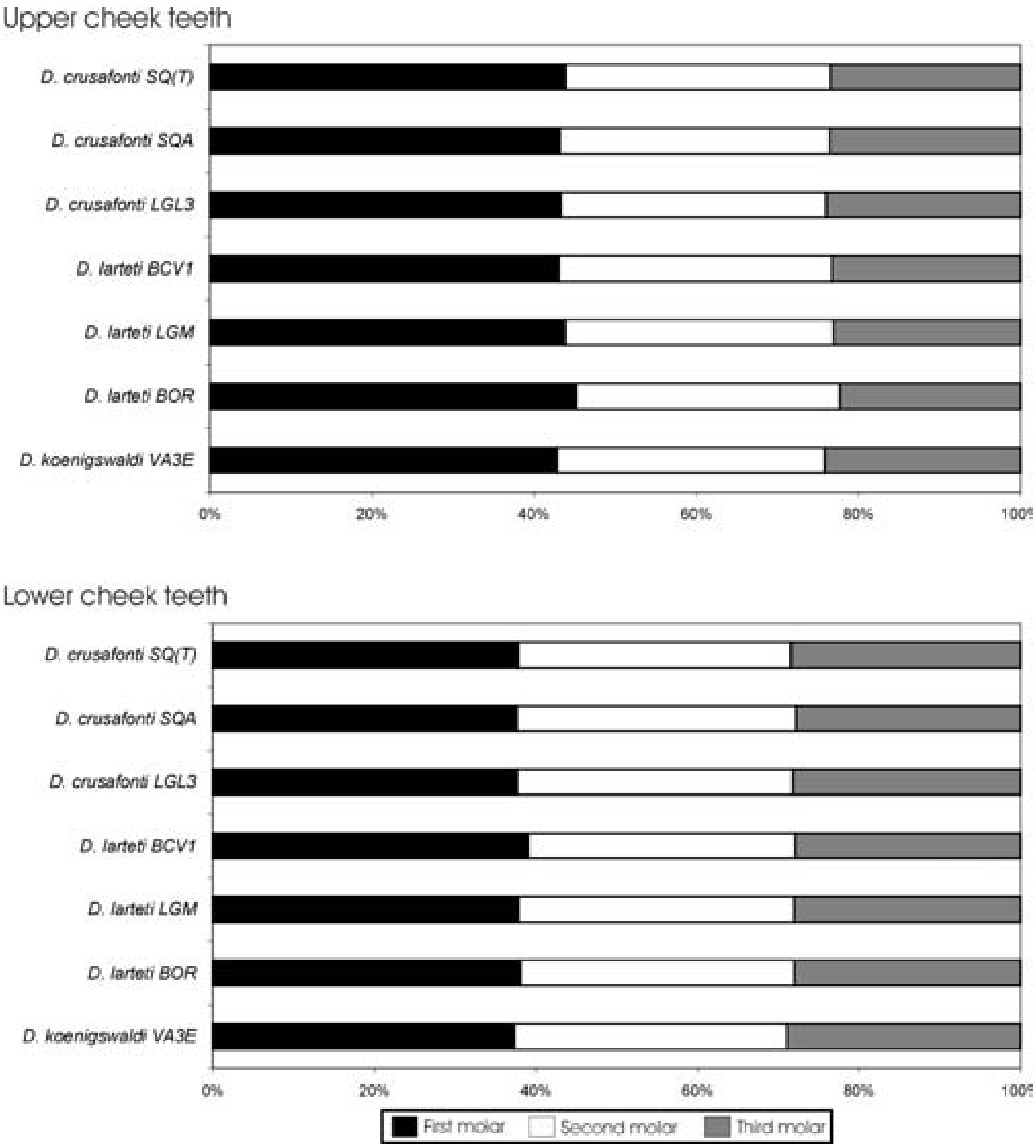


Figure 4.12. Principal Components Analysis (PCA) on the mean length and width for all upper and lower molars of several *Democricetodon* populations. (a) Scores for the different populations on the two first principal components (that account for about 97 % of the variance). *D. koenigswaldi* is represented by squares; *D. larteti* by circles and *D. crusafonti* by triangles. *D. larteti* from BCV1 is represented by a gray circle, while *D.* aff. *crusafonti* from La Grive L3 (LGL3) is represented by a gray triangle. Note the position of BCV1, close to the upper boundary of *D. larteti*. Locality acronyms are as follows: BSC = Barranc de Can Vila 1; LGL3 = La Grive L3; SQ(T) = Sant Quirze (Trinxera); MOL = Molina de Aragón; NOM2 = Nombrevilla 2; SOL = Solera; LGM = La Grive M; TOR3B = Toril 3B; TOR1 = Toril 1; LP4B = Las Planas 4B; LUM14 = Las Umbrias 14; LUM11 = Las Umbrias 11; REG2 = Regajo 2; LUM8 = Las Umbrias 8; VA7F = Valdemoros 7F; VA7E = Valdemoros 7E; LUM4 = Las Umbrias 4; LUM3 = Las Umbrias 3; VR11 = Vargas 11; VA6B = Valdemoros 6B; VA3E = Valdemoros 3E. See appendix 4.1. for the ages assigned to each site and the mean length and width values for all the *Democricetodon* populations considered. (b) Loadings of the variables (i.e. the mean length and width for all the molars) on PC1 and PC2.

Figure 4.13. Length of each molar of both upper and lower series as a percent of the length of the whole series for selected medium-sized *Democricetodon* samples. SQ (T) = Sant Quirze (Trinxera); SQA = Sant Quirze A; LGL3 = La Grive L3; BCV1 = Barranc de Can Vila 1; LGM = La Grive M; BOR = Borjas; VA3E = Valalto 3E.



populations[29]. The loadings of the variables on PC1 are all positive and considerably large, supporting the interpretation of PC1 as a "size axis" (fig. 4.12b). PC2 is more difficult to interpret. The lower molars contribute negatively to PC2 while the upper molars contribution is positive (figure 4.12b). Thus, PC2 may reflect the relative size of the lower series as compared to the upper one. The population of Sant Quirze (SQ), which is the type locality of *D. crusafonti*, has the lowest values in PC2, indicating that the lower molars are relatively large in comparison to the upper ones, as has already been recognized by Van der Meulen *et al.* (2003). The taxa are perfectly separated along PC1; the higher values correspond to *D. crusafonti*, which is hence characterized by a

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[29] The interpretation of PC1 as a "size" axis is open to criticism, since it might also reflect differences that are not attributable to this parameter. Nevertheless, many students consider that the subtle differences within a dataset are better expressed by the remaining principal components and they even do not take the PC1 into account (see Hammer & Harper, 2006 for a discussion on this issue).

higher overall size. The assemblage from BCV1 is close to the upper size limit of *D. larteti* (fig. 4.12b).

The absolute size of the molars appears as clear diagnostic character, although probably this is not the only one. In his diagnosis of *D. crusafonti* Agustí (1978a) considered two diagnostic characters: the absolute size of the molars and the degree of reduction of the M^3. Agustí (1978a) points that the M^3 is not so reduced in the Sant Quirze material as it is in *D. larteti* from La Grive (as already pointed by Schaub, 1944, 1947). In figure 4.13. we have represented the length of each molar of both upper and lower series as a percent of the length of the whole series. The data include *D. koenigswaldi* from Valalto 3E (VA3E); *D. larteti* from Borjas (BOR), La Grive M (LGM) and BCV1; and *D. crusafonti* from Sant Quirze (Trinxera) (SQ(T)), Sant Quirze A (SQA) and La Grive L3 (LGL3). The graphs clearly evidence that the relative proportions of the molars remain stable in this lineage.

Concerning the morphological characters, certain traits, such as the reduced mesolophs/ids or the reduction or absence of the posterosinus, are more common in *D. crusafonti*. Thus, size appears as the only valid diagnostic character at the present state of knowledge.

Subfamily **Cricetodontinae** Schaub, 1925

Genus *Hispanomys* Mein & Freudenthal, 1971

***Hispanomys* sp.**

(fig. 4.3.4-6, fig. 4.14)

Synonymy: *Cricetodon* sp. in Moyà-Solà *et al.* (2004).

Material: 1 broken right mandible with I_2 and M_1-M_3 (IPS 20242), 1 M^1 (IPS 23285), 1 M^2 (IPS 23118), 2 M^3 (IPS 23253, IPS 23338), 1 M_1 (IPS 23286), 1 M_2 (IPS 23119).

Measurements:

Mandible

Description of the measurement	**IPS 20242**
Length of postcanine series at the occlusal level	6.62
Length of postcanine series at the alveolar level	6.65
Symphysis height	-
Height of mandibular body at the lingual side (perpendicular to the alveolar level), at the level of M_1	(3.85)
Height of mandibular body at the lingual side (perpendicular to the alveolar level), at the level of M_2	(3.78)
Height of mandibular body at the lingual side (perpendicular to the alveolar level), at the level of M_3	(3.26)
Breadth of mandibular body (perpendicular to mandibular height), at the level of M_1	2.87
Breadth of mandibular body (perpendicular to mandibular height), at the level of M_2	2.32
Breadth of mandibular body (perpendicular to mandibular height), at the level of M_3	2.20

Lower incisor

Description of the measurement	IPS 20242
anterior width at occlusal level	-
posterior width at occlusal level	0.58
wear facet anteroposterior length	-
whole length of the incisor	-

Cheek teeth

Lower cheek teeth			Upper cheek teeth		
	L	W		L	W
M_1	2.54	1.52	M^1	3.03	1.89
	2.58	1.68			
M_2	2.33	1.74	M^2	2.24	1.83
	2.09	1.94			
M_3	1.97	1.78	M^3	1.79	1.70
				1.78	1.69

Description:

Mandible (fig. 4.3.4-6)**:** Most of the mandibular ramus is broken, while the ventral part of the corpus and the mandibular symphysis are also slightly damaged. Furthermore the tip of the incisor is broken, and the M_1 is broken in two fragments which could be joined again. All the cheek teeth are present and show an advanced degree of wear. Overall, the mandible is quite elongated and the incisor is straight rather than curved. The mandibular corpus is shallow. The incisor is separated from the molar series by a long, shallow and asymmetrical (its lowermost point is placed slightly backwards) diastema. The dimensions of the molar series are very similar at the occlusal and at the alveolar plane. The molar series is procumbent lingually. Albeit damaged, it can be appreciated that the base of the ramus partially originates below the distal margin of M_2 and rises steeply, partially obscuring the M_3. The mental foramen is placed mesially to the anterior root of the M_1, just below the lowest point of the diastema, being situated quite dorsally. This foramen is big and rounded. The masseteric fossa is V-shaped. The masseteric ridges are very marked. The lower masseteric ridge, which is somewhat damaged, appears to have been more prominent than the upper one. Both ridges merge rather ventrally at the level of the distal root of the M_1 defining an inflated masseteric tubercle. In lingual view the insertion of the mylohyoid muscle is faint. At the inner side of the preserved part of the ramus, just posterior to the molar series, there appears to be an insertion scar (presumably for the temporal muscle) which is not well defined.

I_2: The right lower incisor is still attached to the mandible IPS 20242. The incisor is broken at the mesial margin of the wear surface. The incisor is not strongly curved. The tip of the incisor is situated at the level of the alveolar plane of the molars. The wear surface is elongated and slightly concave. The external margin is rounded. The enamel on the anterior surface presents two parallel longitudinal ridges that are clearly visible when the incisor lays on its lingual side. The enamel thickness reaches the midpoint of crown's width at the external side, while at the symphyseal side only a thin enamel layer can be appreciated.

Upper cheek teeth: Moderately hypsodont molars with the buccal cusps clearly higher than the lingual ones (terraced sensu Hershkovitz, 1967). The wear surface tends to be flattened, particularly on the lingual side. The molars are not very elongated (see table 4.1.). The third molars are button-shaped, although not very reduced (see fig. 4.14.3. and table 4.2.). The enamel is slightly wrinkled at the base of some cups, such as on the protocone of M^1 and M^3 (fig. 4.14.1. and 4.14.3.). The distal wall of the protocone appears somewhat inflated and partially closes the sinus. The presence of this "inflation" implies that the sinus may appear to be proverse, when in fact it is transverse in all the molars. This valley is closed by a low cingulum which joins the base of the hypocone to the base of the protocone. There is always a reduced mesocone. All the molars lack the mesoloph, except the M^1 (IPS 23285 fig. 4.14.1.) which shows a vestigial mesoloph. The ectolophs are weak. In buccal view it can be appreciated that these ectolophs merge a very low ridge departing from the cusp immediately distal to them, although this fusion occurs at a very low high of the crown (see figs. 4.14.1b-2b.). The protolophule is short and posterior. A well-developed ridge, which may result of the fusion of a posterior metalophule and the posteroloph, joins the distal wall of the hypocone to that of the metacone in all the molars except one of the recovered M^3 (IPS 23338 fig. 4.14.3.). This fact implies the disappearance of the posterosinus in these teeth. In IPS 23338 there is a posterior metalophule which merges a vestigial posteroloph. In its turn this posteroloph encloses a very reduced posterosinus. The distal ridge which joins the hypocone to the metacone presents two short spurs, buccal and lingual, in M^1 and M^2.

Table 4.1. Length width ratio for each molar in selected *Hispanomys* and *Cricetodon* species from the Late Aragonian and the Early Vallesian of the Iberian Peninsula and France. Locality acronyms are as follows: BCV1 = Barranc de Can Vila 1; SQ(T) = Sant Quirze (Trinxera); CM = Can Missert; CCN22 = Creu Conill 22; HS = Upper Hostalets de Pierola; CP = Can Ponsic; ESC = Escobosa; NOM = Nombrevilla; PED2C = Pedregueras 2C; LG = La Grive (classical collections); LGL5 = La Grive L5; LGM = La Grive M.

species	locality	L/W M^1	L/W M^2	L/W M^3	L/W M_1	L/W M_2	L/W M_3
Hispanomys sp.	BCV1	1.60	1.22	1.00	1.60	1.20	1.11
H. lavocati	SQ(T)	1.61	1.23	1.00	1.54	1.36	1.30
H. daamsi	CM	1.61	1.34	1.08	1.48	1.32	1.30
H. dispectus	CCN22	1.55	1.39	1.06	1.61	1.35	1.30
H. dispectus	HS	1.58	1.24	1.03	1.56	1.33	1.25
H. thaleri	CP	1.56	1.24	1.00	1.60	1.27	1.23
H. aguirrei	ESC	1.50	1.20	1.03	1.47	1.28	1.18
H. nombrevillae	NOM	1.56	1.26	1.05	1.53	1.28	1.23
H. aragonensis	PED2C	1.65	1.31	1.10	1.59	1.31	1.33
H. decedens	LG	1.54	1.26	1.08	1.53	1.30	1.49
H. bijugatus	LGL5	1.58	1.29	1.14	1.56	1.30	1.49
Cricetodon albanensis	LGM	1.62	1.27	1.10	1.02	1.29	1.33

M^1 (fig. 4.14.1.): This molar presents traces of four cylindrical roots, although only two (the one below the anterocone and the one below the hypocone) have been preserved. These roots are placed below each one of the main cusps except the paracone. The root below the anterocone points obliquely forward. The anterocone is divided into two lobes of the same size which are joined by a wide ridge. These lobes are separated by a very weak groove which can be hardly appreciated on the mesial wall of the anterocone. The anterolophule joins the lingual lobe of the anterocone. There is a very low lingual anteroloph which partially closes the protosinus. The labial lobe shows a very short posterior spur (anterior ectoloph) which immediately becomes very low. The paracone shows a better-developed ectoloph which does not reach the metacone.

M^2 (fig. 4.14.2.): The buccal cusps are slightly damaged. There is a vestigial protosinus which can be appreciated at the mesiolingual corner of the tooth. There is also a vestigial lingual arm of the anteroloph in the form of a short spur. The buccal arm of this ridge is high and wide. This labial anteroloph directly departs from the protocone and its buccal end is cusp-like. The anterosinus is not closed by the labial anteroloph but by a very low cingular ridge departing from the base of the paracone. The paracone presents a relatively short ectoloph which does not reach the metacone.

M^3 (fig. 4.14.3.): The distal cusps are more reduced than the mesial ones. The protocone defines most of the surface of the teeth. One of the recovered molars presents a vestigial protosinus which is closed by a very low cingulum (IPS 23253), while in the other one this valley is missing (IPS 23338 fig. 4.14.3.). The anteroloph is defined just by its labial arm which is high, wide and very long, although it does not close the anterosinus. In IPS 23338 the protolophule presents a short spur pointing forwards (IPS 23338 fig. 4.14.3.). The sinus is very narrow. The paracone shows a long and low ectoloph which does not reach the metacone.

Table 4.2. Length ratio between the first and the third molars for selected *Hispanomys* and *Cricetodon* species from the Late Aragonian and the Early Vallesian of the Iberian Peninsula and France. Locality acronyms are as follows: BCV1 = Barranc de Can Vila 1; SQ(T) = Sant Quirze (Trinxera); CM = Can Missert; CCN22 = Creu Conill 22; HS = Upper Hostalets de Pierola; CP = Can Ponsic; ESC = Escobosa; NOM = Nombrevilla; PED2C = Pedregueras 2C; LG = La Grive (classical collections); LGL5 = La Grive L5; LGM = La Grive M.

species	locality	length ratio M^1/M^3	length ratio M_1/M_3
Hispanomys sp.	BCV1	1.69	1.30
Hispanomys lavocati	SQ (T)	1.74	1.13
Hispanomys daamsi	CM	1.72	1.08
Hispanomys dispectus	CCN22	1.79	1.16
Hispanomys dispectus	HS	1.83	1.20
Hispanomys thaleri	CP	1.79	1.17
Hispanomys aguirrei	ESC	1.77	1.20
Hispanomys nombrevillae	NOM	1.98	1.26
Hispanomys aragonensis	PED2C	1.79	1.15
Hispanomys decedens	LG	1.73	1.13
Hispanomys bijugatus	LGL5	1.62	1.04
Cricetodon albanensis	LGM	1.65	1.11

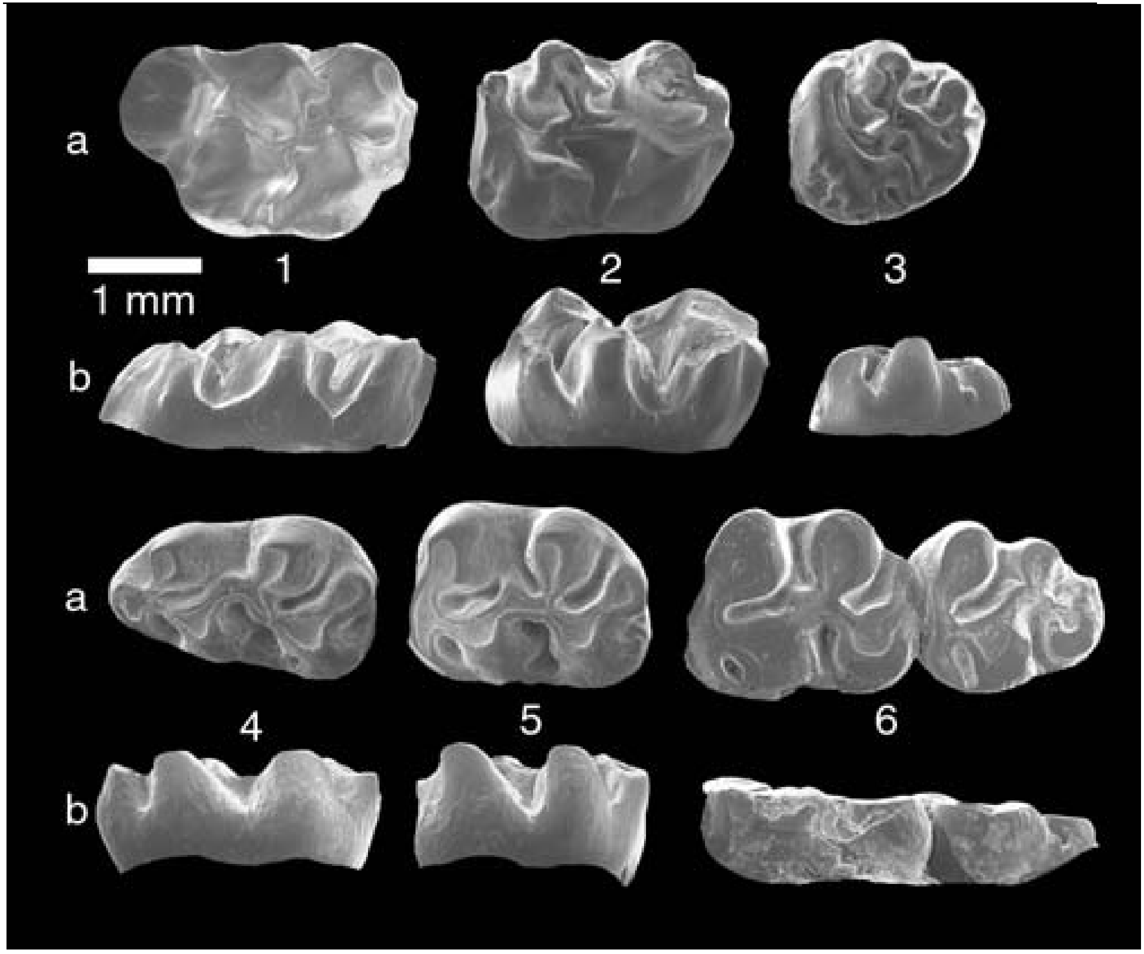


Figure 4.14. SEM micrographs of selected molars of *Hispanomys* sp. from BCV1 in oclusal view (a), labial view for upper molars (b) and lingual view for lower ones (b). The mesial side is always to the left in side view of the molars, accordingly the left ones are reversed in side view. 1. Right M^1 (reversed), IPS 23285. 2. Right M^2 (reversed), IPS 23118. 3. Right M^3 (reversed), IPS 23338. 4. Left M_1, IPS 23286. 5. Left M_2, IPS 23119. 6. Right M_2-M_3 (reversed) of mandible IPS 20242 (see fig. 4.3-4-6.).

Lower cheek teeth: The first and particularly the third molar are relatively more elongated in the lower series than in the upper one. The lower molars are hypsodont and they show a terraced wear pattern. All the molars present a mesial and a distal root only. These roots are always robust and flattened, except in the case of the mesial root of the M_1 and the distal one of the M_3, which are cylindrical. The anterosinusid is very reduced in M_1 and this valley has disappeared in the M_2 and the M_3. The anterolophid is defined by its buccal arm only, which is very short and quite low. This labial anterolophid closes a small protosinusid. The sinusid and the mesosinusid are quite wide. The mesosinusid is open. Apparently there is never a mesolophid (see discussion below). A small mesoconid can be appreciated on the M_1 and the M_2. There is an extremely short anterior hypolophulid. In the case of the M_3 this ridge is so short that the entoconid appears to join the longitudinal ridge directly. The posterosinusid is narrow. The posterolophid is well developed and its lingual end continues in a very low ridge that closes the posterosinusid.

M_1 (fig. 4.14.4.): The anteroconid is placed very mesially and consists in a rounded cusp. A short and wide anterior metalophulid directly joins the metaconid to the anteroconid. The anterolophulid is also wide and quite short. In one molar (IPS 23286 fig. 4.14.4.) there is also a vestigial posterior arm of the metalophulid (or a mesolophid, see below) situated at a very low high of the crown. The sinusid points obliquely

forwards and it is closed by a low cingulum departing from the distal wall of the protoconid.

M_2 (fig. 4.14.5-6.): In one molar (IPS 23119 fig. 4.14.5.) there is a short spur on the longitudinal ridge near the mesoconid which points forwards and merges the base of the metaconid at a very low crown's high. This spur may be interpreted as a vestigial posterior metalophulid, however, its position is closer to that which would occupy the mesolophid. A similar (although much lower) spur exists in one M_1 (IPS 23286 fig. 4.14.4.) and may also be interpreted as a short mesolophid which joins the base of the metaconid.

M_3 (fig. 4.14.6.): The single recovered M_3 is still attached to the mandible IPS 20242 and is highly worn. The four main cusps are clearly distinguishable, although the distal ones, and particularly the entoconid, are somewhat reduced. The protoconid is crescent-shaped and occupies an important part of the molar surface. The sinusid is wide and transverse. This valley is closed by two low cingula departing from the base of the protoconid and the hypoconid, respectively. The posterosinusid is reduced to a small distal valley.

Comments and comparisons:

The material from BCV1 belongs to a small-sized *Hispanomys* species, comparable to *H. decedens* and *H. dispectus* (see figs. 4.15. – 4.16.). The specimens are very close in size to *H. dispectus*, which has been described from the Aragonian and Vallesian classical sites from Els Hostalets de Pierola (Agustí, 1981a, 1981b; Agustí & Gibert, 1982). Nevertheless, it clearly differs from *H. lavocati*, which has also been described from the same set of sites (Freudenthal, 1966; Agustí, 1981a, 1981b; Agustí & Gibert, 1982), given its smaller size. Agustí (1981a, 1981b, 1982b) stressed on the diagnostic value of the relative length of the third molars as compared to the first ones in the genera *Cricetodon*, *Hispanomys* and *Ruscinomys*. Nevertheless, as it can be appreciated in figure 4.17., this parameter shows little variation in the Late Aragonian and Early Vallesian *Hispanomys* species, and the postulated differences are rather subtle. The M^3 are relatively elongated, as in many of the older *Hispanomys* species (*H. decedens*, *H. bijugatus* or *H. lavocati*), on the contrary they are reduced in *H. dispectus* and *H. nombrevillae* (see fig. 4.17. and table 4.2.). On the lower series, the M_3 is relatively short, while the M_1 is long in relation to the whole series (see fig. 4.17. and table 4.2.). Table 4.2. shows that the M_3 is even more reduced than in *H. nombrevillae* and *H. dispectus*. This fact contrasts with the presence of a non-reduced M^3 in the material of BCV1. The molars are not very elongated as compared to other *Hispanomys* species (see table 4.2.) and the L/W ratio for both upper and lower cheek teeth is very similar to that of *H. aguirrei*. As far as size and the relative proportions of the molars are concerned, the BCV1 material belongs to a small-sized species which does not present elongated molars; further being characterized by the presence of a reduced M_3 which contrasts with a non-reduced M^3.

The hypsodonty is moderate, being comparable to *H. decedens*, *H. aguirrei* or *H. dispectus* (cf. our fig. 4.14.1b to plate 1, figure 2 of Agustí, 1980b). In the upper molars the ectolophs are always present, although they are incomplete. Partial ectolophs

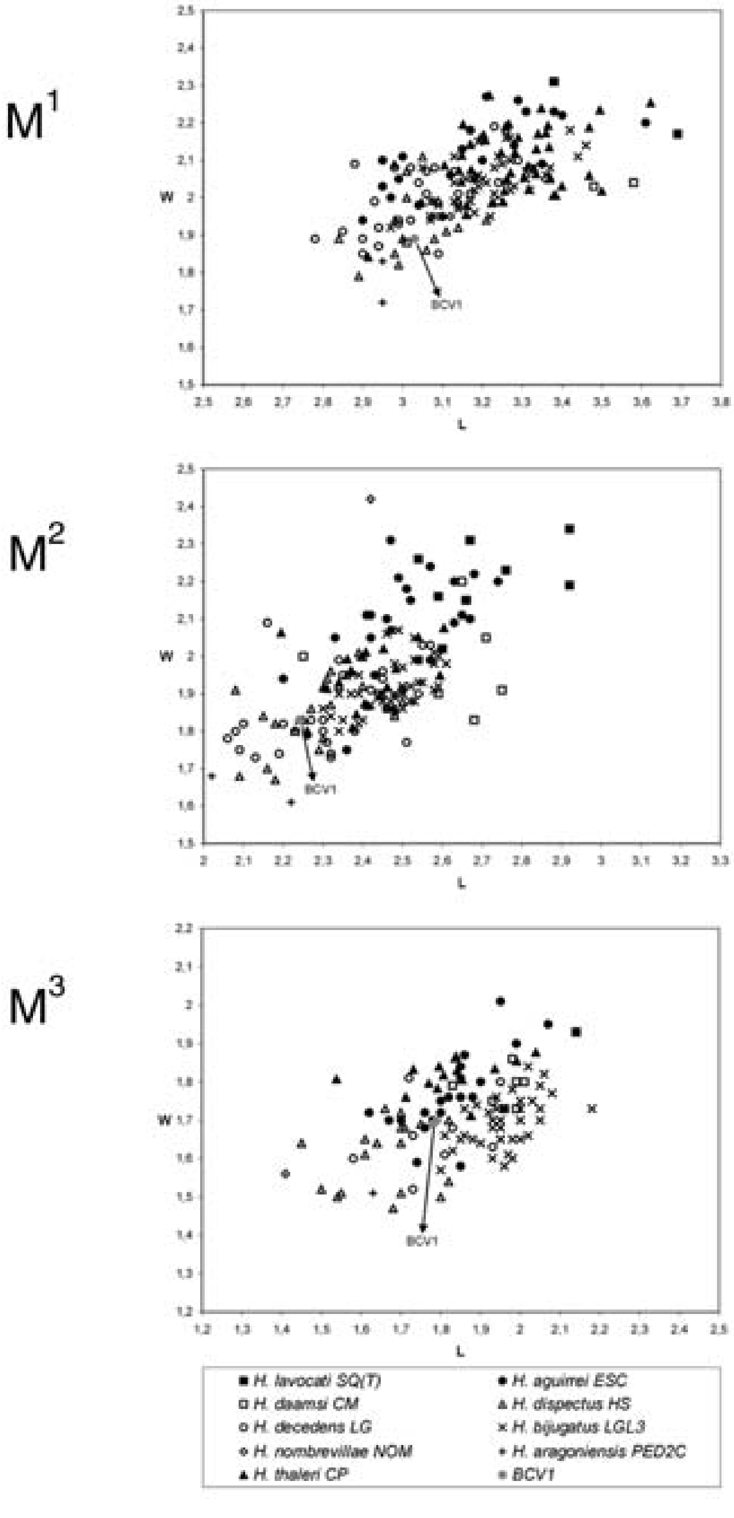


Figure 4.15. Scatter diagrams of the length and width values for the upper molars of selected *Hispanomys* species from the Late Aragonian and the Early Vallesian of the Iberian Peninsula and France. Locality acronyms are as follows: BCV1 = Barranc de Can Vila 1; SQ(T) = Sant Quirze (Trinxera); CM = Can Missert; HS = Upper Hostalets de Pierola; CP = Can Ponsic; ESC = Escobosa; NOM = Nombrevilla; PED2C = Pedregueras 2C; LG = La Grive (classical collections); LGL5 = La Grive L5.

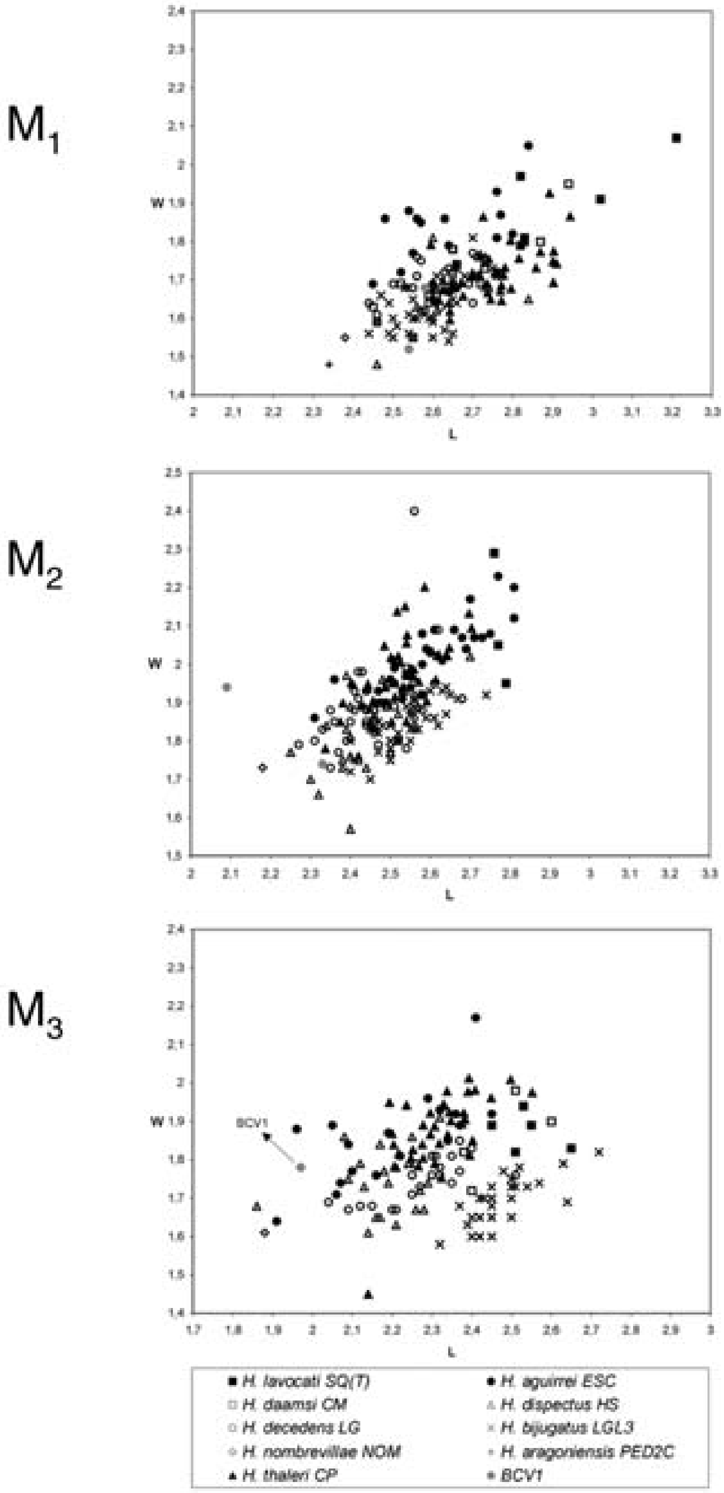


Figure 4.16. Scatter diagrams of the length and width values for the lower molars of selected *Hispanomys* species from the Late Aragonian and the Early Vallesian of the Iberian Peninsula and France. Locality acronyms are as follows: BCV1 = Barranc de Can Vila 1; SQ(T) = Sant Quirze (Trinxera); CM = Can Missert; HS = Upper Hostalets de Pierola; CP = Can Ponsic; ESC = Escobosa; NOM = Nombrevilla; PED2C = Pedregueras 2C; LG = La Grive (classical collections); LGL5 = La Grive L5.

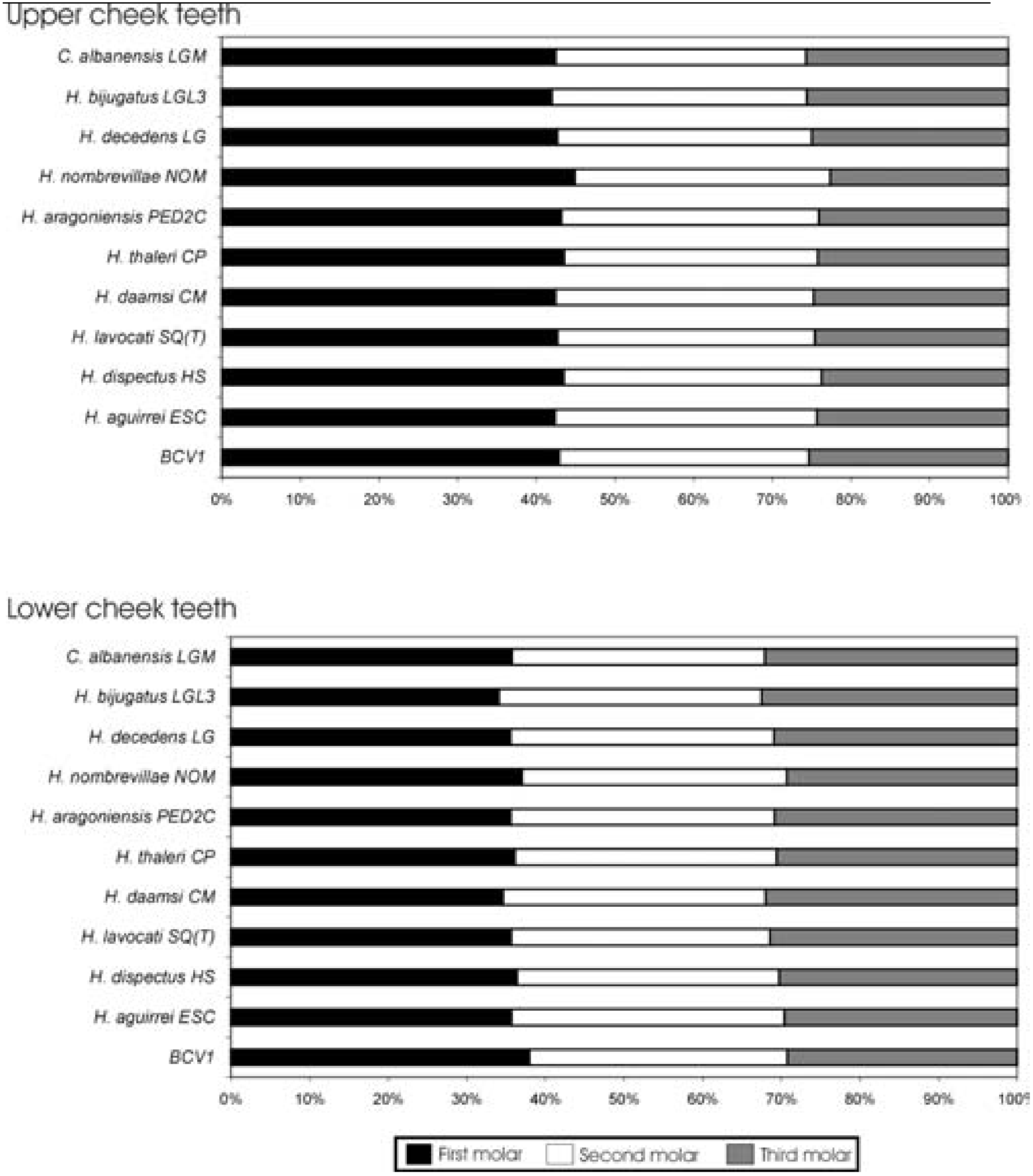


Figure 4.17. Length of each molar of both upper and lower series as a percent of the length of the whole series for selected *Hispanomys* and *Cricetodon* species from the Late Aragonian and the Early Vallesian of the Iberian Peninsula and France. Locality acronyms are as follows: BCV1 = Barranc de Can Vila 1; SQ(T) = Sant Quirze (Trinxera); CM = Can Missert; CCN22 = Creu Conill 22; HS = Upper Hostalets de Pierola; CP = Can Ponsic; ESC = Escobosa; NOM = Nombrevilla; PED2C = Pedregueras 2C; LG = La Grive (classical collections); LGL3 = La Grive L3; LGM = La Grive M.

are very common in many of the earlier *Hispanomys* species such as *H. aguirrei* (Sesé, 1977), *H. decedens*, *H. bijugatus*, *H. dispectus* or *H. lavocati* (Agustí 1981a, 1981b; Agustí & Gibert, 1982). Partial ectolophs occur more rarely in more advanced species such as *H. aragoniensis* (Freudenthal, 1966) or *H. thaleri* (Hartenberger & Crusafont, 1979; Agustí, 1981a, 1981b). Unfortunately, this is a highly variable character, so it cannot be evaluated on the basis of the scarce material recovered at BCV1. A vestigial mesoloph is present in the M^1, while a short spur, which may be homologous to the posterior metalophulid or to a short mesolophid, is observed in one M_1 and one M_2. Short mesolophs/ids tend to be present in many of the earlier *Hispanomys* species (*H. aguirrei*, *H. dispectus*, *H. daamsi*). To sum up, the material recovered at BCV1 belongs to a small-sized plesiomorphic species of the genus *Hispanomys* which is characterized by its reduced M_3. However, since the material is very scarce it cannot be discarded that it might be referred to one of the already described *Hispanomys* species.

4.4. Biochronology

The BCV1 fauna can be confidently correlated to the widely used MN zones (Mein, 1975 with modifications after De Bruijn *et al.*, 1992). The presence of a significant number of micromammal species (such as *Democricetodon larteti, Democricetodon brevis brevis, Megacricetodon minor minor* or *Glirudinus undosus*) point towards an MN 7+8 age (late Middle Miocene) for BCV1 since they are also recorded in the reference site for this MN: La Grive M (cf. to the updated faunal list given by Mein & Ginsburg, 2002; see also chapter 2). Mein & Ginsburg (2002) have claimed for a distinction between MN 7 and MN 8 according to the different composition of the faunas recovered at the several fissure infillings of La Grive (see also chapter 2). La Grive M is proposed as the MN 7 reference locality, being characterized by the presence of *Democricetodon larteti* amongst other species, as well as by the absence of some supposed MN 8 immigrants (such as *Megacricetodon* aff. *ibericus*, *Muscardinus hispanicus*, *Crusafontina endemica* and *Dryopithecus fontani*) (Mein & Ginsburg, 2002). In contrast, La Grive L3 is chosen by these authors as the reference site for MN 8. Interestingly, in La Grive L3, *Democricetodon crusafonti* is found instead of its putative ancestor, *Democricetodon larteti*. This fact, besides the absence of many of the immigrant taxa listed by Mein & Ginsburg (2002), indicates that BCV1 should be correlated to the lower part of the MN 7+8, and so, between 12 and 12.5-13 Ma (Agustí *et al.*, 2001).

Further chronological precision may be achieved by comparison of the fauna of BCV1 with the assemblages of the Calatayud-Daroca area (Inner Spain), since magnetostratigraphical calibrations are available for many sections (Krijgsman *et al.*, 1994; Krijgsman *et al.*, 1996; Daams *et al.*, 1999a; Garcés *et al.*, 2003). However, we must note that the resolution is poorer for the late MN 7+8 (see also chapter 2). On the basis of the occurrence of *Megacricetodon minor minor* and *Democricetodon larteti* (= *Fahlbuschia darocensis* in Daams *et al.*, 1999a), BCV1 is correlated to zone G of the Aragonian type area (Daams *et al.*, 1999a). Daams *et al.* (1999a) subdivided zone G according to the evolution of larger-sized *Megacricetodon* species and considering the presence of some glirid and “cricetid” species. Unfortunately, larger-sized *Megacricetodon* species have not been recovered from BCV1. Furthermore, the faunal composition of the localities in the Calatayud-Daroca area is markedly different from that of the Vallès-Penedès Basin, and many of the recorded Gliridae species as well as common elements such as *Eumyarion* do not occur inner Spanish basins. Accordingly, a direct correlation to the local subzones of the Calatayud-Daroca Basin may be controversial.

Instead of considering the whole fauna, which may differ in chronologically close sites from different areas just because of local environmental conditions, it seems preferable to study the morphology of particular species with a wider geographical distribution, such as *Democricetodon larteti*. This “cricetid” is a common element in the late Middle Miocene assemblages from the Iberian Peninsula and Southern France. Since many of the Calatayud-Daroca sites have been magnetostratigraphically characterized it is possible to infer a relative age for BCV1 assuming that the assigned ages to the other sites considered are correct. As we have already discussed, *D. larteti* is part of the *D. franconicus* – *D. crusafonti* anagenetic lineage (Van der Meulen *et al.*, 2003). An increase in size is recorded throughout the geological history of this lineage, culminating in *D. crusafonti*. We have demonstrated that size is a valid diagnostic character (see comments on *D. larteti* on section 4.3.) and the only trait that can be used to distinguish *D. crusafonti* from *D. larteti*. The *D. larteti* sample from BCV1 is situated close to the upper size limit for this species (fig. 4.12.). If it is assumed that the different local populations of *D. larteti* from the Calatayud-Daroca and the Vallès-Penedès basins increased in size synchronously, the population from BCV1 must be interpreted as close to that from Toril 3B (TOR3B), although somewhat younger. The former would be also close in age to La Grive M (LGM), older than Sant Quirze A (SQA), Solera (SOL) and La Grive L3 (LGL3), and clearly younger than Borjas (BOR).

The age assigned to TOR3B is 12.59 Ma, while SOL is dated to 11.75 Ma (Daams *et al.*, 1999a). We tentatively assign an age between 12.5 and 12 Ma to BCV1, being half a million of years younger than the age previously proposed by Moyà-Solà *et al.* (2004). Ongoing magnetostratigraphic studies in the Abocador de Can Mata series (Els Hostalets de Pierola) and nearby areas will refine the dating of this and other macromammal sites. For the moment, BCV1 is clearly placed in the lower part of the MN 7+8, being older than other Late Aragonian sites of the Vallès-Penedès area, such as Sant Quirze, Castell de Barberà or Can Missert (see also chapter 2).

4.5. Conclusions

The small mammal fauna from BCV1 includes eleven rodent species distributed amongst sciurids (2), glirids (4) and "cricetids" (5). The sciurids include the ground squirrel *Spermophilinus bredai*, which is a common component in Middle and early Late Miocene small mammal faunas. This species is fairly abundant and represents about 10 % of the total sample of rodent cheek teeth. The remains of flying squirrels are very rare and consist in just three teeth attributed to *Miopetaurista* cf. *crusafonti*. The glirids are nearly as diverse as the "cricetids" but much less abundant. The "cricetids" represent more than 80 % of the cheek teeth, while the glirids are less than the 5 %. *Glirudinus undosus* is the most abundant dormice (Gliridae), being represented by only eight teeth. The remaining Gliridae species include *Muscardinus sansaniensis* and *Microdyromys complicatus*, which are here reported for the first time from the Vallès-Penedès Basin. The fourth dormice identified is *Bransatoglis* sp., which is represented by just one M^3. Concerning the "cricetids", *Eumyarion leemani*, which-represents 40 % of the assemblage, is by far the most abundant rodent in the sample. The genus *Democricetodon* includes two species: a small-sized one, *D. brevis brevis*; and a larger-sized one, *D. larteti*. *D. brevis brevis* is here quoted for the first time in the Vallès-Penedès Basin. The remaining "cricetids" include the small-sized *Megacricetodon minor minor*, which is also quite abundant (about 12 % of the cheek teeth) and the numerically rare *Hispanomys* sp.

The composition of the rodent assemblage indicates an early MN 7+8 age for the fauna. Further biochronological resolution may be achieved by a close comparison of the *Democricetodon larteti* population from BCV1 with those from several sites from the Calatayud-Daroca Basin, which have been magnetostratigraphically calibrated. The size and morphology of *D. larteti* from BCV1 indicates that this is a derived population, clearly younger than the youngest populations of this species in the Calatayud-Daroca Basin (Toril 3B). Accordingly, the age of BCV1 is inferred to lie between 12.5 and 12 Ma, being half a million of years younger than the age previously proposed by Moyà-Solà *et al.* (2004). This site is also clearly older than other MN 7+8 "classical" sites from the Vallès-Penedès Basin, such as Sant Quirze or Castell de Barberà. Therefore BCV1 records the first occurrence of the hominoid primates in basin.

Appendix 4.1.

Mean length and width of the *Democricetodon* populations included in the PCA of figure 4.12. The data sources include Van der Meulen *et al.* (2003) for the sites from the Calatayud-Daroca Basin, Freudenthal & Mein (1987) for La Grive fissure infillings, and Agustí (1978a) for Sant Quirze (Trinxera). The numerical ages assigned to the Caltayud-Daroca Basin sites are taken from Van der Meulen *et al.* (2003). The locality acronyms correspond to those of figure 4.12a.

locality	**acronym**	**age**	**species**	**M^1**		**M^2**		**M^3**	
				L	W	L	W	L	W
Barranc de Can Vila 1	BCV1	see section 4.4.	*D. larteti*	2.49	1.63	1.95	1.60	1.34	1.37
La Grive L3	LGL3	late MN 7+8	*D.* aff. *crusafonti*	2.68	1.80	2.02	1.74	1.48	1.47
Sant Quirze (Trinx.)	SQ(T)	late MN 7+8	*D. crusafonti*	2.67	1.68	1.99	1.79	1.43	1.49
Molina de Aragón	MOL	MN 9	*D. crusafonti*	2.73	1.67	2.12	1.62	1.43	1.36
Nombrevilla 2	NOM2	11.5	*D. crusafonti*	2.73	1.70	2.02	1.63	1.42	1.44
Solera	SOL	11.75	*D. crusafonti*	2.69	1.69	1.96	1.64	1.34	1.46
La Grive M	LGM	early MN 7+8	*D. larteti*	2.47	1.66	1.87	1.64	1.30	1.42
Toril 3B	TOR3B	12.59	*D. larteti*	2.54	1.62	1.89	1.60	1.28	1.38
Toril 1	TOR1	12.62	*D. larteti*	2.48	1.58	1.83	1.53	1.20	1.26
Borjas	BOR	13.2	*D. larteti*	2.47	1.54	1.78	1.52	1.22	1.32
Las Planas 4B	LP4B	13.94	*D. larteti*	2.35	1.52	1.75	1.55	1.23	1.37
Las Umbrias 14	LUM14	13.97	*D. larteti*	2.37	1.53	1.72	1.51	1.24	1.29
Las Umbrias 11	LUM11	14.04	*D. larteti*	2.31	1.55	1.72	1.51	1.20	1.30
Regajo 2	RG2	14.16	*D. larteti*	2.32	1.50	1.72	1.49	1.21	1.27
Las Umbrias 8	LUM8	14.17	*D. larteti*	2.33	1.54	1.70	1.50	1.20	1.29
Valdemoros 7F	VA7F	14.26	*D. koenigswaldi*	2.27	1.52	1.65	1.46	1.21	1.23
Valdemoros 7E	VA7E	14.29	*D. koenigswaldi*	2.23	1.48	1.63	1.44	1.19	1.23
Las Umbrias 4	LUM4	14.32	*D. koenigswaldi*	2.21	1.47	1.62	1.43	1.16	1.20
Las Umbrias 3	LUM3	14.37	*D. koenigswaldi*	2.18	1.44	1.60	1.41	1.16	1.20
Vargas 11	VR11	14.39	*D. koenigswaldi*	2.07	1.38	1.55	1.37	1.09	1.15
Valdemoros 6B	VA6B	14.4	*D. koenigswaldi*	2.10	1.40	1.57	1.39	1.16	1.18
Valdemoros 3E	VA3E	14.55	*D. koenigswaldi*	2.10	1.41	1.62	1.38	1.18	1.21

locality	**acronym**	**age**	**species**	**M_1**		**M_2**		**M_3**	
				L	W	L	W	L	W
Barranc de Can Vila 1	BCV1	see section 4.4.	*D. larteti*	2.24	1.37	1.89	1.50	1.60	1.37
La Grive L3	LGL3	late MN 7+8	*D.* aff. *crusafonti*	2.26	1.46	2.04	1.64	1.69	1.39
Sant Quirze (Trinx.)	SQ(T)	late MN 7+8	*D. crusafonti*	2.48	1.62	2.21	1.73	1.86	1.48
Molina de Aragón	MOL	MN 9	*D. crusafonti*	2.31	1.47	2.06	1.59	1.63	1.38
Nombrevilla 2	NOM2	11.5	*D. crusafonti*	2.27	1.50	2.01	1.62	1.66	1.38
Solera	SOL	11.75	*D. crusafonti*	2.13	1.41	1.93	1.58	1.65	1.37
La Grive M	LGM	early MN 7+8	*D. larteti*	2.08	1.43	1.87	1.54	1.54	1.39
Toril 3B	TOR3B	12.59	*D. larteti*	2.07	1.41	1.88	1.52	1.58	1.32
Toril 1	TOR1	12.62	*D. larteti*	1.99	1.35	1.80	1.48	1.62	1.36
Borjas	BOR	13.2	*D. larteti*	2.04	1.36	1.81	1.48	1.50	1.29
Las Planas 4B	LP4B	13.94	*D. larteti*	1.94	1.37	1.77	1.46	1.48	1.28
Las Umbrias 14	LUM14	13.97	*D. larteti*	1.98	1.35	1.78	1.42	1.49	1.26
Las Umbrias 11	LUM11	14.04	*D. larteti*	1.97	1.35	1.77	1.44	1.46	1.24
Regajo 2	RG2	14.16	*D. larteti*	1.92	1.35	1.75	1.44	1.51	1.28
Las Umbrias 8	LUM8	14.17	*D. larteti*	1.95	1.36	1.76	1.42	1.51	1.25
Valdemoros 7F	VA7F	14.26	*D. koenigswaldi*	1.83	1.32	1.69	1.38	1.44	1.21
Valdemoros 7E	VA7E	14.29	*D. koenigswaldi*	1.86	1.29	1.69	1.38	1.45	1.20
Las Umbrias 4	LUM4	14.32	*D. koenigswaldi*	1.83	1.30	1.66	1.35	1.42	1.18
Las Umbrias 3	LUM3	14.37	*D. koenigswaldi*	1.81	1.26	1.64	1.34	1.41	1.17
Vargas 11	VR11	14.39	*D. koenigswaldi*	1.79	1.24	1.60	1.31	1.35	1.14
Valdemoros 6B	VA6B	14.4	*D. koenigswaldi*	1.79	1.25	1.62	1.32	1.38	1.15
Valdemoros 3E	VA3E	14.55	*D. koenigswaldi*	1.80	1.26	1.63	1.34	1.39	1.19

Chapter 5

The Barranc de Can Vila 1 site: taphonomy and paleoecology

5.1. Introduction

Taphonomy was first defined by Efremov (1940: 85) as “the study of the transition (in all its details) of animal remains from the biosphere into the lithosphere”, naming a field that we characterize more generally as “the study of processes of preservation and how they affect information in the fossil record” (Beherensmeyer & Kidwell, 1985). A detailed study of the taphonomical processes that have affected a fossil assemblage will provide us with a valuable information that will surely affect paleobiological conclusions, even leading to a reconsideration of the results. Thus, for a detailed paleoecological study an adequate understanding of site taphonomy is necessary, since it will serve us to evaluate the compositional fidelity of the assemblage, i. e., the quantitative faithfulness of the record of species richness, species abundances, trophic structure, etc. Furthermore, a detailed taphonomical study will also provide us complementary paleoenviromental information regarding the deposition site or area. In the case of larger-scale paleoecological studies, when we are only interested in showing meaningful differences between different sites or regions, a taphonomic study that may indicate us possible biases affecting the data is often not possible. However, it is assumed that the major ecological aspects are still reflected by the dataset.

Taphonomical studies in mammal paleontology have traditionally focused on macromammals. Although some authors devoted important works to the preservation biases that may affect small mammals earlier (see Mellet, 1974 and Korth, 1979 for example), a renewed interest in micromammal taphonomy started in the 1980s, specially after the publication of the book “Owls, caves and fossils” by P. Andrews (1990). The interest of the so-called “small-mammal taphonomists” has been mainly directed to the study of Pleistocene sites with hominines (Fernández-Jalvo & Andrews, 1992, and Fernández-Jalvo *et al.*, 1998 are good examples), with few studies on earlier sites.

The accurate excavation of the Barranc de Can Vila 1 (BCV1) site during the 2003 and 2004 field campaigns has provided us with a detailed information regarding the spatial distribution and state of preservation of macrovertebrate remains. Furthermore, most of the sediment removed during the excavation process has been washed and sieved, providing an abundant microvertebrate sample (see chapter 4). The taphonomical analysis of the BCV1 fauna, comprising micromammals and macromammals, is one of the subjects of this chapter. The second one concerns the reconstruction of the paleoenvironment associated to *Pierolapithecus catalaunicus* from BCV1. Finally we also discuss the distribution pattern of great apes in Europe during the late Middle Miocene.

5.2. Taphonomy

The material concerned by the taphonomic analysis comes from the excavation at BCV1 in 2003. During this field campaign a surface of about 50 m^2 was excavated, resulting in the recovery of more than 300 macrovertebrate remains including 83 identifiable primate bones or bone fragmets. A large amount of the sediment removed during the excavation was screen-washed in order to recover the microvertebrate remains and small macrovertebrate fossils. In 2004, a new field campaign was carried out at BCV1. The excavation focused on the 2003 outcrop, though more distant parts of the same layer were also excavated. No further primate remains appeared, and fewer (less than 100) macrovertebrate fossils were recovered, which have not been prepared yet. Therefore, these remains are only considered as far as their spatial distribution and orientation is concerned, but they are not included in the study of their state of preservation. We have divided the taphonomic analysis into four parts: the first and second ones are devoted to the macro- and micromammal taphonomy, respectively; the third one discusses the results in relation to the sedimentary environment; and in the fourth and final one, to the taphonomical biases that may affect our paleoenvironmental interpretations are assessed.

5.2.1. Macromammal taphonomy

Material and methods

The position of each bone (in a system of x, y and z coordinates), together with bone orientation (when a clear major axis existed), were recorded in the field. The presence of a high voltage line in the site surroundings caused an average deviation of the compass pointer of 31º. As a result, the orientation of the bones had to be corrected *a posteriori*. The dip angle was recorded in very few cases, since most of the bones appeared to be subparallel to the stratiphication. For the study of the state of preservation, the bones were examined by two observers before deciding what state to record. The preservation state was compared between different taxa in order to investigate for the existence of potentially different taphonomic stories. We distinguished up to three groupings: *P. catalaunicus*, megahervibores (including *Deinotherium giganteum* as well as undetermined remains of large mammals) and other remains (including some carnivore and artyodactyl remains, plus turtle shell fragments and mostly undetermined small- to medium-sized bone fragments).

Spatial distribution and orientation

Many remains clearly cluster in a semicircular front with an approximate northeast-southwest trace (figure 5.1.) surrounded by relatively poorer zones. There is no apparent pattern in bone distribution related to depth, and bones do not seem to be concentrated vertically. Most of the remains of the *P. catalaunicus* individual are concentrated in five squares: Pk, Ok, Ol, Qm and Qn; only two pelvic fragments have been recovered from Lk (see figure 5.1. and table 5.1.). Despite there is no anatomical connection, the bones belonging to different parts of the primate skeleton are spatially associated, phalanges being close to associated metapodials and podials. This fact suggests that the primate skeleton was affected by little transport. No spatial association of bones belonging to any other single taxon or individual is observed among the remaining taxa.

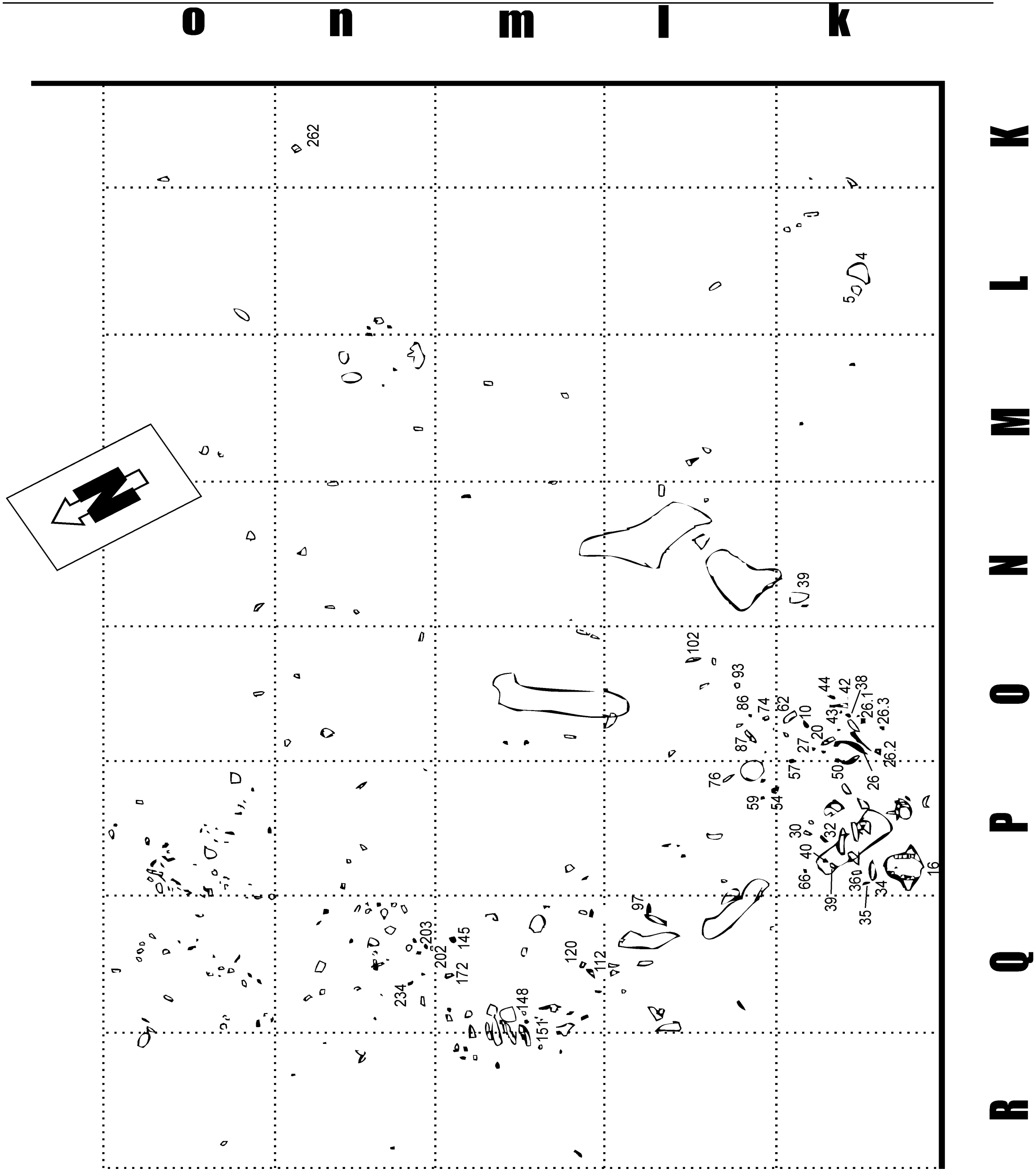


Figure 5.1. Map of the area excavated in BCV1 during the 2003 field campaign indicating the position of the recovered material. The side of each square of the grid measures 1 m. The small bone fragments are not represented. The numbered specimens correspond to elements of the *Pierolapithecus catalaunicus* individual (see table 5.1. for identification of these skeletal elements). Note the concentration of the primate elements in Pk, Ok, Ol, Qm and Qn.

In figure 5.2. we have represented the orientation of the long bones of *P. catalaunicus* (figure 5.2.a) and of all other orientable bones (figure 5.2.b) separately. Apparently, orientation is random in both cases. We tested the null hypothesis that all the directions are equally likely using the Rayleigh's test as well as a chi-square test for uniform distribution (see table 5.2.; for details on the calculation see Hammer & Harper, 2006). Due to the different assumptions and alternative hypotheses of the two tests, Hammer & Harper (2006) recommend to use them together to investigate a number of different situations. Rayleigh's test rejects the null hypothesis (directions uniformly distributed) when there is a single preferred direction, but not when there are two or

Table 5.1. Recovered anatomical elements of the *Pierolapithecus catalaunicus* skeleton. Numbers refer to the map of the excavated area in figure 5.1. Complete elements are indicated in bold and parcial elements in italics, otherwise the numbers indicate element fragments. The asterisk means that additional material was recovered but its spatial position was not recorded. This happened in two cases: when the material was extracted before a systematic excavation had been planned; and when small fragments were recovered by sediment screen-washing. While screen-washing the sediment we treated the different squares separately, so the approximate precedence (grid square) of the remains recovered by these means can still be established. That is the reason for including a third column in the table showing the squares where the different anatomical remains were found, including those not represented in figure 5.1.

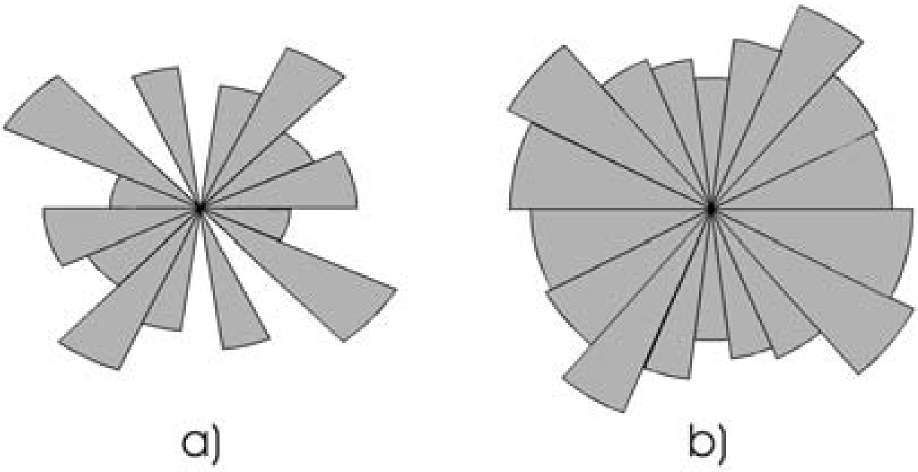
anatomical element	numbers	square
skull	16	Pk
mandible	-	-
isolated teeth	**34**, **36**	Pk
vertebrae	42.1, *148* *	Ok, Ql, Qm
ribs	*26*, *30*, *32*, *35*, *39*, *42.2*, *42.3*, *62*, *40*, *29*, 50 *	Ok, Pk, Pl, Ql
clavicle	22	Pk
scapula	-	-
pelvis	*4, 39*	Lk, Nk
humerus	position not recorded	Ok
radius-ulna	*5*, *42.1*, *112*, *120* *	Lk , Nl, Ok, Pk, Qm
carpals	**20**, **26.3**, **27**, **38**, **54**, **59**, **74**, **86** *	Ok, Ol, Pk, Pl
metacarpals	**43**, 76, 87, 97 *	Ok, Ol, Pk, Pl, Ql, Qm
hand phalanges	**10**, **26.1**, **26.2**, **44**, **57**, **66** *	Ok, Pk, Pl
femur	*102*	Ol
patella	**93**	Ol
tibia-fibula	-	-
tarsals	**145**, **202**, **203** *	Pk, Qk, Qm, Qn
metatarsals	234, 262 *	Kn, Ql, Qm, Qn
foot phalanges	151, 172 *	Qm, Ok

more preferred directions. In contrast, the chi-square test would also reject the null hypothesis in the latter case. The results indicate that a random orientation cannot be rejected when the primate bones are considered alone. For the rest of the bones, only the chi-square test for a random distribution gives a significant result at $p < 0.05$. This means that some directions are more common than others. In the rose plot of figure 5.2.b, there is a hint of a northeast-southwest trend, which would coincide with the trace of the arc where many bones are clustered; moreover, a second perpendicular axis is sketched. This orientation pattern, with a preferred axis and a secondary axis at a right angle to the first one, has been observed in flume experiments in which the bones are partially emergent from the current (Voorhies, 1969).

Table 5.2. Point distribution statistics for the macromammal remains from BCV1 (see text for details). Bold indicates significant values.

	Rayleigh's test		Chi-square test	
	R	p (random)	χ^2	p (random)
Pierolapithecus	0.1203	> 0.1	1.4	0.7055
rest of remains	0.1021	> 0.1	8.12	**0.0436**

Figure 5.2. Rose plots showing the orientations of the macromammal remains from BCV1. Area of the segments is proportional to frequency. a) Orientations of *Pierolapithecus catalaunicus* long bones. b) Orientations of all other orientable bones.



Abundance and breakage of anatomical elements

The skeletal parts most commonly preserved vary depending on the considered taxa (see figure 5.3.); however, in all cases the chi-square test points out that the distribution of elements differs from a random one, consisting of the same number of total items, with very high significance levels ($p < 10^{-8}$ in all instances). Therefore, some kind of bone sorting cannot be rejected, either by density or due to other factors. The percentage of breakage is very high and many bones display more than two fractures. These may be either parallel or perpendicular to the major axis of the bone. Oblique fractures are also common. In order to check a possible action of water, we considered the susceptibility of bones to hydraulic transport by classifying them into the Voorhies categories (Voorhies, 1969, with modifications by Beherensmeyer, 1975, and Hunt, 1978). In the case of *P. catalaunicus* (Figure 5.3.a), hand and foot bones are the most abundant ones, though rib fragments are also common. Highly compact bones, such as podials, are usually complete, while metapodials and phalanges are usually fragmented. Only blade-like cortical fragments of long bone diaphyses have been recovered. The primate material is attributed to a single individual, since all the bones were found close to one another, and no duplicated elements were recovered. These elements include a mixture of easily transportable bones (such as ribs and vertebrae, Voorhies category I) together with denser ones (such as the skull, category III), so that a selection by density can be rejected. The preferential removal and destruction of long bones is attributed to the action of carnivores. This interpretation is supported by the presence of carnivore marks on many dyaphyseal fragments (see following section).

Concerning macromammal remains other than those belonging to *P. catalaunicus*, ribs also appear to be one of the most common elements, even equaling isolated cheek teeth (figure 5.3.c). Megaherbivores, for example, are nearly exclusively

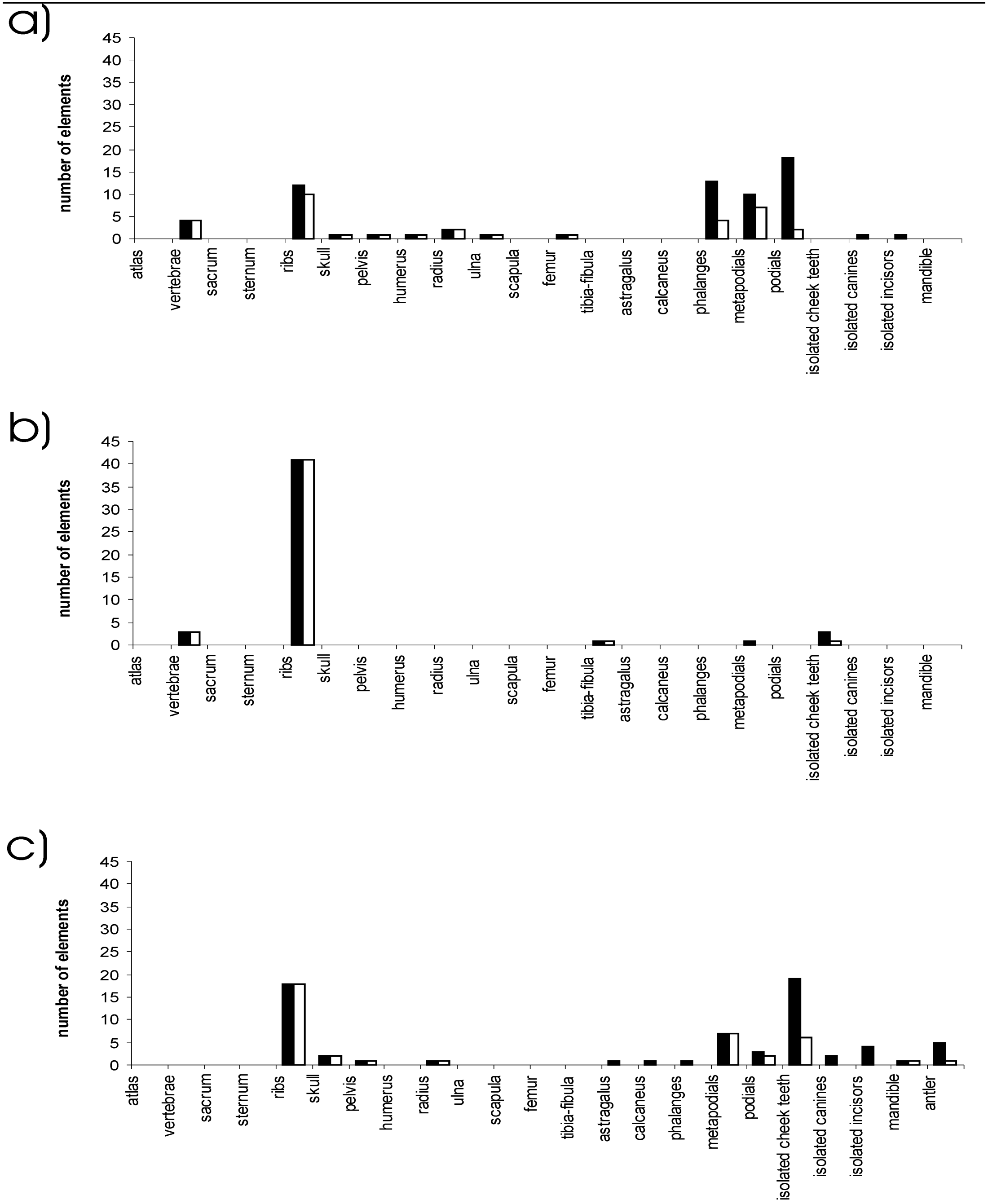


Figure 5.3. Number and kind of macromammal anatomical elements recovered from BCV1. The black bar represents the total number of elements recovered of each kind, while the white bar shows the proportion of those that are fragmented. Data shown include: (a) *Pierolapithecus catalaunicus*; (b) megaherbivores; (c) rest of the remains.

represented by rib fragments (Figure 5.3.b). Given the fact that ribs are amongst the least dense elements (category I) of the skeleton and can be easily transported, we must conclude that the megahervibore remains were removed and driven to the place of burial by water currents. Artiodactyls and carnivores are mostly represented by dental remains, although in the case of the cervid *Euprox furcatus* two shed antlers have also been recovered. Rib fragments of undetermined small- to medium-sized mammals are the second most common elements within this group. Unlike ribs, isolated cheek teeth are very dense (category III) and are supposed to define lag deposits. This also points towards the existence of hydraulic sorting in the case of these groups, although a mixture of transported and locally-derived lag elements defines the assemblage.

To sum up, there are evidences of at least two different accumulation processes. The first one would be the responsible for the deposition of the megaherbivore remains and, to a lesser degree, of the carnivore and artyodactyl ones. The accumulation of these elements would be the product of hydraulic transport from site surroundings. The second accumulation process is referred to the *P. catalaunicus* individual. In the latter case, carnivores must have played a major role in the accumulation, determining which skeletal parts were preserved.

Carnivore marks

Carnivore marks such as pits, scratches and grooves are almost entirely restricted to the primate bones. 27 out of 83 bones show tooth marks (see figure 5.4. for an example). Punctures and pits are observed in 14 bones, while scratches and grooves are found in 13. These marks are predominantly found on diaphyseal fragments. However, they also occur in one pelvic fragment, the partial clavicle and some of the metapodials and phalanges. This point confirms the action of carnivores as the main factor producing breakage and/or destruction of some of the skeletal elements of the *P. catalaunicus* skeleton. Carnivore marks are also observed in 11 bones belonging to other taxa. These include mainly diaphyseal cortical fragments of undetermined mammals and a distal epiphysis of tibia of an undetermined ruminant showing scratches, punctures and big pits. In conclusion, accumulation due to carnivore activity seems to have played a preponderant role only in the case of *P. catalaunicus*.

Weathering

Weathering mainly depends on atmospheric agents and has been generally used to estimate the time elapsed between the loss of the soft parts and the definitive burial of the bones (Beherensmeyer, 1978). However, recent studies have shown that weathering depends on important parameters such as climate (Andrews & Armour-Chelu, 1998) and the extent of the vegetable cover at the place of deposit (Tappen, 1994). Thus, the rate of weathering varies depending on the habitat and cannot be directly related to the burial time when no detailed information about the first parameter is available. Furthermore, the relation between burial time and weathering has been only extensively studied in the African savanna (Beherensmeyer, 1978). When coding the weathering stages, we followed the methodology described by Alcalá (1994) by distinguishing three categories: intact bone (stage 1), weathering of superficial bone tissues (stage 2), and weathering of the whole bone tissue (stage 3). Following Beherensmeyer (1978), we neglected small, compact bones such as podials, phalanges or isolated cheek teeth. Our results show a relationship between certain weathering stages and the different groupings considered (see table 5.3.). In the case of *P. catalaunicus*, most of the elements show only superficial weathering, although an important proportion (more than 30 %) show no weathering at all; weathering stage 3 is very rare (see figure 5.5.). In contrast, the megaherbivore remains are heavily weathered (about 75 % of them belong to stage 3), and there are not fresh bones. The third group (mainly consisting in artyodactyl and carnivore remains) includes a minor proportion of fresh bones (less than 10 %) and abundant superficially or heavily weathered bones.

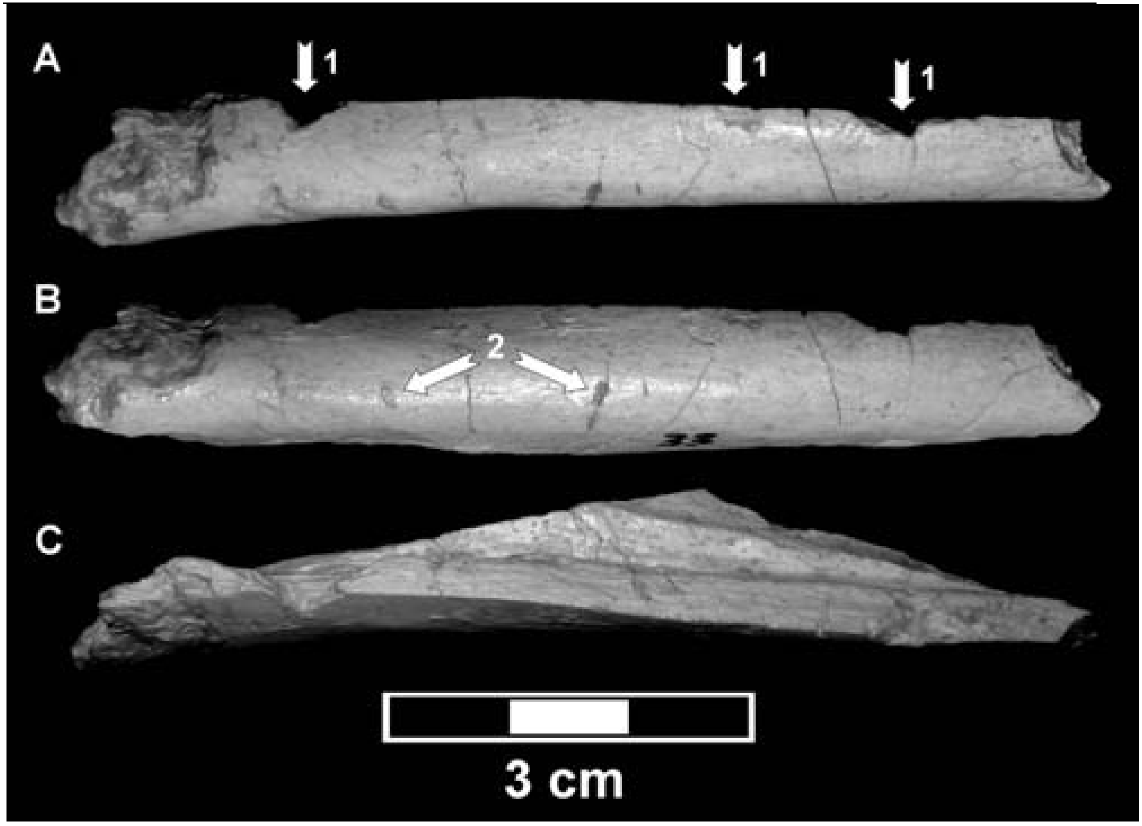


Figure 5.4. Carnivore marks on a diaphyseal cortical fragment of ulna of *Pierolapithecus catalaunicus* (IPS 21350-78). Two scratches can be seen in the bone surface (2), while pits appear in the margin of the shaft (1). Two of these pits completely perforate the cortical bone.

Highly weathered remains concentrate outside the main arch-like bone accumulation (in the southeastern side of the excavated area and in the northwestern one). Nevertheless, bones showing extensive weathering are also found in the main accumulation. This fact may suggest that weathering may have occurred *in situ*. We explored this possibility by testing the correlation between the spatial position of the bones (in x, y and z coordinates) and weathering stage using Kendall's test (for details on calculation see Hammer & Harper, 2006). The null hypothesis (no correlation) was only rejected in the case of the y coordinate ($\tau = 0.12$, $p = 0.03$). In the remaining situations, the correlation between both variables could not be rejected at $p < 0.05$. Thus, weathering may be related to spatial position, though variation in weathering depending on the taxa considered is more evident. All the remains were exposed for some time, although the primate parcial skeleton was buried faster than most of the remaining bones, particularly the megaherbivore ones.

Abrasion

Although wind can also produce bone abrasion, the degree of abrasion is usually interpreted as indicative of a possible hydraulic transport. We followed Alcalá (1994) in the coding of the abrasion stage. Three stages were distinguished: intact bone (stage 1), polishing of the edges of bone or fractures (stage 2 or rounding sensu Alcalá, 1994), and heavy polishing of the bone even leading to the loss of its original morphology (stage 3 or polishing sensu Alcalá, 1994). The primate bones show only very light abrasion in a few cases. Concerning the megaherbivores and the rest of the remains, half of the bones do not show any evidence of abrasion. In the other half, rounding is more common, and

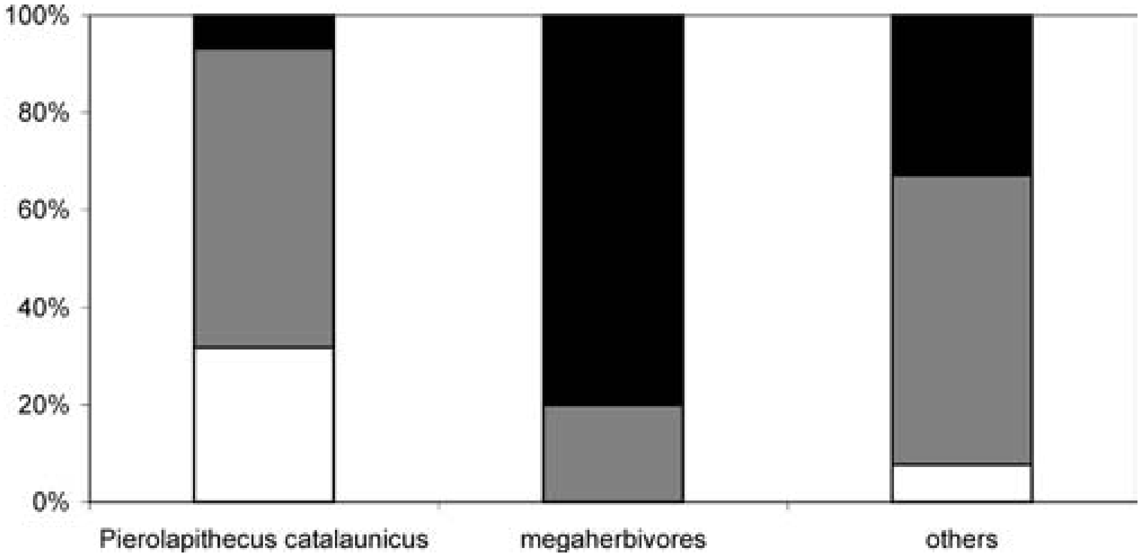
	Pierolapithecus	megaherbivores	others

Pierolapithecus	-	**χ^2= 39,45 ; p = 2,71 · 10^{-9}**	**χ^2= 23,82 ; p = 6,72 · 10^{-6}**
megaherbivores	**χ^2= 39,45 ; p = 2,71 · 10^{-9}**	-	**χ^2= 20,23 ; p = 4,05 · 10^{-5}**
others	**χ^2= 23,82 ; p = 6,72 · 10^{-6}**	**χ^2= 20,23 ; p = 4,05 · 10^{-5}**	-

Table 5.3. Comparison of the distribution of weathering stages amongst three groups of taxa (*Pierolapithecus catalaunicus*, megaherbivores and rest of the remains) using chi-square tests. Bold indicates significant values. Note that there is always a relationship between certain weathering stages and the group of taxa considered.

polishing (stage 3) may appear as well, although affecting a minor proportion of the assemblage. Polishing is more common in the megaherbivore bones. The presence of light abrasion in the primate bones might indicate some hydraulic transport. Nevertheless, given the fact that all the bones belong to a single individual, and that only some bones show abrasion, this transport appears to have been very short. This transport must necessarily postdate bone breakage, since fracture edges are often polished. In the case of other remains, and especially in the megaherbivore bones, transport seems to have been greater, since the occurrence of rounded bones is common and polished bones also occur.

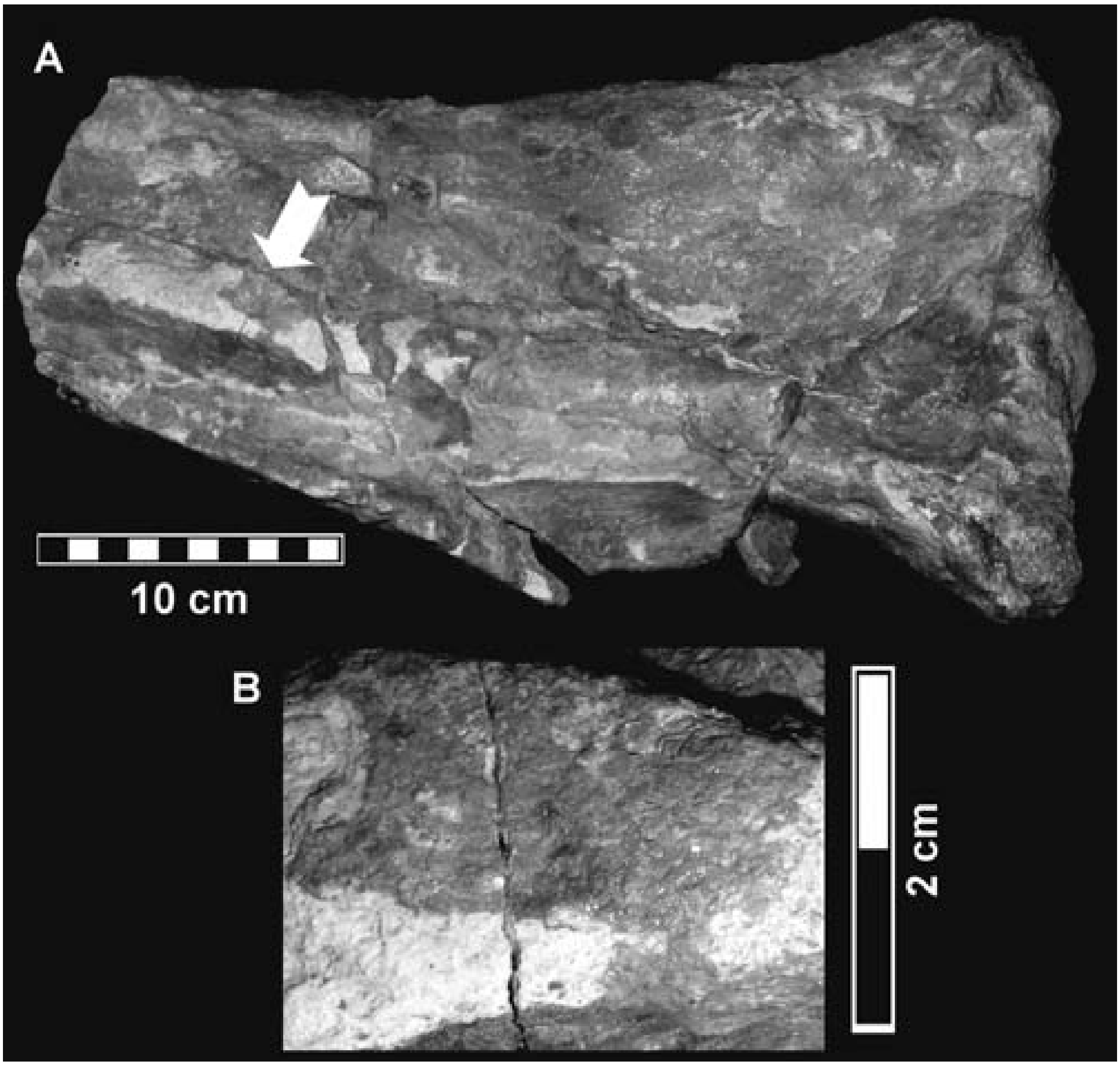
Figure 5.5. Weathering stages recorded in the macromammal remains from BCV1. Colors show the proportion of bones assigned to each one of the weathering stages by Alcalá (1994). White indicates stage 1 (intact bone), grey stage 2 (weathering of superficial bone tissues), while black indicates stage 3 (weathering of the whole bone tissue). In order to compare the occurrence of the different weathering stages the remains are classified in three groups as follows: *Pierolapithecus catalaunicus*, megaherbivores and the remaining bones.



Post-burial alterations

Once bones are embodied in the sediment they may undergo further alterations depending on the composition and water content of the burial environment. A significant proportion of unidentified bone fragments and also some megaherbivore bones have a fragile and dusty texture that blurs the original bone shape and complicates their separation from the surrounding matrix. The presence of hard and thin grey carbonate crusts is relatively common and affects all taxa. In a significant portion of the larger bones (20 % in the case of megaherbivore ones), this crust is more developed, being sometimes even associated with the growing of calcite crystals in the surface of the bone and inside the bone cavities (for an example see figure 5.6.). Encrusting and crystal growing occur preferably in the zone of oscillation of the ground-water table, near the interphase between the vadose and phreatic zones (Polonio & López-Martínez, 2000). In some cases the inner cavities are filled with a limonitic matrix that includes the crumbled cancellous bone. This is rather common and affects at least 20 % of the material, thought it is more frequent in the megaherbivore bones. All these modifications are related to the burial of the bones in water saturated acid conditions.

Figure 5.6. A fragment of an undetermined long bone of a proboscidean (IPS 4395) (A). The bone is broken into several fragments that are joined by the surrounding matrix blurring the original bone shape. Arrow indicates the area enlarged in B, which shows a gray carbonate crust that is common in the surface of many bones (gray area above the bone fragments in B).

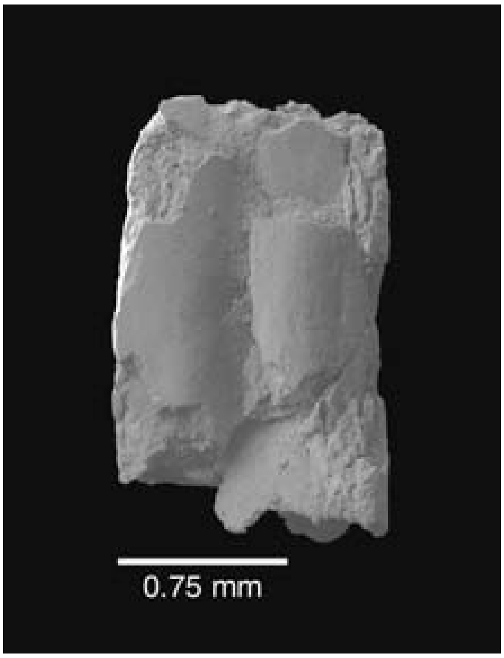


5.2.2. Micromammal taphonomy

Material and methods

The sediment removed during the 2004 campaign at the BCV1 site was screen-washed using a minimum mesh size of 0.7 mm (see chapter 1 for a description of the methods). This technique may imply some degree of destruction of the material. In this case most of the teeth were not affected, but a large percentage of bones were broken. This resulted from the action of water during washing as well as from the fact that some bones were already broken by pressure while buried (see figure 5.7.). In the latter case, the sediment that joined the broken parts was removed during washing, so that further separation of the fragments occurred. Given the fact that bone remains from BCV1 are extremely broken because of collecting methods, it is not possible to apply many of the taphonomic criteria based on bone breakage (see Andrews, 1990) in order to determine their origin. The fossil collection includes about 100 postcranial bones, 43 isolated incisors, a couple of mandibles and 414 isolated cheek teeth. These remains were examined under a stereomicroscope at a variable magnification (x 8 to x 40), while microphotographs (figures 5.7, 5.8 and 5.9.) were taken using a scanning electron microscope (SEM).

Figure 5.7. SEM micrograph of a small mammal bone from BCV1 broken by pressure. Notice that the fragments are still attached. Screen-washing often produces further separation and destruction of the bone fragments.



Relative abundance of the different taxa

Up to 21 different small mammal taxa have been recognized (see chapter 4 and table 5.4.). However, most of them are represented by just a few specimens and are very rare. This applies to all the dormice, the flying squirrel *Miopetaurista* cf. *crusafonti*, the ochotonid *Prolagus oeningensis*, the "cricetid" *Hispanomys* sp. and most of the insectivores. The "cricetids" *Eumyarion leemani* and *Democricetodon larteti* are the most abundant taxa, followed by another "cricetid", (*Megacricetodon minor minor*), the ground squirrel *Spermophilinus bredai*, and the insectivores *Parasorex socialis*, *Dinosorex sansaniensis* and *Plesiodimylus chantrei*. The dormice and the flying squirrels tend to be rare in the Late Aragonian and Vallesian rodent assemblages, and their rarity is probably a result of their arboreal habits. Thus, as it happens with many primates, they are often underrepresented in the samples. Other rare taxa, such as many of the insectivores as well as the "cricetid" *Hispanomys* sp., probably were not arboreal, and their scantiness should be related to other factors.

Table 5.4. Micromammal cheek teeth recovered from BCV1, distributed in eleven rodent species, eight insectivores and one lagomorph. The undetermined Crocidosoricinae is only represented by an upper incisor. n is the total number of cheek teeth recovered in each case, while MNI is the minimum number of individuals. MNI is calculated counting the most abundant teeth typologies in each case, considering only those teeth belonging to the same side. A is the relative abundance of the different taxa calculated using n, while B repeats the calculation using the MNI. Note that the abundance pattern is roughly similar in A and B, although in B the relative abundance of some rare taxa is increased. However, the rare taxa such as the dormice and the flying squirrels are still very rare even when the MNI is considered.

taxon	n	MNI	A	B
Dinosorex sansaniensis	29	5	6.89	6.94
Crocidosoricinae indet.	-	-	-	-
Soricidae indet.	1	1	0.24	1.39
Parasorex socialis	32	3	7.60	4.17
Erinaceidae sp. 2	5	2	1.19	2.78
Talpa minuta	9	3	2.14	4.17
cf. *Proscapanus* sp.	4	2	0.95	2.78
Plesiodimylus chantrei	21	5	4.99	1.39
Prolagus oeningensis	7	1	1.66	2.78
Spermophilinus bredai	35	8	8.31	11.11
Miopetaurista cf. *crusafonti*	3	1	0.71	1.39
Glirudinus undosus	9	3	2.14	4.17
Muscardinus sansaniensis	6	2	1.43	2.78
Microdyromys complicatus	5	2	1.19	2.78
Bransatoglis sp.	1	1	0.24	1.39
Eumyarion leemani	121	15	28.74	20.83
Hispanomys sp.	9	1	2.14	1.39
Democricetodon brevis brevis	15	2	3.56	2.78
Democricetodon larteti	71	10	16.86	13.89
Megacricetodon minor minor	38	8	9.03	11.11
TOTAL	421	72		

Predation

Predation has been proposed as the most important process involved on the origin of small mammal fossil assemblages (Mellet, 1974; Korth, 1979; Andrews & Evans, 1983; Andrews, 1990). Since the hunting habits of the predator (s) involved in the accumulation may introduce biases in the paleoecological interpretation, a considerable effort has been devoted to identify it by recognizing characteristic patterns of bone breakage and modifications on teeth and bones (Andrews, 1990). This procedure is based on the comparison with recent small mammal prey assemblages, and has been successfully applied to many Pleistocene sites (Andrews, 1990; Fernández-Jalvo & Andrews, 1992; Fernández-Jalvo *et al.*, 1998). Since many of the recent small mammal predators already existed in the Pleistocene, the correction of the bias introduced by them in these cases seems justified. However, only a few genera of these predators have been found in Miocene deposits, and the identification of the predators involved in accumulations older than the Pleistocene is therefore controversial. In pre-Pleistocene predator-derived accumulations, the identity of the predator should stay unknown, and no correction of the bias introduced by the predator should be applied on the basis of recent standards.

Because of the considerable recent breakage of the bones, in the case of BCV1 we have only focused on the degree of digestion of both bones and teeth. The definition of digestion categories follows Andrews (1990). Most of the remains (more than 90 %) do not show any trace of digestion. In the case of the cheek teeth, moderate to heavy digestion, consisting in pitting of the surface of the teeth as well as partial removal of the enamel along the edge of wear facets, is observed in some “cricetid” and insectivore cheek teeth (22 out of 425 teeth). This category of digestion has been identified in some “cricetids” (*Eumyarion leemani*, *Democricetodon larteti*, *Hispanomys* sp., *Democricetodon brevis brevis*), the ground squirrel *Spermophilinus bredai* and the erinaceid *Parasorex socialis*. Extreme digestion is very rare, being only observed in *Eumyarion leemani* (6 teeth) and *Democricetodon larteti* (2) (figures 5.8.a and 5.8.b). Digestion seems to affect particularly *Hispanomys* sp., since half of the molars recovered (4) show heavy digestion. Digestion of rodent incisors is also uncommon, but two different categories can be distinguished: light digestion concentrated at the tips of the incisors (3 out of 42 incisors) (figure 5.8.c); and moderate to heavy digestion reducing the enamel to islands on the surface of the dentine, which is also affected (1 incisor; figures 5.8.e and 5.8.f). Digestion of postcranial bones is often masked by postdepositional modifications such as weathering and soil corrosion. However, signs of light to moderate digestion are observed in a few bones (figure 5.8.d).

In the light of this evidence, predators do not seem to be the primary responsible for the origin of the small mammal assemblage of BCV1. However, category-1 predators (Andrews, 1990) usually do not produce appreciable damage to molars and incisors; accordingly, the possibility that this kind of predators may play any kind of role in the genesis of the accumulation cannot be ruled out. It should be noted that the remains of rare, presumably arboreal taxa (dormice, flying squirrels) do not seem to derive from the predator contribution to the assemblage.

Other pre-burial alterations

Abrasion is very uncommon in the studied sample and only a light degree of rounding has been recognized on a few postcranial bones. It is clearly distinguished from polishing caused by digestion because the whole bone is affected instead of more localized bone areas. Wheathering, which would indicate the exposition of remains on the ground surface, affects approximately 20 % of the recovered postcranial bones. Splitting and, in advanced stages, flaking, is present in the bones. Weathering patterns differ from those described for large mammals (Beherensmeyer, 1978) and also from the effects of digestion (Andrews, 1990). Concerning the teeth, weathering produces cracking and splitting of the dentine and, in more advanced stages, may result in the loss of parts of the crown. Since enamel is more resistant to weathering than bones, this may account for the very rare occurrence of wheatering in teeth, although cracking of the dentine has been observed in a few molars. Microscopic grooves are common, especially in the bone diaphyses (17 %) but also in a few incisors, were they may affect the dentine (figure 5.9.a). This kind of marks is often attributed to insect damage (Fernández-Jalvo *et al.*, 1998). Possible rodent gnawing marks have also been identified in a small mammal incisor. All these alterations show that a high proportion of the

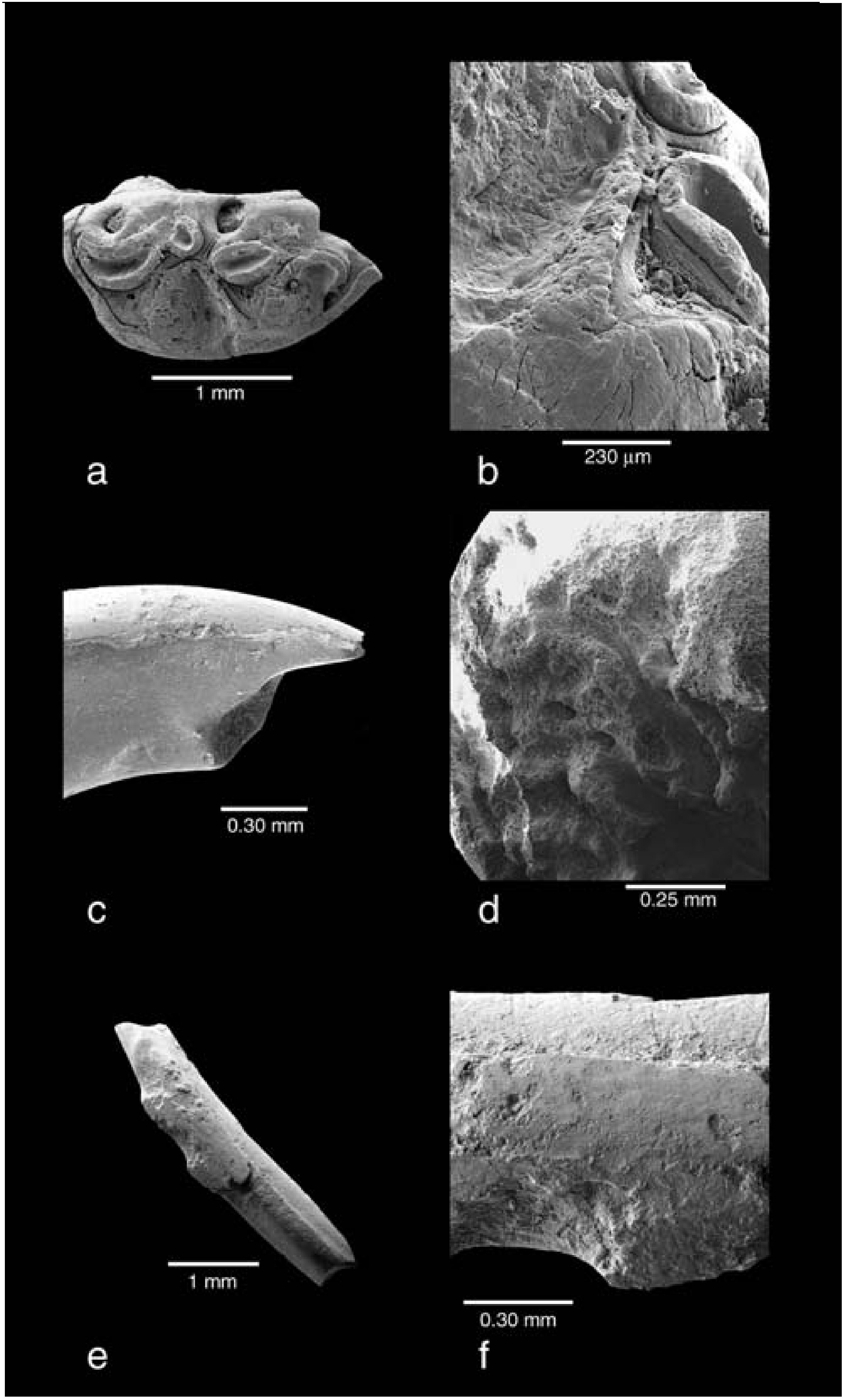

1 mm
a
b
230 µm
0.30 mm
c
d
0.25 mm
1 mm
0.30 mm
e
f

Figure 5.8. (previous page) SEM microphotographs of small mammal remains from BCV1 showing traces of digestion. (a) Right M^1 of *Democricetodon larteti* very heavily digested. The mesial end of the tooth is broken. The whole surface is heavily cracked and pitted. Note that digestion is greater at the buccal margin: enamel has been nearly removed and the dentine is also affected, resulting in polishing and rounding of the buccal cusps. (b) Detail of the protocone of the same specimen showing the collapse of dentine inside this cusp as well as extensive cracking and splitting of the enamel. (c) Very light digestion of the tip of a rodent lower incisor. Note slight pitting of the enamel and digestion of the dentine resulting in a polished occlusal surface. (d) Femoral head of a juvenile specimen showing moderate digestion. (e) Very heavy to extreme digestion of a rodent lower incisor. Note that most of enamel has been removed and that dentine is also affected, producing a waved outline. (f) Detail of the same specimen showing extensive pitting and removal of incisor enamel.

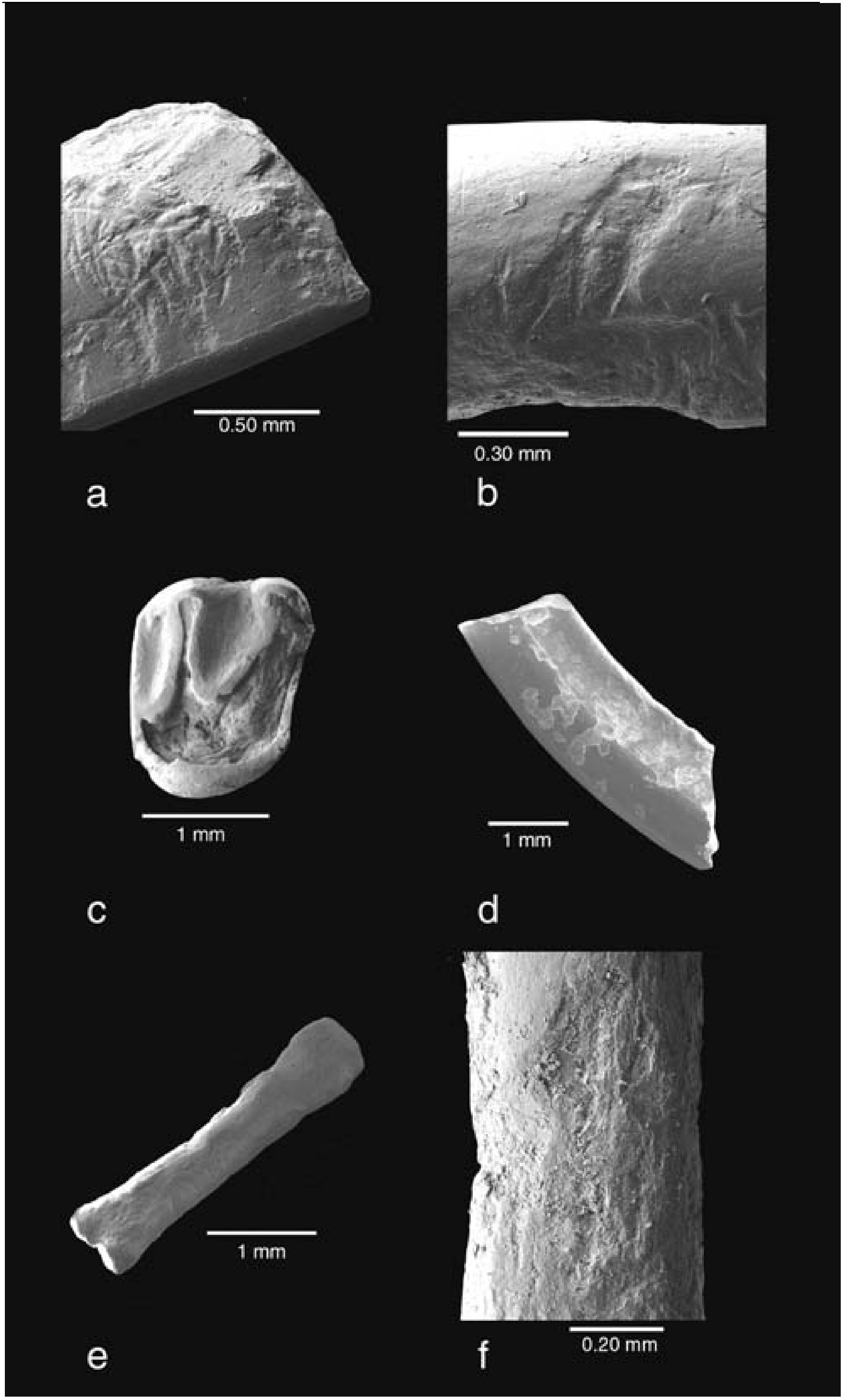
remains were exposed to meteorological agents for some time prior to burial. The low occurrence of abrasion also indicates that they experienced little transport.

Post-burial alterations

As in the case of the macromammals, once buried, micromammal remains still persist for some time in a biologically and chemically active environment. Root marks may be present in bone surfaces, but in BCV1 they are restricted to a few bones and incisors (figure 5.9.b). In contrast, chemical corrosion, consisting in the removal of parts of the surface of bones and teeth, is common, particularly in the case of incisors (more than 30 % affected) and postcranial bones (close to 22 %), while the cheek teeth are rarely affected (5 %). In some of the affected cheek teeth and incisors, the effects of corrosion are more important on the dentine than on the enamel (figure 5.9.c). In these cheek teeth, the dentine has been partially removed from the main cusps and, in some extreme cases, small holes are defined. In cave environments, similar alterations have been related to the existence of highly alkaline soils (Fernández-Jalvo & Andrews, 1992). In the rest of the material affected by chemical corrosion, dentine and enamel are equally damaged (Figure 5.9.d). On the postcranial bones, extensive pitting is observed on the whole surface of the bone, and it may be accompanied by the loss of some bone layers (Figures 5.9.e and 5.9.f).

5.2.3. Congruence with the sedimentary and early diagenetic environments

Our results indicate that both large and small mammals derive from several different sources; moreover, different accumulation processes have been identified. Predators do not represent the main agent, but play an important role, since they may be responsible for the presence of the primate individual in the assemblage. The *P. catalaunicus* specimen was hunted and/or scavenged very close to the deposit area and later buried. The rest of the large mammal remains mostly seem to derive from isolated bones scattered around the alluvial plain, next to the burial area. This would account for the differences in weathering and the preservation stages described, since the bones exposed at the floodplain may have remained there for variable amounts of time, depending on the case. However, it should be noted that weathering is more intense in the megaherbivore bones, which may have been exposed for a longer time. In megaherbivores, abrasion is intense in some bones, and there seems to be a hydraulic selection of the bones with lower density (mainly ribs). This suggests a greater transport in the latter case. The statistical analysis of bone distribution also shows the presence of some hydraulic transport affecting the macromammal remains other than those of *P. catalaunicus*.


0.50 mm
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1 mm
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d
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e
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0.20 mm

Figure 5.9. (previous page) SEM microphotographs of small mammal remains from BCV1 showing some surface alterations. (a) Broken rodent incisor showing some small irregular scratches that may be attributed to insect damage. (b) Root mark in a long bone diaphysis fragment of a small mammal. The same fragment shows small scratches and surface corrosion. (c) Left $M^{1/2}$ of *Spermophilinus bredai* showing preferential dissolution of dentine in worn areas, especially in the protocone. (d) Fragment of a lower incisor of a rodent showing post-depositional corrosion of both enamel and dentine. (e) Small mammal metapodial with post-depositional corrosion of the whole surface. (f) Detail of the same specimen showing the loss of some bone layers.

Concerning the micromammals, the action of predators seems generally absent. However, many of the recovered cheek teeth of the rare “cricetid” *Hispanomys* sp. show traces of heavy digestion, and its presence in the assemblage is inferred to be related to the predator contribution. In the case of other rare rodents (flying squirrels, dormice), their rarity is probably related to other factors that define the majority of the assemblage, such as their arboreal lifestyle and/or their population density, much lower than that of “cricetids” (French *et al.*, 1975). Abrasion only affects a few remains, so the whole micromammal assemblage is supposed to derive from areas close to the burial site.

All the remains would have been buried by a low energy muddy current flow and soon afterwards underwent some early diagenetic modifications related to its shallow burial in the alluvial deposits. In accordance to this early diagenetic setting, the chemical corrosion of a few of the micromammal remains is similar to that produced under moderate to relatively high-alkalinity soil conditions (Fernández-Jalvo & Andrews, 1992). The high carbonate solute contribution related to the groundwater would account for these alkaline conditions. The thin surrounding carbonate precipitates and calcite growing crystals on bone surfaces and cavities accord well with the diagenetic processes developed around the boundary between the phreatic and vadose zones (Polonio & López-Martínez, 2000). On the other hand, the bone fragments and also the megaherbivore bones show a fragile and dusty texture that accords better to decalcification in an at least slightly acid environment (Polonio & López-Martínez, 2000). This diagenetic alteration might have resulted either from the direct influence of meteoric waters in the upper vadose zone or from the action of acid waters related to organic matter rich soils.

5.2.4. Evaluation of the taphonomical biases and conclusions

The richness of the BCV1 fossiliferous level, is not exceedingly high, with a bone concentration per surface unit being five to ten times lower than the richest localities in the Abocador de Can Mata series (ACM), such as C3-Ak and C4-C2. This means that macromammal paleodiversity is relatively undersampled at BCV1, especially regarding carnivores and possibly several ungulate families. Accordingly the macromammal fauna from BCV1 does not provide much data for paleoenvironmental inferences.

In contrast, the abundant small mammal sample may provide a more adequate estimate of the existing paleodiversity. The small mammal remains do not seem to have experienced an important transport, and the action of predators is mostly rare, only significantly affecting *Hispanomys* sp. Thus, the material appears to be suitable for paleoecological analysis, since no major biases are detected. However, we must keep in mind that, for several reasons (low population density, life-history strategy, arboreal habitat…), some taxa (Sciuridae and Gliridae) are most probably underrepresented. Van Dam (1997) tried to correct in part this bias by adjusting the relative abundances of the different rodents in the sample. This correction is based on the classification of rodent families into three groups according to their life-history patterns, as devised by French *et al.* (1975). By calculating the mean life-expectancy for each group of rodents, and assuming attritional dead, "life assemblages" may be estimated from fossil ones. The adjustment of the relative abundances according to Van Dam (1997) does not seem adequate, especially taking into account that it requires many additional assumptions. Accordingly, the abundances of the several taxa will not be modified in the paleoecological analysis.

5.3. Paleoecology and paleobiogeography

The earliest hominoid record in Europe corresponds to MN 5, with the appearance of *Griphopithecus* in Germany and Turkey (Heizmann & Begun, 2001; Begun *et al*., 2002). This is slightly before or during the Langhian age, thus coinciding with the Middle Miocene climatic optimum (Wright *et al*., 1992; Zachos *et al*., 2001), a brief warm phase that lasted from 17 to 15 Ma. The first European hominoids encountered a warm and humid environment dominated by evergreen broad-leafed forests in Central Europe (Kovar-Eder, 2003). In the regions closer to the Mediterranean, such as the Iberian Peninsula, the environment was warm and also seasonally dry, as evidenced by pollen records (Bessedik, 1984) and macrofloral remains (Sanz de Siria, 1994). However, this warm climatic optimum was followed by a global, stepwise cooling and the progressive growth of a major ice-sheet on Antarctica, which would become more important during the Late Miocene (Zachos *et al*., 2001). The climatic deterioration implied the disappearance of some megathermic elements, a decrease in the abundance of evergreen woody taxa, and an increase in deciduous ones, especially at higher latitudes (Kovar-Eder, 2003).

These environmental changes, which had already started by the late Middle Miocene, surely affected the geographic distribution of great apes, given their ecological requirements. The ACM sites record part of this critical period, thus providing an environmental background that may help to explain the evolution and geographic distribution of great apes in southwestern Europe. Our goal in this section is to provide such environmental reconstruction, always focusing on BCV1. Since no plant remains have been recovered from ACM so far, our interpretation is entirely based on the mammal fauna, which is compared to chronologically close European fossil faunas.

5.3.1. The evidence provided by macromammals

Crusafont (1950b) first made some tentative inferences on the paleoenvironmental conditions of the classical Lower Hostalets assemblage on the basis of sedimentological and faunal data, suggesting less humid conditions than for Sant Quirze, the other then-known Vallès-Penedès locality from the Late Aragonian. Recently, Hernández Fernández *et al.* (2003) concluded that Lower Hostalets should be interpreted as a savanna environment. Certainly, the presence of some taxa such as tragulids and castorids in the ACM sites but not in Lower Hostalets, suggests some more humid and densely forested conditions in at least part of the ACM series. However, the faunal compositions of both sets of localities are not so strikingly different as to infer such open and more semi-arid conditions for Lower Hostalets. It should be always kept in mind that both ACM and Lower Hostalets are not localities in a strict paleontological sense, but rather a set of localities of somewhat different ages that span a considerable time interval of about a million years. In the case of Lower Hostalets, many remains came from locality Can Mata I, which is confidently attributed to the late MN 7+8 (see Alba *et al*., 2007 in press); the stratigraphic series of ACM, in contrast, ranges from the latest MN 6 to the late MN 7+8, although most currently sampled localities (including

BCV1) correspond to the early MN 7+8 (see Alba *et al.*, 2007 in press). Given the present state of knowledge, it is not possible to assess the several large mammal localities from ACM separately. Hernández Fernández *et al.* (2003) used a discriminant analysis employing the relative contribution in species of several selected groups to the total number of non-carnivore large mammals. A close inspection of the data employed by Hernández Fernández *et al.* (2003) reveals that the authors did not compute any of the suiform and primate species recorded from Lower Hostalets. This derives from the data compiled by Morales *et al.* (1999, their Table 6.1), who inadvertently omitted some of the taxa from Lower Hostalets (suoids, primates, rhinocerotids and chalicotheriids). These omissions were only partially emended by Hernández Fernández *et al.* (2003). We replicated the discriminant analysis in order to correctly classify Lower Hostalets (on the basis of emended data) as well as the ACM series taken as a whole (on the basis of our own data; see appendix 2.2. and Alba *et al.*, 2007 in press). The results (not shown) classify Lower Hostalets and ACM between tropical deciduous forests, which are characterized by tropical temperatures and a summer rain season. It is worth mentioning that Hernández Fernández *et al.* (2003) did not employ carnivore data on their analysis, because “this group, due to various ecological and taphonomical processes, is often underrepresented in paleontological sites and their use might introduce a non-quantifiable bias in the results” (ibid., p. 258, our translation from the Spanish original). It is reasonable to assume that primates might introduce a comparable, if not greater, taphonomical bias. Anyway, when the analysis is repeated by excluding primate taxa, a similar discrimination level is attained. Moreover, similar conclusions can be drawn, albeit ACM is now classified between evergreen tropical rain forests, which are characterized by higher levels of humidity throughout the year as compared to tropical deciduous forests. This kind of paleonvironmental characterization of fossil localities should be taken with great care: the analysis is based on a restricted number of recent localities, and it is likely that Miocene environments are not accurately described by this classification. Be that as it may, the analysis permits to reject the depiction of Lower Hostalets as a savanna. The existence of some paleoenvironmental differences between Lower Hostalets and the ACM sites is not unreasonable taking into account that they represent different intervals of time.

5.3.2. The evidence provided by micromammals

The small mammal fauna of BCV1 includes more than 400 isolated cheek teeth, representing up to 20 different taxa (eleven rodents, eight insectivores and one lagomorph). The presence of several arboreal taxa, albeit rare, indicates the existence of forest environments in the area of Hostalets de Pierola. As in the case of macromammals, this contrasts with previous paleoenvironmental interpretations based on the rodents of Lower Hostalets. As previously stated, Lower Hostalets is not a site in an strict sense, but rather represents an aggregate of material recovered from a more or less restricted stratigraphic interval that probably corresponds to the late MN 7+8 (Agustí, 1981a, 1981b, 1982a; Agustí & Gibert, 1982; Agustí *et al.*, 1984), thus being younger than BCV1. The small mammal fauna of Lower Hostalets is dominated by “cricetids”, but the most abundant genera is *Hispanomys* (including *Cricetodon lavocati*, see chapter 2), while *Eumyarion*, which is the most abundant one in BCV1, is completely absent (see chapter 2 and Alba *et al.*, 2007 in press). The dormice are also absent from Lower Hostalets, while the insectivores are diverse (up to, at least, six different genera). This faunal composition has been interpreted as indicative of an open environment, markedly different from other Late Aragonian sites from the Vallès area (such as Sant Quirze or Castell de Barberà), which are placed slightly to the north (Crusafont, 1950; Agustí *et al.*, 1984). At the present state of the art, two different interpretations are possible: either the environment within the Vallès-Penedès Basin was different in the northern and southern areas; or environmental conditions markedly changed in a relatively short interval of time.

In order to outline an environmental scenario that would account not only for the differences observed between the sites of the Vallès-Penedès Basin, but also between other Spanish and European localities, we compiled a qualitative database that is explored using multivariate ordination techniques. These are preferred because, in contrast to classification techniques such as cluster analysis, they do not force the data into groups but still reveal grouping structure if it exists (Shi, 2001; see also chapter 6). Ordination methods order localities as well as taxa in a multivariate space, so that their disposition may be related to some underlying biogeographical and/or ecological determinants. The database includes up to 19 sites dated to MN 7+8 and covering a geographical range from Central Spain to Poland. In the case of the several sites for which magnetostratigraphic data are not available, it is impossible to further precise their age, so it must be assumed that they are comparable to this regard. However, when age has been more accurately established, such as in the Calatayud-Daroca and Vallès-Penedès Basins, the role of temporal factors is discussed. Raw data for the analysis consist in a presence/absence matrix recording all the rodent and insectivore genera confidently identified in these sites. Uncertain determinations were not taken into account. Lagomorphs had to be excluded from the calculations since they have not been studied in many of the sites considered. We chose to use qualitative instead of quantitative data for two main reasons. First, sample sizes are not always comparable; just to cite an example, in Anwil (Switzerland) more than 3000 micromammal cheek teeth have been recovered, while in Can Missert (Vallès-Penedès Basin) the sample size is of 90 cheek teeth. Second, quantitative data are usually not available in the case of insectivores. The localities included and data sources are indicated in table 5.5.

We have performed a correspondence analysis (CA) (see chapter 6 and Hammer & Harper, 2006 for details) on our genera-presence-by-localities matrix. The scatter of points along the two first axes is shown in figure 5.10. For locality acronyms see table 5.5. The first axis explains about 20 % of the similarity (eigenvalue 0.39), while the second explains a 12 % (eigenvalue 0.23). Thus, the sum of the two first axes accounts for more than 30 % of the similarity between samples. Each of the following third and fourth axes accounts for 9 % of the similarity. It must be noticed that many variables are needed to explain the differences between the samples, and thus the reduction to only two or three is not possible. However, subsequent axes do not change the major pattern shown by the two first ones, with differences being related to the position of certain localities and particular taxa. It can be seen in figure 5.10.a that the first axis discriminates between the sites of Inner Spain and the rest of the localities. The Vallès-Penedès sites, including BCV1, are mixed with the Central-European and French sites.

acronym	locality	area	data sources
BCV1	Barranc de Can Vila 1	Vallès-Penedès Basin (Spain)	this paper
SQA	Sant Quirze A	Vallès-Penedès Basin (Spain)	chapter 6; Van den Hoek Ostende & Furió, 2005
CB	Castell de Barberà	Vallès-Penedès Basin (Spain)	Aguilar *et al*., 1979; Agustí *et al*., 1985; Van den Hoek Ostende & Furió, 2005
HI	Hostalets de Pierola (lower levels)	Vallès-Penedès Basin (Spain)	Agustí & Gibert, 1982; Aldana, 1991; Van den Hoek Ostende & Furió, 2005; Alba *et al*., 2007 in press
CM	Can Missert	Vallès-Penedès Basin (Spain)	Agustí *et al*., 2005
VF9	Villafeliche 9	Calatayud-Daroca Basin (Spain)	Daams *et al*., 1988; Van den Hoek Ostende & Furió, 2005
ALC2	Alcocer 2	Calatayud-Daroca Basin (Spain)	Daams *et al*., 1988; Van den Hoek Ostende & Furió, 2005
TOR	Toril	Calatayud-Daroca Basin (Spain)	Daams *et al*., 1988; Van den Hoek Ostende & Furió, 2005
LP5H	La Planas 5H	Calatayud-Daroca Basin (Spain)	Daams *et al*., 1988; Van den Hoek Ostende & Furió, 2005
SOL	Solera	Calatayud-Daroca Basin (Spain)	Daams *et al*., 1988; Van den Hoek Ostende & Furió, 2005
ESC	Escobosa de Calatañazor	Soria (Spain)	López Martínez *et al*., 1977; Sesé, 1977; Van den Hoek Ostende & Furió, 2005
LGM	La Grive M	Isère (France)	Mein & Ginsburg, 2002
LGL7	La Grive L7	Isère (France)	Mein & Ginsburg, 2002
LGL3	La Grive L3	Isère (France)	Mein & Ginsburg, 2002
I	Isère	Isère (France)	NOW database
ANW	Anwil	Bassel (Switzerland)	Engesser, 1972; Mein, 1990
SLS-C13	Sous le Stand C-13	Upper Freshwater Molasse (Switzerland)	Kälin *et al*., 2001
STEIN	Steinheim	southwestern Germany	Mein, 1990
OP2	Opole 2	southwestern Poland	Kowalski, 1990

Table 5.5. Sites included in the CA of figure 10a. The acronym used for each site in the figure is given, as well as the sources for the rodent and insectivore presence/absence data.

Figure 5.10.b represents the ordination of the genera present in the sites considered in the same multivariate space. As a rule of thumb, the genera characteristic of an association will plot in the vicinity of this association. It must be noted that most of the genera plot in the positive half of the first axis, while the negative part of this axis, where the sites of Inner Spain plot, is occupied by fewer genera, some of them being endemic to Spain. The genera typically interpreted as forest-dwellers (many dormice, flying squirrels, small-sized eomyids) plot at very high values of the first axis, while intermediate values are occupied by different kinds of “cricetids”. At first sight, this axis can be hence interpreted as a gradient of increasing humidity. If we inspect closely the genera present in each region (Inner Spain, Vallès-Penedès Basin, France and Central Europe), a clarifying pattern emerges (see table 5.6.). First, diversity seems to increase with latitude, and the number of genera present in Inner Spain is about the half of the number present at France or Central Europe. The small mammal assemblages from the Central Spanish basins are characterized by the presence of very few dormice genera as well as very few insectivores. In most of the sites, the insectivore fauna only includes two genera: the erinaceid *Galerix* and the soricid *Miosorex*. The arboreal dormice are usually absent or they are very rare. In contrast the ground-dwelling dormice, such as *Myomimus* or the endemic hypsodont dormouse *Armantomys* are

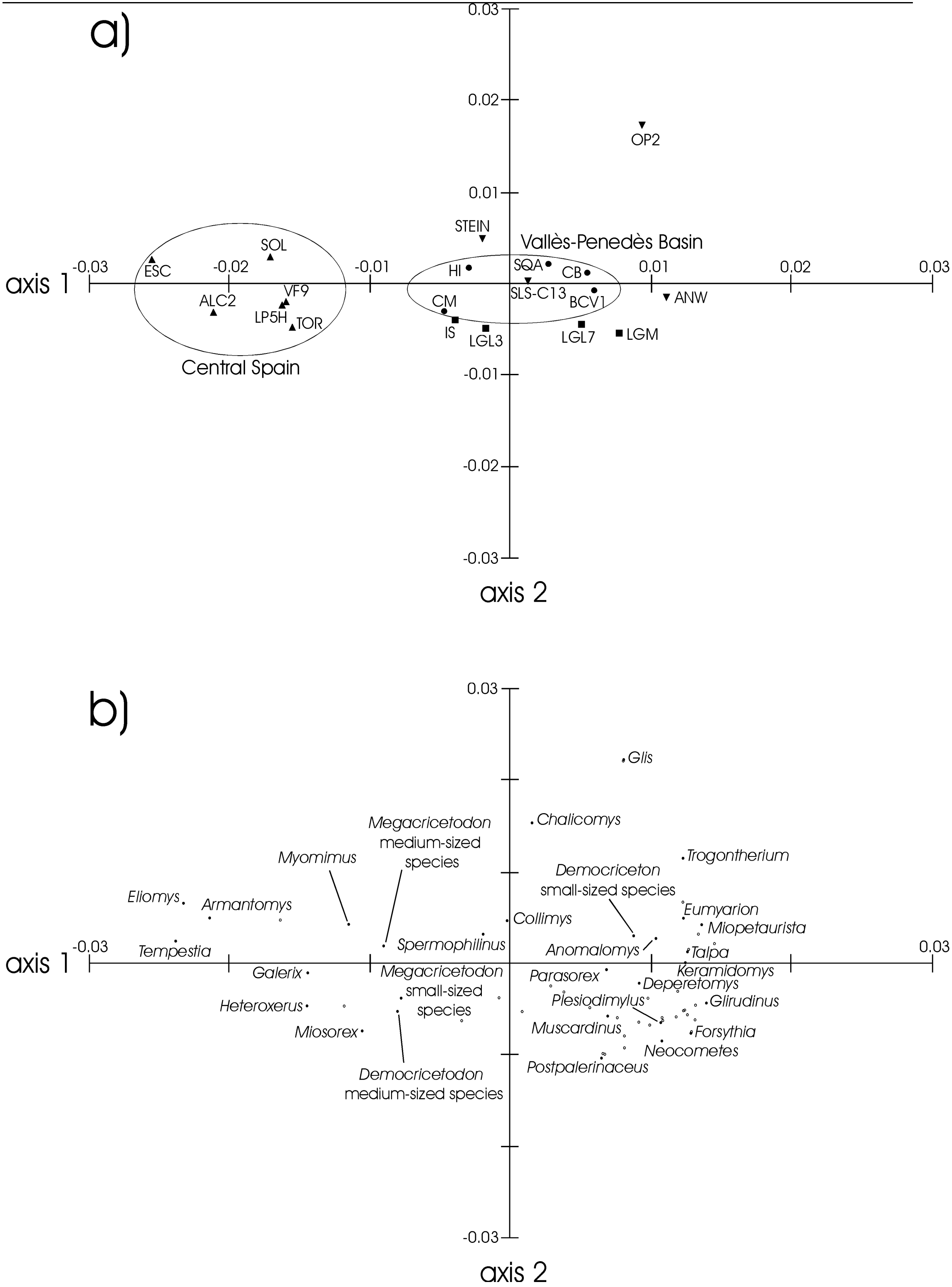

Figure 5.10. The two first axes of the Correspondence Analysis (CA). (a) Position of the localities considered (see table 5.5. for locality acronyms and data sources of the presence/absence data). The sites of the basins of Central Spain are indicated by a triangle; the sites from the Vallès-Penedès Basin by a circle; the sites from France by a Square; and the sites from Central Europe by a reversed triangle. (b) Plotting of the genera present in the sites considered. We have distinguished between small- and medium-sized *Megacricetodon* and *Democricetodon* species since opposite ecological preferences have been suggested for small- and medium-sized ones (Daams *et al.*, 1988). The name of certain characteristic genera is indicated, and their exact position in the CA is indicated with a filled circle. The position of the rest of the genera is marked with open circles. The scale of the axes is the same in (a) and (b).

common in some sites (for faunal preferences for the different genera of Gliridae we follow Van der Meulen & De Bruijn, 1982; see also discussion in chapter 6). The flying squirrels are also absent, and beavers are present in just one site. The fauna is dominated by medium-sized “cricetid” species, especially by *Megacricetodon ibericus* or closely related forms (see Daams *et al.*, 1988, Van der Meulen & Daams, 1992). In Central Europe and France up to 19 insectivore genera have been recorded, including families unknown in Inner Spain, such as talpids or dimylids. The flying squirrels are very diverse, and they may be represented by more than three genera in a single site. The arboreal dormice are also very diverse, while the ground dormice are absent. The ground squirrels are represented by several genera, *Spermophilinus* being the most common one. Eomyids, anomalomyids and plathacanthomyids are recorded both in France and Central Europe, though they are always rare. Regarding “cricetids”, there are a few genera present in Central Europe (*Collimys*, *Deperetomys*) that have not been recorded in France, but differences between both areas are minimal. Certain “cricetid” genera, such as *Eumyarion*, are not recorded in the Central Spanish basins.

According to the small mammal fauna, Inner Spain must be recognized as a distinct bioprovince characterized by a dryer climate. The Vallès-Penedès Basin appears as a zone of transition between both areas. This transitional character applies to its total generic richness (33 small mammal genera, while there are 18 in Inner Spain and up to 45 in France) as well as faunal composition. Rodent genera endemic to Spain, such as *Armantomys*, have not been recorded in the Vallès-Penedès. In contrast, many of the rodent genera recorded in France and Central Europe, but not in inner Spain, are recorded in the Vallès-Penedès, although their relative abundance is lower. These shared genera are usually considered forest dwellers. For example, the flying squirrels *Albanensia* and *Miopetaurista* are present in the Vallès-Penedès (and maybe *Blackia* as well), but the rest of genera recorded in France (*Hylopetes*, *Forsythia*) are absent. All the dormice genera recorded in Central Europe (excluding *Glis*, which in its turn has been neither cited from France) are present in the Vallès-Penedès , although some of them, such as *Bransatoglis*, are very rare. Eomyids and anomalomyids are also present in some sites, but no plathacanthomyid remains have appeared so far. The “cricetid” *Eumyarion* is present and may be very common in some sites such as Castell de Barberà or BCV1. Concerning the insectivores, the diversity is clearly lower, and some genera, such as the talpids *Urotrichtus* and *Scaptonyx*, are absent from the basin.

The fact that the Vallès-Penedès Basin was characterized by wetter environments than inner basins has been previously suggested (Agustí, 1978b, 1981 and 1990; Sesé, 1988; see also chapter 6). This contention is reinforced by the presence of primates, tapirids and other macromammals, which are unknown in Inner Spain. However, within the Vallès-Penedès Basin there appears to be some differences between the Late Aragonian sites. According to the CA (figure 5.10.), BCV1 and Castell de Barberà appear to have been more humid than Lower Hostalets and Can Missert. The rodent faunas of these latter sites are dominated by an association of the “cricetid” *Hispanomys* and the ground squirrel *Spermophilinus*. The medium-sized *Megacricetodon* species also tend to be abundant, while *Eumyarion*, small-sized “cricetid” species, dormice and the flying squirrels are very rare or totally absent. These sites may have been relatively dryer, since they plot closer to the localities of Inner Spain (figure 5.10.). Lower Hostalets and Can Missert are placed in the late MN 7+8 (see chapter 2 and Alba *et al.*, 2007 in press) while BCV1 and probably Castell de Barberà and Sant Quirze are older. This would indicate that paleoenvironmental

genus	Vallès-Penedès	Inner Spain	France	Central Europe
Parasorex	1	-	-	1
Postpalerinaceus	-	-	**1**	-
Amphechinus	-	1	-	-
Mioechinus	-	-	1	1
Lanthanotherium	1	-	1	1
Galerix	1	**1**	1	1
Proscapanus	1	-	1	**1**
Talpa	1	-	**1**	1
Urotrichus	-	-	1	-
Scaptonyx	-	-	1	1
Desmanella	1	-	1	1
Blarinella	-	-	1	-
Paenelimnoecus	-	-	1	-
Lartetium	-	-	1	-
Dinosorex	1	-	1	1
Miosorex	1	1	**1**	-
Metacordylodon	1	-	1	1
Plesiodimylus	1	-	**1**	1
Heteroxerus	1	1	1	-
Palaeosciurus	-	-	1	1
Tamias	-	-	1	-
Spermophilinus	**1**	1	**1**	1
Albanensia	1	-	1	1
Blackia	1	-	1	1
Hylopetes	-	-	1	-
Forsythia	-	-	1	1
Miopetaurista	1	-	1	1
Trogontherium	1	-	-	1
Steneofiber	-	-	-	1
Chalicomys	1	1	-	1
Armantomys	-	1	-	-
Eliomys	-	1	-	-
Glirudinus	1	-	1	1
Glis	-	-	-	1
Muscardinus	**1**	1	**1**	1
Myoglis	1	1	1	1
Microdyromys	1	1	**1**	1
Paraglirulus	1	-	1	1
Miodyromys	1	-	1	1
Myomimus	-	1	-	-
Tempestia	-	1	-	-
Bransatoglis	1	-	1	1
Eomyops	1	-	1	1
Keramidomys	1	-	**1**	1
Cricetodon	1	**1**	**1**	1
Lartetomys	-	-	1	-
Deperetomys	-	-	-	1
Hispanomys	1	-	1	-
Collimys	-	-	-	1
Eumyarion	**1**	-	1	1
Democricetodon small-sized species	1	1	**1**	**1**
Democricetodon medium-sized species	**1**	1	**1**	1
Megacricetodon small-sized species	1	1	**1**	1
Megacricetodon medium-sized species	1	**1**	**1**	1
Neocometes	-	-	1	1
Anomalomys	1	-	**1**	**1**
GENERA RICHNESS	35	18	45	40

Table 5.6. (previous page) Occurrence of the rodent and insectivores genera from the sites included in the Correspondence Analysis (CA) (see also figure 5.10. and table 5.5.) in the different areas considered. 1 indicates presence, dash absence. Bold indicates the presence of the corresponding genus in all the sites of the considered area. The last row shows the total number of genera recoreded in each region. Note that genera richness, especially in the case of the insectivores, appears to increase at higher latitudes.

conditions in the Vallès-Penedès Basin were relatively dryer in the latest MN 7+8 than in previous times.

Paleobotanical data further support our interpretations. As previously noted, during the late Middle Miocene a large part of Central Europe was covered by mixed mesophytic forests, including a significative proportion of deciduous forms but also with a hard core of evergreen ones (Kovar-Eder, 2003). Unfortunately there is no direct paleobotanical evidence in the Vallès-Penedès Basin for the same timespan. The macrofloral remains and palynological assemblages from the site of Montjuïc, in Barcelona, next to the Vallès-Penedès Basin, may provide a glimpse of the environments that would have existed in the area. This flora, which has been assigned to the Serravallian (Sanz de Siria, 1994; Gómez Gras *et al*., 2001) and would be approximately equivalent to MN 6 plus MN 7+8, records the occurrence of warm temperate[30] evergreen forests close to the coastal areas. The paleofloral assemblage includes some taxa indicating a warm climate (*Cinnamomum*, *Daphnogene*, *Laurus*) and also an important proportion of deciduous trees (*Acer*, *Populus*, *Juglans*, *Salix*). This forest assemblage appears to have been similar to that existing in northern latitudes, although mean annual temperatures were probably higher in the Vallès-Penedès (Sanz de Siria, 1994). In contrast, the palynological data from the Torremormojón section (Late Aragonian of the Duero Basin, West-Central Spain) revealed the existence of a temperate, open woodland in that area (Rivas Carballo & Valle, 1986; the age estimation for the locality of Torremormojón 9 is taken from García Moreno, 1987). On the basis of the limited available paleobotanical information, Inner Spain is hence also interpreted as a warm but dryer area, which was probably not suitable for some macromammal taxa such as primates. Accordingly, the Vallès-Penedès Basin may well represent the southernmost limit of the biogeographic range of this mammal group in Western Europe during the Middle Miocene.

5.4. Conclusions

The taphonomical study of the micro- and macrovertebrates from the Barranc de Can Vila 1 (BCV1) site allows us to infer different taphonomical agents involved in the accumulation. All the remains of *P. catalaunicus* are attributable to a single individual. Moreover, they are spatially associated and randomly oriented, suggesting little transport. Given the fact that carnivore marks are present in some of the primate bones, predation is proposed as the main accumulation agent. In contrast, predation marks are mostly absent in other macromammal remains. These seem to derive from isolated bones scattered around the alluvial plain, next to the burial area. This would account for the differences in weathering and the preservation stages that they present. The statistical analysis of bone distribution shows the existence of some hydraulic transport affecting the macromammal remains other than those of *P. catalaunicus*.

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[30] Following the climatic classification by Walter (1970) warm temperate climates refer to those climatic regimes characterized by the absence of cold winters and by high degrees of humidity, specially on summers. Warm temperate forests are evergreen forests characterized by the presence of several kinds of trees and no clear dominance of any of them. Deciduous taxa may also be present.

Concerning the micromammals, the rare occurrence of alterations produced by digestion is quite a remarkable fact, since predation has been proposed as the main accumulation agent for small mammal remains in many sites. Only a minor proportion of teeth and bones show traces of digestion, although in the case of *Hispanomys* sp. a significant number of the recovered cheek teeth are heavily digested. The presence of this hamster, which is very rare, should be related to predator contribution to the assemblage. Other rare micromammals such as flying squirrels or dormice do not show any trace of digestion, and their rarity in the assemblage must be related to other factors, such as their lifestyle and/or to life-history aspects. Evidences of transport are very rare. The remains were buried in water-saturated sediments and during early diagenesis, characterized by changing pH conditions, they experienced processes of corrosion, encrusting and crystal growing that affected most of the remains. The large mammal fauna from BCV1 does not provide an adequate estimate of paleodiversity, while the large sample of micromammals is considerate adequate for paleoecological analyses, since it more accurately reflects paleodiversity and taphonomical biases (transport, predation) do not seem to have been important.

In contrast with previous paleoenvironmental reconstructions, which had interpreted the Late Aragonian levels of els Hostalets de Pierola as a savanna, the large mammal fauna from the ACM series indicates the presence of a relatively humid warm temperate forest environment at least during certain time intervals. Concerning the composition of the small mammal fauna from BCV1, correspondence analysis, in particular, shows that BCV1 and all the remaining small mammal localities from the Late Aragonian of the Vallès-Penedès Basin are closer to those from France and Central Europe than to other Spanish localities. The higher diversity of insectivores, arboreal dormice plus the presence of flying squirrels confirms that the environment was more humid in the Vallès-Penedès than in inner Spain basins. The latest Aragonian sites of the Vallès-Penedès Basin, such as Can Missert, appear to have been characterized by more open environments, closer to those of Central Spain. Paleobotanical data suggest that the evergreen warm temperate forests present at higher latitudes extended to the Vallès-Penedès Basin during the Late Aragonian, in contrast open woodland environments seem to have existed in inner Spain, thus precluding the spread of hominoid primates into that area.

Chapter 6

Ecogeographical stability and climate forcing in the Late Miocene (Vallesian) rodent record of Spain

6.1. Introduction

The Vallesian, that is, the period of time comprised between 11.1 Ma and 8.7 Ma, is a crucial moment in the evolution of the terrestrial faunas in Europe. The beginning of this period is characterized by the entry and quick dispersal throughout Eurasia of the hipparionine horses (Garcés *et al.*, 1997a; see also chapter 2). From this time on, the so-called “*Hipparion*-faunas” characterize the terrestrial ecosystems of the late Neogene. After the entry in Western Europe of hipparionine horses, a major turnover event is recorded at the Early-Late Vallesian boundary (Agustí & Moyà-Solà, 1990; Moyà-solà & Agustí, 1990; Agustí *et al.*, 1999; see also chapter 7). The so-called Vallesian Crisis determined the extinction of several mammalian taxa characteristic of the previous Middle Miocene faunas. This event appears as a true extinction event in Western Europe, while in Anatolia it coincides with a significant turnover. It has also been suggested that the Vallesian Crisis is noted in Central European mammal faunas (Fortelius *et al.*, 1996b; Franzen & Storch, 1999). The end of the Vallesian and the beginning of the Turolian is also a significant boundary, which records a new turnover pulse, and the extension to the west of the bovid and giraffid dominated faunas that characterize the so-called “sub-Paratethyan” (Bernor, 1984) or “Greek-Iranian” province (De Bonis *et al.*, 1992) (see chapter 7).

Therefore, the Vallesian can be regarded as a critical period when the highly diversified Middle Miocene forest mammalian faunas were replaced by dry-adapted, open country faunas in the latest Miocene. As we have seen, this change was not a sudden one, and seems to have been accomplished throughout a number of punctuated events. In this chapter, we analyze the evolution of the rodent faunas in the three basins of the Iberian Peninsula that present a more detailed record of the complete succession, ranging from the Late Aragonian to the latest Vallesian. The changes in the composition of rodent taxocenoses are related to different environmental contexts.

6.2. Material and methods

6.2.1. Material and basic assumptions

In our analysis we include 36[31] localities fairly rich in rodent teeth from three Iberian basins (Calatayud-Teruel, Duero and Vallès-Penedès). We have chosen basins presenting a reasonably complete record for the studied time-span (between 12.8 and 8.7 Ma). However, the record is poor for the Duero Basin, so results in this case should be taken with caution. The best rodent record for this time-span is the one of the Calatayud-Teruel Basin; so more than half of the localities included in the present paper correspond to this one. Having more than 50 rodent cheek teeth has been the main criterion for the selection of the localities. Other studies consider that the minimum sample size to include a locality in the analysis should exceed at least 100 cheek teeth

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[31] In an earlier version of this chapter Barranc de Can Vila 1 (BCV1) was not included in the analysis because a study of the rodent fauna was on course. In the present version this site has been included, and all the calculations have been repeated.

(see Van der Meulen & Daams, 1992). In the case of the Aragonian rodent assemblages of the Calatayud-Daroca Basin, Daams *et al*. (1999c) have shown that in most cases species richness and abundance does not vary significantly from test samples (which included between 50-250 first and second molars approximately) and final samples (which usually exceed 1000 first and second molars). More sampling only added one or two species with an abundance of less than 1 % in the assemblage. Similar studies on the effects of sample size on species richness and abundance have not been performed in the other basins, and they are out of the scope of this work, thus we will assume that 50 cheek teeth is an adequate sample in every case. Since our analysis will focus on the most abundant species the use of sample size smaller than about 100 cheek teeth is not a critical issue. Furthermore less than half of the localities considered in our study have a sample size of less than 100 cheek teeth (see fig. 6.1.). In each locality we have considered the relative abundances of all the genera present. Abundance data for the Calatayud-Teruel Basin are based on the number of first and second molars and are taken from different sources including the works by Daams *et al*. (1988), Van Dam (1997) and Van Dam & Weltje (1999). Additional data were compiled by one of us (I. C-V). Abundance data from the Duero Basin are taken from García Moreno (1987) and are based on the total number of cheek teeth. One of us (J. A.) compiled the relative abundances of rodent genera for most of the localities from the Vallès-Penedès Basin. In this last case we also considered the total number of cheek teeth. Since some rodents have premolars (in our case the Gliridae, Sciuridae, Castoridae and Eomyidae) and others not ("cricetids", Muridae and Anomalomyidae in the localities considered), the abundance of the first is somewhat over-represented[32]. However, in most of the cases these rodents do not define a major part of the assemblage. We have only taken into account the material recovered by sediment washing and sieving, discarding the rodent remains found during macropaleontological excavations. For this reason we have excluded large beavers (such as *Chalicomys*) because in many cases the material was stored within the macromammal collections and it was recovered using different methods.

All the localities are framed in comparable sedimentary contexts, being placed in layers of alluvial/colluvial origin. Nevertheless, this fact does not imply isotaphonomy. A detailed taphonomic study would be required before one could assume equality in the taphonomic processes for all the sites. In the discussion of the results we will assume similar taphonomic conditions (or similar taphonomic biases) for all the localities, thus the validity of our conclusions is ultimately linked to this point and may be compromised if major variations in these parameters are shown. The samples are supposed to present some degree of time and spatial averaging and as a direct consequence of these phenomena the data on the relative abundances of the different taxa may not exactly reflect the relative abundances of those taxa as they were in the

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[32] We have compared the minimum and maximum number of individuals in the case of BCV1 (see chapter 4), and we have seen that the pattern of species abundances is not significantly different in each case. When calculations are repeated omitting the premolars and the third molars (results not shown) only a slight decrease in the abundance of the sciurid *Spermophilinus* is detected. Similar comparisons have not been attempted in other sites, however, the results in the case of BCV1 suggest that the pattern of abundances when the total number of cheek teeth is considered instead of just first and second molars is not significantly different if rodents with premolars do not constitute an important portion of the assemblage.

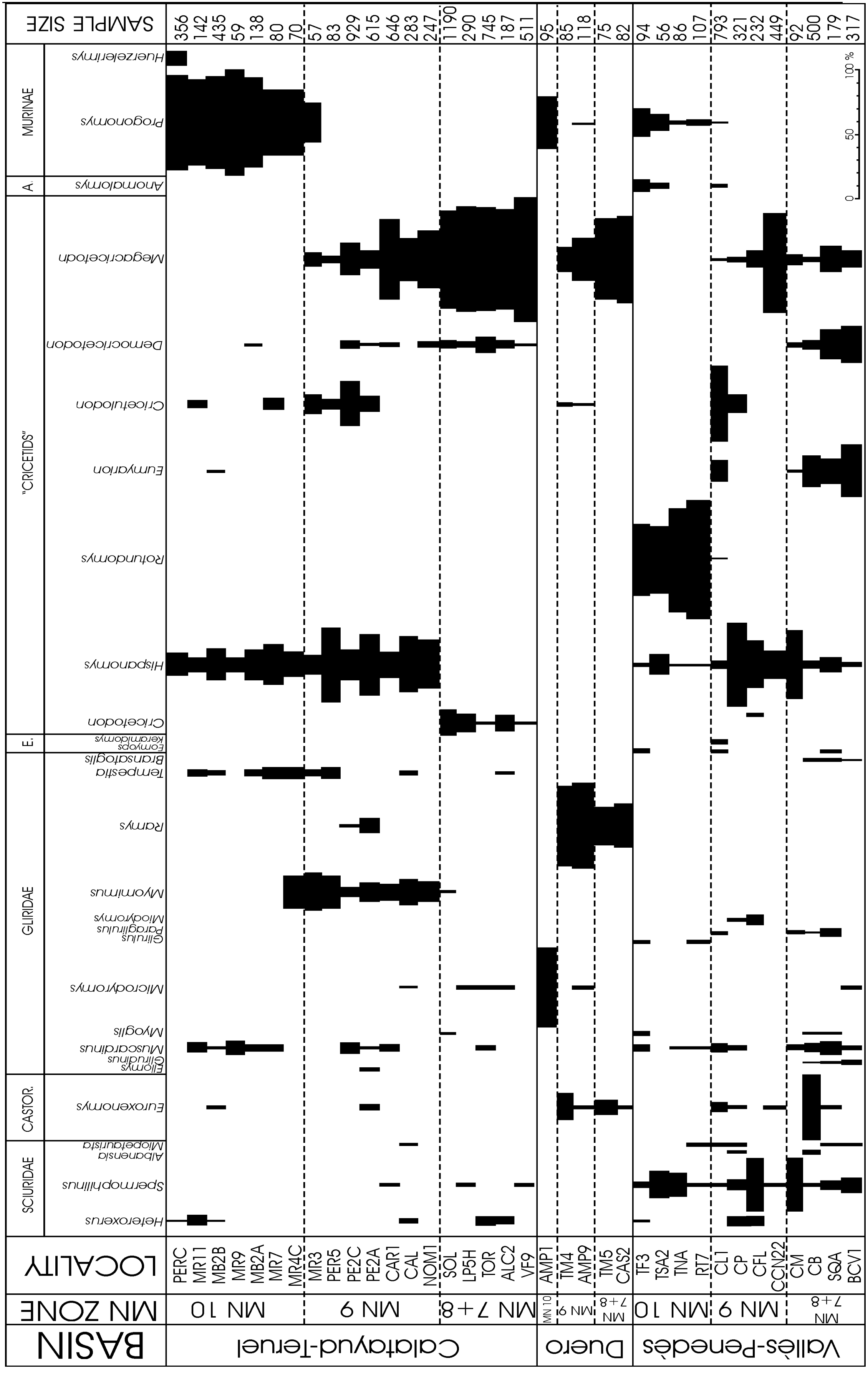

BASIN
MN ZONE
LOCALITY
SAMPLE SIZE
Calatayud-Teruel
Duero
Vallès-Penedès
MN 10
MN 9
MN 7+8
SCIURIDAE
CASTOR.
GLIRIDAE
E.
"CRICETIDS"
A
MURINAE
Heteroxerus
Spermophilinus
Albanensia
Miopetaurista
Euroxenomys
Eliomys
Glirulus
Muscardinus
Myoglis
Microdyromys
Glirudinus
Paraglirulus
Miodyromys
Myomimus
Ramys
Tempestia
Bransatoglis
Eomyops
Keramidomys
Cricetodon
Hispanomys
Rotundomys
Eumyarion
Cricetulodon
Democricetodon
Megacricetodon
Anomalomys
Progonomys
Huerzelerimys
PERC
MR11
MB2B
MR9
MB2A
MR7
MR4C
MR3
PER5
PE2C
PE2A
CAR1
CAL
NOM1
SOL
LP5H
TOR
ALC2
VF9
AMP1
TM4
AMP9
TM5
CAS2
TF3
TSA2
TNA
RT7
CL1
CP
CFL
CCN22
CM
CB
SQA
BCV1
356
142
435
59
138
80
70
57
83
929
615
646
283
247
1190
290
745
187
511
95
85
118
75
82
94
56
86
107
793
321
232
449
92
500
179
317
0
50
100 %

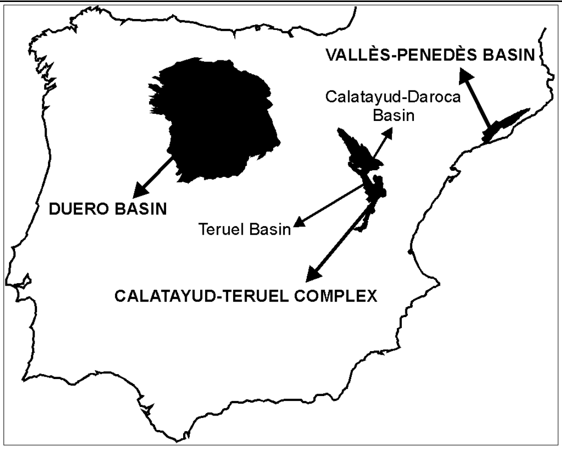
Fig. 6.1. (previous page) Percentages of rodent genera in the latest Aragonian and Vallesian succession of the considered basins. Localities are classified in basins and given in temporal sequence. Sample size is based in the number of first and second molars in the case of Calatayud-Teruel Basin and in the total number of molars in the case of the Duero and Vallès-Penedès Basin. See table 6.1. for locality acronyms.

biocenosis. If the objective of this study was the accurate reconstruction of the life assemblage time and spatial averaging should be corrected in any way. In contrast, we are just interested in showing meaningful differences between the localities considered, and such corrections may not be necessary for this kind of study. Furthermore, it has been suggested that time-averaged assemblages do indeed reflect a time-weighted average of environmental conditions during the entire interval of time (Kowaleski *et al.*, 1998). On one hand, fossil assemblages with little or no time-averaging provide valuable glimpses of ancient communities sampled as an ecologist might sample a living community today (Kidwell & Bosence, 1991). On the other hand, time and spatial averaged assemblages provide a longer record and a broader view of the environmental conditions in an area.

The ages of the sites from the Calatayud-Daroca area are taken from Daams *et al.* (1999a) and the numerical ages for the localities of the Teruel area are from Krijgsman *et al.* (1996), Garcés *et al.* (1997b) and Van Dam *et al.* (2001). Dating for the Duero Basin was obtained by interpolation based on evolution of rodent faunas (except the numerical ages of the localities in the Torremormojón section, which are based on the work by Krijgsman *et al.* (1996)). Numerical ages based on magnetostratigraphical correlation for some of the localities of the Vallès-Penedès Basin are available: Creu Conill 22 (Garcés *et al.*, 1996; Garcés *et al.*, 1997a); Can Llobateres 1 (Garcés *et al.*, 1996; Agustí *et al.*, 1996); Rubí-Terrassa 7 and Torrent de Febulines 3 (Garcés *et al.*, 1996; Agustí *et al.*, 1997). The numerical age of the remaining sites has been interpolated according to unpublished bio- (see chapter 2) and magnetostratigraphical data. See table 6.1. for the sites included, their geographic position and assigned age. The database used in this chapter is available from the author upon request.

6.2.2. Transformation of the data

The analyses are carried at the genus level. Some authors have claimed that ecological interpretations based on genera or higher taxonomical groups are bound to be unreliable and that they should be based on taxonomical units at species level (for an example focusing in rodent paleontology see Martín-Suárez *et al.* (2001). It is assumed that ecological preferences may not have been the same for all the species in a genus. However, carrying the analysis at the species level would have added several methodological problems. First many species would be absent in a several sites; and second the analysis would have shown many differences that are attributable to temporal factors and would have obscured those due to ecological differences. A usual procedure in carrying paleoecological analysis based on rodents begins with the definition of ecological groups. These groups may simply discriminate between forms adapted to open or closed environments as well as ubiquists (Van de Weerd & Daams, 1978; Daams *et al.*, 1988), or may consist in several complex groups (Van Dam & Weltje, 1999). Justification and definition of ecological grouping is probably correct in many cases and offers the advantage of providing a database for a taxon-free analysis. However a large number of assumptions must be made before carrying the calculations. In a considerable number of cases broad ecological preferences of rodents extend beyond the species level into the genus and even the subfamily/family level (for



locality	locality acronym	MN zone	age
DUERO BASIN			
Casasola 2	CAS2	MN 7+8	11.5*
Torremormojón 5	TM5	MN 7+8	10.7
Ampudia 9	AMP9	MN 9	10.2*
Torremormojón 4	TM4	MN 9	10.2
Ampudia 1	AMP1	MN 10	9.0*
CALATAYUD-TERUEL COMPLEX			
Calatayud-Daroca Basin			
Villafeliche 9	VF9	MN 7+8	12.85
Alcocer 2	ALC2	MN 7+8	12.7
Toril	TOR	MN 7+8	12.6
Las Planas 5H	LP5H	MN 7+8	12.52
Solera	SOL	MN 7+8	11.75
Nombrevilla 1	NOM1	MN 9	11.0
Carrilanga 1	CAR1	MN9	10.5
Pedregueras 2A	PE2A	MN9	10.25
Pedregueras 2C	PE2C	MN9	10.0
Teruel Basin			
Casas Altas	CAL	MN9	10.7
Peralejos 5	PER5	MN9	9.7
Masía de la Roma 3	MR3	MN9	9.7
Masía de la Roma 4C	MR4C	MN10	9.5
Masía de la Roma 7	MR7	MN10	9.4
Masía del Barbo 2A	MB2A	MN10	9.4
Masía de la Roma 9	MR9	MN10	9.4
Masía del Barbo 2B	MB2B	MN10	9.2
Masía de la Roma 11	MR11	MN10	9.2
Peralejos C	PERC	MN10	8.8
VALLÈS-PENEDÈS BASIN			
Barranc de Can Vila 1	BCV1	MN 7+8	12.0*
Sant Quirze A	SQA	MN 7+8	11.5*
Castell de Barberà	CB	MN 7+8	11.3*
Can Missert	CM	MN 7+8	11.2*
Creu Conill 22	CCN22	MN9	11.1
Can Flaquer	CFL	MN9	10.6*
Can Ponsic	CP	MN9	10.2*
Can Llobateres 1	CL1	MN9	9.7
Autopista Rubí-Terrassa 7	RT7	MN10	9.6
Trinxera Nord Autopista	TNA	MN10	9.2
Trinxera Sud Autopista 2	TSA2	MN10	9.2
Torrent de Febulines 3	TF3	MN10	8.7

* = numerical ages interpolated for this work

Table 6.1. Localities included in our analysis. Map (upper left corner) shows the geographic position of the basins compared. We have assigned an absolute age to each locality. Numerical ages interpolated for this work are marked with an asterisk (see text for details). The acronyms of the localities correspond to those of figures 6.1, 6.2a and 6.4.

example all living Pteromyinae inhabit densely forested environments, as well as most of the living Glirinae). That is the reason why the ecological grouping carried out by many authors sometimes may closely follow taxonomy (see for example Van Dam & Weltje, 1999). Since we are interested in detecting large-scale ecological differences rather than providing a detailed reconstruction of the environment, the genus level is considered adequate for our analysis. Furthermore the use of genera reduces the assumptions that have to be made before any statistical analysis is attempted. Nonetheless, as we have comented above, carrying out the calculations at this level (or at the species level) introduces a problem: some differences shown by the analysis are likely to be biassed because of temporal factors. Such kind of situations is discussed *a posteriori*.

Genera abundances are expressed as percentages and not as numbers of molars. That is, depending on the situation, the number of cheek teeth of a genus divided by the total number of cheek teeth in the sample, or in the Calatayud-Teruel sites, the number of first and second molars of a genus divided by the total number of first and second molars. Applying this transformation the differences in absolute sample size are removed and the samples become comparable (Clifford & Stephenson, 1975). This procedure can be useful when differences in abundances between localities seem to have a sedimentologic/taphonomic and not an ecological cause (Etter, 1999). The resulting genera-abundance-by-localities-matrix was used as input for the Correspondence Analysis described in 6.2.3. (carried out using the program PAST 1.65 (Hammer *et al*., 2001).

6.2.3. Ordination using Correspondence Analysis

Multivariate ordination and classification techniques have become very popular in paleobiogeographic and paleoecological studies. These techniques are used to explore the data matrix in order to search for some underlying pattern. In our case we will use ordination techniques to group and order the localities according to the composition of their rodent assemblage. The most widely used classification method is perhaps cluster analysis, which is an heuristic classification technique devised to recognize discrete groups within a dataset. Thus, cluster analysis implicitly assumes the existence of discrete groupings, and because of this underlying assuption it always forces data into groups, even if the data points are randomly distributed (Shi, 2001). Ordination methods will order both samples and taxa in a multivariate space so that their disposition may be related to some underlying biogeographical or ecological determinants. In this treatment, no assumption is made about the existence of discrete groups in the data. Instead ordination assumes continuity, but still reveals grouping structure where it exists (Shi, 2001). The ordination method mostly used by mammal paleontologists is principal components analysis (PCA) (see Van der Meulen & Daams (1992) for an example dealing with rodent paleocommunities). Correspondence analysis (CA) is another ordination technique, somewhat similar to PCA, but for counted or discrete data. Correspondence analysis can compare associations containing counts of taxa. Also, CA is more suitable if it is expected that species have unimodal responses to the underlying parameters, that is they favor a certain range of the parameter and become rare under lower and higher values (this is in contrast to PCA, which assumes a linear response) (Hammer *et al*., 2001; Hammer & Harper, 2006). CA tries to position both samples and taxa in the same space maintaining correspondence between the two. The algorithm used is taken from Davis (1986). CA was performed on our genera-abundance-by-localities-matrix and results are displayed in figure 6.2.

6.2.4. Analysis of similarities (ANOSIM)

Once the CA has ordered or grouped the localities according to their faunal compositions we have to test if the differences showed by the CA are statistically significant. This important issue may be assessed using ANOSIM (ANalysis Of SIMilarities), which needs an *a priori* definition of the groups to be compared, that in our case will derive of the results of the CA. ANOSIM is based on the distances between all pairs of samples, computed from a distance index of choice. We have choosen the Bray-Curtis distance measure (*BC*; Bray & Curtis, 1957), which is highly recommended because it places more emphasis on the difference between the common species (Bray & Curtis, 1957; Faith *et al*., 1987; Etter, 1999). ANOSIM works by comparing within group and across-group distances; thus, if two groups were different in their taxonomic compositions, we would expect the distances within each group to be small relative to the distances across groups. A test statistic R is constructed based on this idea (see Hammer & Harper, 2006 for a brief description of the details on calculation), and its significance is computed by permutation of group membership (we will compute 5000 permutations). R is given together with the probability of all groups being equal.

We have used ANOSIM not only to test for significant differences (at $p = 0.05$) between the groups recognized by the CA, but also within these groups. When one of the groups includes localities belonging to different basins, we have used ANOSIM to test if there are significant differences between the sites included in this group according to their geographic position. Calculations have been carried using the software PAST 1.65 (Hammer *et al*., 2001).

6.2.5. Correlation tests

The similarity between samples may be the result of the existence of similar environments, but the age of the sites may play an important role. In order to explore the influence of temporal patterns in the results of the CA we have tested the correlation between the age of the sites and their eigenvalue in the two first axes of the CA. Since the data are obviously not normally distributed we have proceeded using non-parametric tests. We have calculated two correlation coefficients: Spearman rank-order correlation coefficient and Kendall's τ (results are displayed in table 6.4.; the calculations have been carried using PAST 1.65, see Hammer & Harper (2006) for a brief description of the tests).

6.3. Results and interpretation: Rodent Paleocommunity Types

6.3.1. Ordination and classification of the rodent assemblages

Figure 6.2.a shows the two first axes of a CA performed over a genera-abundance-by-localities-matrix. For locality acronyms see table 6.1. The first axis explains close to 18 % of the similarity between samples (eigenvalue 0.81), while the second axis accounts for about 16 % of the similarity (eigenvalue 0.72). The following third and fourth axes explain close to a 12 % and an 11 % of the similarity. It must be

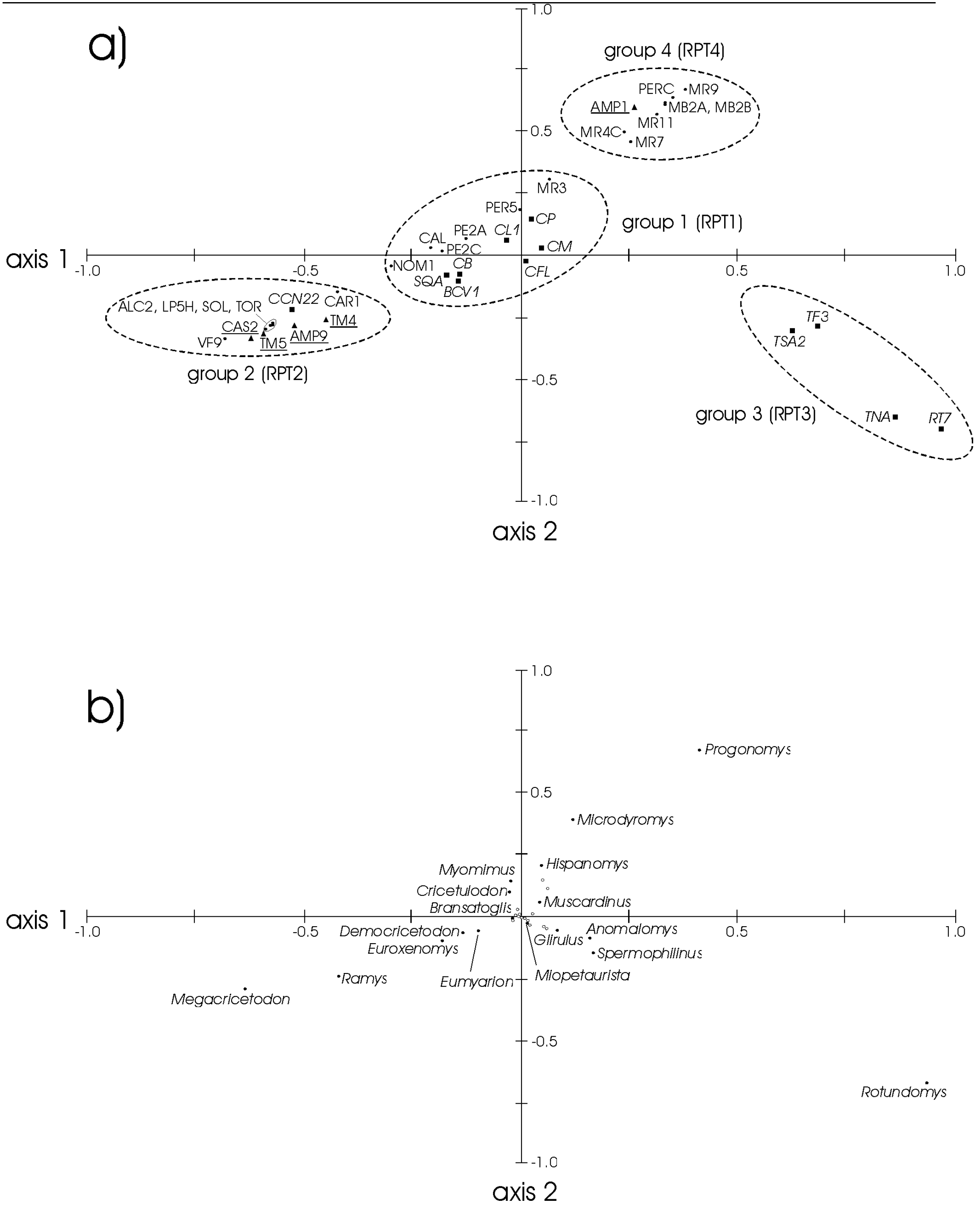


Figure 6.2. The two first axes of the Correspondence Analysis (CA). a) Position of the localities considered (see table 6.1. for locality acronyms). The position of the localities from the Calatayud-Teruel Basin is indicated with a full circle; for the Vallès-Penedès it is indicated with a square and the acronym is in italics; for the Duero we use a triangle and the acronym is underlined. The main groups (= rodent paleocommunity types or RPTs) that can be recognized are encircled and numbered (see text for details). b) Plotting of the rodent genera present in the sites considered. The genera typical of an association plot in the vicinity of that association. Note that most of the genera plot near the origin of coordinates. The name of certain characteristic genera is indicated, and their exact position in the CA is marked with a filled circle. The position of the rest of the genera is marked with open circles. The scale of axis 1 and axis 2 is the same in both figures.

noticed that there are many variables to explain the main differences observed between samples, and that the reduction to only two or three is not possible. However, axes 3 and 4 show approximately the same pattern exhibited by axis 2, so they can be assimilated to this one. In fact, many variables may be related to the first and more important axes. In our discussion only axes 1 and 2 have been considered. The sum of these two axes explains about 35 % of the similarity between samples. In the multivariate space represented by the two first axes of the CA the localities appear to be clustered in four groups instead of being arranged in a continuum. Group 1 and 2 include all the Late Aragonian and Early Vallesian sites of our analysis, and mix localities from the three basins. Group 3 includes only four localities, all from the Late Vallesian of the Vallès-Penedès Basin (TNA, TSA2, TF3 and RT7). In group 4 we find all the Late Vallesian localities from basins other than Vallès-Penedès. We have performed an ANOSIM over the groups recognized by the CA. The results show significant differences (probability of equality always lower than 0.05) between all possible pairs (see table 6.2.).

In figure 6.2.b the rodent genera included in our analysis are plotted in the two first axes of the CA. Filled circles and a corresponding label indicate the position of some selected genera, while the remaining genera are represented by open circles and are not labeled. The genera characteristic of a certain locality group distinguished by the CA plot in the vicinity of this group. As becomes evident from figure 6.2.b, most of the genera plot near the origin of both axes, coinciding with some of the localities of group 1. Therefore a diverse association characterizes group 1 sites. This situation contrasts with the composition of the remaining groups, which shows a less diverse association dominated by one or a few rodent genera.

Table 6.2. Results of the ANOSIM (using Bray-Curtis distance and bootstrapping by 5000) performed over groups of localities recognized by the CA. Bold indicates significant values. The results show significant differences (probability of equality always lower than 0.05) between all possible pairs.

	RPT1		RPT2		RPT3		RPT4	
RPT1	-		mean rank within groups	94,2	mean rank within groups	47	mean rank within groups	73.64
			mean rank between groups	179,7	mean rank between groups	103.2	mean rank between groups	138
			R	0.6196	R	0.8269	R	0.6127
			p (same)	**$<2\cdot10^{-4}$**	p (same)	**$8\cdot10^{-4}$**	p (same)	**$<2\cdot10^{-4}$**
RPT2	mean rank within groups	94,2	-		mean rank within groups	31	mean rank within groups	42.61
	mean rank between groups	179,7			mean rank between groups	83.5	mean rank between groups	126.9
	R	0.6196			R	1	R	0.986
	p (same)	**$<2\cdot10^{-4}$**			p (same)	**$6\cdot10^{-4}$**	p (same)	**$<2\cdot10^{-4}$**
RPT3	mean rank within groups	47	mean rank within groups	31	-		mean rank within groups	17.5
	mean rank between groups	103.2	mean rank between groups	83.5			mean rank between groups	50.5
	R	0.8269	R	1			R	1
	p (same)	**$8\cdot10^{-4}$**	p (same)	**$6\cdot10^{-4}$**			p (same)	**$18\cdot10^{-4}$**
RPT4	mean rank within groups	73.64	mean rank within groups	42.61	mean rank within groups	17.5	-	
	mean rank between groups	138	mean rank between groups	126.9	mean rank between groups	50.5		
	R	0.6127	R	0.986	R	1		
	p (same)	**$<2\cdot10^{-4}$**	p (same)	**$<2\cdot10^{-4}$**	p (same)	**$18\cdot10^{-4}$**		

Bennington and Bambach (1996) define the concept of community type as "the aggregate of local communities and communities that have similar, but not identical, taxonomic membership and occur in similar, but not necessarily the same, environments" (Bennington & Bambach, 1996: 112). As we will discuss in this section, each one of the groups distinguished by the CA is characterized by a similar rodent association with certain dominant taxa. Thus, the groups that appear in the multivariate space may be viewed as community types. In the following subsections we will describe the composition and structure of the rodent assemblages in each one of the rodent paleocommunity types recognized.

6.3.2. Rodent Paleocommunity Type 1

Group 1 includes 13 localities from the Calatayud-Teruel and Vallès-Penedès basins that cluster in a wide region around the origin of coordinates. We will refer to the rodent assemblage of the sites in this group as Rodent Paleocommunity Type 1 (RPT1). The age of the localities from the Vallès-Penedès ranges from the latest Aragonian to the Early Vallesian, while the localities of the Calatayud-Teruel Basin included in this group belong exclusively to the Early Vallesian. In table 6.3. we have represented the mean relative abundance of the rodent genera present in each one of the groups. When the relative abundance of a genus exceeds 5 % it is marked in bold. Clearly, localities of group 1 are the ones with higher genera richness in our database. Equitability of the rodent assemblage is also higher than in the remaining groups. Most of the sites of group 1 include a "cricetid"-dominated fauna, although glirids and sciurids (both ground and flying squirrels) are quite diverse and may be locally common. The eomyids, anomalomyids and murids are present, but they are very rare. RPT1 usually includes one or two "cricetid" genera that account for about the 50 % of the association. One of the most common "cricetids" is *Hispanomys* (mean relative abundance of about 40 %), which is especially common in some latest Aragonian (CM) and earliest Vallesian (CFL, CP) sites of the Vallès-Penedès. It is also very abundant in the Calatayud-Teruel Basin during the whole Vallesian. The following genus in abundance is another "cricetid", *Megacricetodon* (close to 19 %), which includes species belonging to two different lineages: a small-sized lineage and a larger-sized one (Daams & Freudenthal, 1988b). One member of the larger-sized lineage, *Megacricetodon ibericus*, is very common in the earliest Vallesian localities (NOM1, CAL, CFL), but this species disappears about the middle of the Early Vallesian, coinciding with a marked increase in the abundance of the genus *Cricetulodon* (Agustí *et al.*, 2001). *Cricetulodon* is a medium-sized "cricetid" which may be very abundant in some localities of the late Early Vallesian (CL1, PE2C). There are some differences between most of the sites from the Vallès-Penedès and those from Calatayud-Teruel. In the Vallès-Penedès the arboreal dormice are always more diverse, nevertheless, as it happens in the case of the Calatayud-Teruel Basin, they are not abundant. Some Gliridae genera are not recorded in the sites of the Calatayud-Teruel Basin included in group 1 (*Bransatoglis*, *Miodyromys*, *Paraglirulus*, *Glirulus*, *Glirudinus* and *Myoglis*) (see also chapter 5). The ground dormouse *Myomimus* seems to characterize the Early Vallesian sites of Calatayud-Teruel, where it is very common. On the contrary, this genus is not recorded in the Vallès-Penedès. The family Eomyidae is only present in the Catalan basin. Some genera may be very abundant in many sites of the Vallès-Penedès, such as the "cricetid" *Eumyarion* (BCV1, SQA, CB, CL1), the ground squirrel *Spermophilinus* (CM, CP) or the small beaver *Euroxenomys* (CB). These genera are absent or very rare in the localities of the Calatayud-Teruel Basin.

Table 6.3. Mean relative abundance of the rodent genera present in each one of the recognized RPTs. When the relative abundance of a genus exceeds 5 % it is marked in bold. Dash indicates that the genus is absent in this RPT, while italics indicate that it is present in all the sites included in this group.

Genus	Group 1 (RPT1)	Group 2 (RPT2)	Group 3 (RPT3)	Group 4 (RPT4)
Heteroxerus	1.11	1.02	0.25	1.25
Spermophilinus	**8.17**	0.66	**10.20**	-
Albanensia	0.24	-	-	-
Miopetaurista	0.45	-	0.25	-
Euroxenomys	4.74	3.02	-	0.25
Eliomys	0.12	0.02	-	-
Glirudinus	0.31	-	-	-
Muscardinus	2.89	0.57	1.54	3.25
Myoglis	0.14	0.02	0.75	-
Microdyromys	0.22	0.54	-	**7.50**
Glirulus	-	-	0.50	-
Paraglirulus	0.63	-	-	-
Miodyromys	0.59	0.04	-	-
Myomimus	**8.06**	1.16	-	3.00
Ramys	1.17	**17.86**	-	-
Tempestia	1.59	0.10	-	3.25
Bransatoglis	0.41	-	-	-
Eomyops	0.33	-	0.75	-
Keramidomys	0.21	-	-	-
Cricetodon	-	5.39	-	-
Hispanomys	***41.54***	4.75	*4.61*	**16.12**
Rotundomys	-	-	***68.52***	-
Eumyarion	**10.31**	-	-	0.12
Cricetulodon	**14.47**	0.26	-	1.62
Democricetodon	**7.21**	3.33	-	0.12
Megacricetodon	***19.35***	***86.22***	-	-
Anomalomys	0.19	-	3.14	-
Progonomys	3.22	0.06	***9.42***	***62.25***
Huerzelerimys	-	-	-	1.25
Number of genera	26	18	11	12

6.3.3. Rodent Paleocommunity Type 2

Group 2 includes 11 localities ranging from the Late Aragonian to the Early Vallesian. All the localities of the Duero Basin but one (AMP1) are included in this group as well as all the Late Aragonian sites of the Calatayud-Teruel Basin. Also included are CAR1, an Early Vallesian site from Calatayud-Teruel, as well as CCN22, the site which records the First Appearance Datum (FAD) of the hipparionine horses in the Vallès-Penedès Basin (Garcés *et al.*, 1996; Garcés *et al.*, 1997a). We will refer to the rodent assemblage of the sites in this group as Rodent Paleocommunity Type 2 (RPT2). The dominance of the genus *Megacricetodon* (mean relative abundance of about 85 %) characterizes the localities within this group. Usually two lineages of *Megacricetodon* are present, but the larger-sized lineage is the most abundant, so in many localities a single species of this lineage (*M. ibericus* or closely related forms) represents more than 70 % of the recovered cheek teeth (CCN22, and all the Late Aragonian sites from the Calatayud-Teruel Basin). In the case of CAR1, the small-sized lineage is more abundant, and the assemblage is more similar to that of RPT1. The Late Aragonian and Early Vallesian localities of the Duero Basin also include high proportions of *Megacricetodon ibericus* (between 20 % and 60 %), but they are characterized by a high abundance of *Ramys* (also between 20 % and 60 %). *Ramys* is an endemic dormouse of this latter basin even though it made an incursion in the Calatayud-Teruel Basin by the end of the Early Vallesian (PE2A, PE2C), where it never became abundant. The richness in the Duero Basin is very low, usually including no more than five genera. The rest of the rodent assemblage of RPT2 resembles that of RPT1, with the absence of the Eomyidae, the Anomalomyidae, the Pteromyinae and many Gliridae genera (*Glirudinus*, *Glirulus*, *Paraglirulus*, *Bransatoglis*). The Muridae are present only in one site (AMP9), where they are very rare.

6.3.4. Rodent Paleocommunity Type 3

Group 3 is the smallest of the groups distinguished by the CA and it includes all the Late Vallesian localities from the Vallès-Penedès Basin. We refer to the rodent assemblage of the sites in group 3 as Rodent Paleocommunity Type 3 (RPT3). The genera richness is much lower than in RPT1 and RPT2. The rodent assemblage is overwhelmingly dominated by the "cricetid" *Rotundomys* (mean relative abundance of about 70 %). The ground squirrel *Spermophilinus* and the mouse *Progonomys* have approximately the same mean relative abundances (close to 10 %). The "cricetid" *Hispanomys* and the Anomalomyidae may be quite abundant in many sites. Apart from *Rotundomys* and *Hispanomys* there are no more "cricetid" genera. The Pteromyinae and Eomyidae may be present but they are quite rare. The Gliridae are relatively rare and they are represented by few genera, of which *Muscardinus* is the most abundant one.

6.3.5. Rodent Paleocommunity Type 4

Group 4 includes only Late Vallesian localities, all but one (AMP1, from the Duero Basin) belonging to the Calatayud-Teruel Basin. We will refer to the rodent assemblage of the sites in this group as Rodent Paleocommunity Type 4 (RPT4). The dominance of the murid *Progonomys* (mean relative abundance of about 62 %) characterizes RPT4. The rodent assemblage is nearly as poor as that of RPT3. In the case of AMP1 only two genera are recorded, *Progonomys* and the dormice *Microdyromys*, the latter one being very abundant in this site (close to 60 % of the assemblage). *Microdyromys* is absent of the rest of the sites of the group, although it has been recorded in the Late Aragonian and Early Vallesian of the other basins. The mean richness of the assemblage in the localities of the Calatayud-Teruel Basin is of about five genera, the "cricetid" *Hispanomys* (mean relative abundance close to 16 %) being the following rodent in abundance after *Progonomys*. The dormice are represented by three genera apart from *Microdyromys*. These are *Muscardinus*, *Myomimus* and *Tempestia* which may be relatively common in many sites. Only three "cricetid" genera are recorded in RPT4: *Cricetulodon*, *Democricetodon* and *Eumyarion*. The presence of *Democricetodon* (MB2A) and *Eumyarion* (MB2B) is anecdotic, while *Cricetulodon* is present at two sites where it is rare. A remarkable fact is the absence of the "cricetid" *Rotundomys*, so common in the Late Vallesian of the Vallès-Penedès. The Xerini *Heteroxerus* is the only Sciuridae in the localities of this group. The Eomyidae are absent and the Castoridae are only present in MB2B, where they are not abundant.

6.3.6. The role of temporal patterns

There are three main factors that can explain the similarity between samples: temporal distribution of the genera considered, geographic distribution of rodent genera and paleoenvironmental variables. Unfortunately the methods cannot discriminate between the three factors, so one must decide which are the most important in explaining the differences *a posteriori*. We should emphasize those differences attributable to paleoenvironmental factors and discard those that may be better explained by temporal or geographic causes. Because of this, we have tested the correlation between the age of the sites and their eigenvalue in the two first axes of the

CA shown in figure 6.2.a (see table 6.4.). From visual appreciation of figure 6.2.a it seems clear that the first axis mainly discriminates between Aragonian and Early Vallesian sites, which take values below or close to 0, and Late Vallesian ones, which take higher positive values. Therefore, the relation of this axis to the age of the sites seems evident. However, the pattern shown by axis 2 is not so clear. In figure 6.3. the age of the sites is plotted against their values in both axis of the CA. The age seems to decrease with increasing values in axis 1, although there is a wide dispersion of the points for values below 0 (fig. 6.3.a). In the case of axis 2 the pattern is similar (fig. 6.3.b). In both cases the probability that the CA values are not correlated with the age of the sites is small ($p<<0.05$ see table 6.4.). We must conclude that time plays an important role in the differentiation of the groups.

Nevertheless, this does not exclude the possibility that the different RPTs may be associated to different paleoenvironments. In order to investigate this point we have plotted in the space defined by the two first axes of the CA additional paleobotanical and paleomastological information available for some localities.

Table 6.4. Results of correlation test between the age of the sites and their score in the two first axes of the CA. Two tests of correlation are computed: Spearman's rank-order correlation coefficient (r_s) and Kendall's τ. The probability of no correlation between the two variables is given in both cases. Bold indicates significant values.

	age			
	τ	p (uncorrelated)	r_s	p (uncorrelated)
CA axis 1	-0.66457	**$1.18\cdot10^{-8}$**	-0.84976	**$5.56\cdot10^{-11}$**
CA axis 2	-0.42	**$2.76\cdot10^{-4}$**	-0.47275	**$3.60\cdot10^{-3}$**

6.4. Ecological characteritzation of the Rodent Paleocommunity Types

The discussion and interpretation of the RPTs is not only based in the information provided by the relative abundance of the different kinds of rodents but also on associated paleobotanical and paleomastological data. Combining these sources of information, the different RPTs are linked to a paleoenvironmental frame. In the following sections we will expose the available paleobotanical and paleomastological data and in section 6.4.4. all the available information will be revised in order to ecologically characterize the distinct RPTs.

6.4.1. The paleobotanical evidence

Paleobotanical data refer to leaf assemblages or palynological data depending on the site. The palynological data from the Torremormojón section in the Duero Basin (Rivas-Carballo & Valle, 1986) include the sites T-13 and T-16, which are approximately time equivalent to Torremormojón 5 and Ampudia 1, respectively (García Moreno, 1987). The leaf assemblage from Tal·lús Sud Autopista 2 (TSA2), in the Vallès-Penedès Basin, occurs in the same fossiliferous level that has delivered the micromammal remains (Agustí *et al.*, 2003). The paleobotanical information from these sites is plotted in the position of the micromammal localities that are closer in age. Each

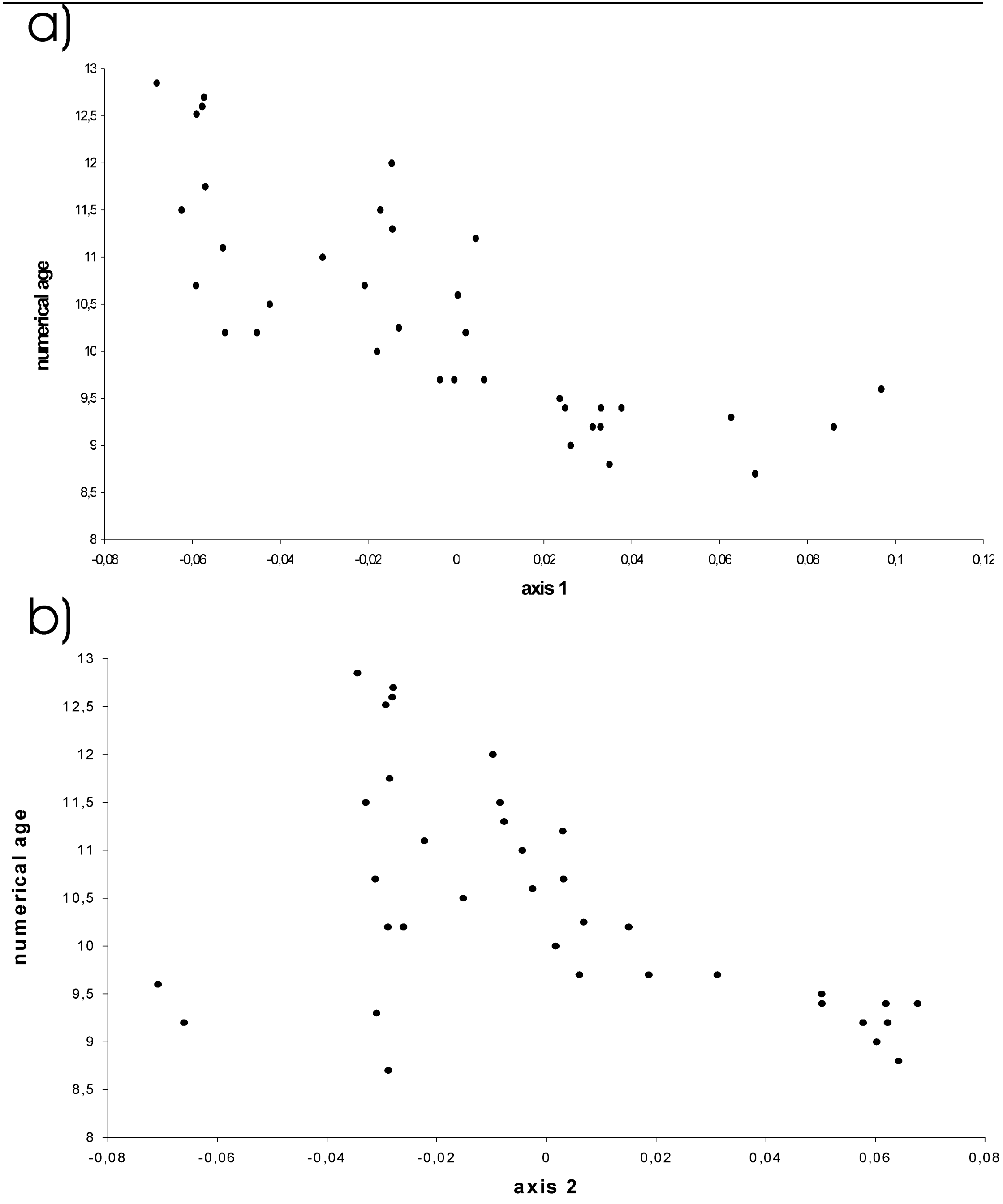


Figure 6.3. Age of the rodent sites plotted against their values in both axes of the CA. a) Age of the sites versus their score in CA axis 1. b) Age of the sites versus their score in CA axis 2. In both situations exists an statistically significant correlation between the age of the sites and their score on the CA (see table 6.4. and text for more details).

one of these localities is plotted in a different group recognized by the CA, thus representing different paleoenvironments. The floral remains have been classified in categories: arboreal elements and non-arboreal elements; and in their turn arboreal elements are classified as Mediterranean, deciduous and evergreen (fig. 6.4.). The paleobotanical information is represented as a bar chart were the left column represents arboreal against non-arboreal elements and the right column the kind of arboreal taxa. We have only considered the presence or absence of taxa of these categories, not the relative abundance of each one in the assemblage.

6.4.2. Evidence provided by macromammals

Many of the sites considered, especially those of the Vallès-Penedès, have delivered abundant macromammal remains apart from small mammal ones. In this latter basin this applies to CB, CP and CL1. Furthermore, BCV1, CCN22 and CM have a poorer macromammal sample. Similarly some sites of the Calatayud-Teruel Basin have also provided macromammal remains, these are: TOR, NOM1 and MBB. In our discussion we will assimilate some micromammal sites to approximately equivalent macromammal ones. These include the rich macromammal site of Viladecavalls (VC), from the Vallès-Penedès Basin, which is only slightly younger than RT7 (Garcés *et al.*, 1996). The macromammal remains from Sant Quirze (SQ) were recovered in stratigraphic levels just above the micromammal site SQA. The macromammal fauna known in the literature as Hostalets Superior (HS; *sensu* Agustí *et al.*, 1984) includes remains from Can Mata III and nearby sites. All these sites are stratigraphically very close to the micromammal site of Can Flaquer (CFL), which is often also called Hostalets Superior, but in this case the term refers to an homogeneus sample. The fauna of Terrassa (TR; *sensu* Morales *et al.*, 1999) includes large mammal remains from TNA, TSA2 and TF. All these sites are chronologically and stratigraphycally very close (see Garcés *et al.*, 1996) and their large mammal fauna is often united in the literature (Agustí *et al.*, 1984; Moyà-Solà & Agustí, 1987; Morales *et al.*, 1999). The macromammal site of La Roma 2 (R2) is stratigraphycally very close to PERC (Van Dam, 1997), and it is assimilated to this one. Faunal information has been taken from Alcalá (1994) and Morales *et al.* (1999), in the case of the Calatayud-Teruel Basin. In the case of the Vallès-Penedès Basin it is based in the works by Agustí *et al.* (1984), Agustí *et al.* (1999), Morales *et al.* (1999) and additional unpublished data.

The ecological characterization of some large mammals is given in table 6.5. The genera present in the assemblages considered are classified in ecomorphological groups in the case of suoids (after Fortelius *et al.*, 1996a) and ruminants (after Köhler, 1993). Fortelius *et al.* (1996a) distinguished up to four suoid ecomorphological groups, but we have only considered the extreme classes, since they are believed to be better paleocological indicators. The information provided by other groups (such as primates, or perissodactyls) is also presented. In figure 6.4 we have plotted the generic richness of two groups of ruminants and two groups of suoids which are believed to be good ecological indicators coinciding with the position of equivalent (or time-equivalent) micromammal sites. We have only represented these two great groups of herbivorous mammals because they are always present in the sites considered, where they are often quite diverse and abundant.

6.4.3. A discussion on the ecology of some fossil rodents

The efforts in paleoenvironmental reconstruction based on fossil rodents have led to a precise ecological characterization of some genera and species based on ecomorphology, biogeography and ultimately actualism. In the following lines we will present and discuss the information on the ecology of most of the genera included in our analysis.

Van der Meulen & de Bruijn (1982) grouped living and fossil Gliridae species on the basis of characteristic features of the upper first and second molars and extrapolated the ecology of the living representatives to the fossil species. The Glirinae,

ecological grouping	taxa	ecology	references
Type A ruminants	*Dorcatherium* *Micromeryx* *Hispanomeryx* *Euprox* *Heteroprox* *Amphiprox* *Stehlinoceros* *Dicrocerus* *Palaeomeryx* *Decennatherium* *Tragoportax* *Austroportax* *Miotragocerus*	browsers, wooded an humid habitats. *Dorcatherium* and *Miotragocerus* show skeletal adaptations for a semiaquatic life-style	Köhler, 1993
Type B ruminants	*Aragoral* *Palaeotragus* *Samotragus*	browsers, open habitats	Köhler, 1993
Class 1 Suoidea	*Albanohyus*	small omnivore (less than 20 kg), forest environments	Fortelius et al., 1996b
Class 4 Suoidea	*Microstonyx*	large omnivores (more than 200 kg), open habitats	Fortelius et al., 1996b
	Aceratherium	browser, forest environments maybe near water masses	Heissig, 1999a
	Acerorhinus	browser with adaptation to hard and dry brush vegetation	Heissig, 1999a
	Alicornops	browser, forest environments maybe near water masses	Heissig, 1999a
	Brachypotherium	browser, forest and woodland environments maybe near water masses	Heissig, 1999a
	Stephanorhinus	browser with adaptation to hard and dry brush vegetation	Heissig, 1999a
	Chalicotherium	browser, forest and woodland environments	De Bonis et al., 1999
	Tapirus	browser, forest and woodland environments	Heissig, 1999b
	Pierolapithecus	arboreal, mainly frugivorous, warm and wet forest environments	Moyà-Solà *et al.*, 2004 ; Moyà-Solà *et al.*, 2005
	Dryopithecus	arboreal, mainly frugivorous, warm and wet forest environments	Moyà-Solà & Köhler, 1996 ; Andrews et al., 1997
	Pliopithecus	arboreal, mainly frugivorous, warm and wet forest environments	Ginsburg & Mein, 1980; Ungar & Kay, 1995
	Egarapithecus	arboreal, mainly folivorous, forest environments	Moyà-Solà et al., 2001

Table 6.5. Ecological preferences for some macromammal genera associated to the rodent sites included in our analysis. The ecology of large mammals is based on different works in each case, references are given in the last column. For ruminants and suoids we follow the ecological groupings by Köhler (1993) and Fortelius et al. (1996b), respectively. The generic richness of these ecological groups in selected sites is presented in figure 6.4. (see text for details).

the Leithiini and the mouse-like dormouse *Ramys* (tribe Myomimini) are considered to have been mainly frugivorous arboreal/scansorial dormice. In contrast, the remaining Myomimini are supposed to have been terrestrial and to have inhabited open, moderately dry habitats, as seen in the living genus *Myomimus*. The flying squirrels would have preferred forest environments since they are gliders (Daams *et al.*, 1988; Van Dam & Weltje, 1999). Storch *et al.* (1996) have provided unquestionable evidence of gliding locomotion in an exceptionally preserved Oligocene eomyid (*Eomys querci*). Nothing is known so far about the postcranial skeleton of other European eomyid taxa. But it should not be expected that all rodents in a such diverse family were gliders. However, these minute rodents tend to be more abundant in faunas that include a high proportion of forest-dwelling dormice and flying squirrels and are considered forest-dwellers (Daams *et al.*, 1988; Van Dam & Weltje, 1999). Recent Castoridae present a number of skeletal adaptations linked to their semiaquatic lifestyle that have also been recognized in some Miocene genera such *Steneofiber* (Hugueney & Escuillié,1995, 1996) and *Chalicomys* (Daxner-Höck, 2004; see also chapter 3). In our analysis we only include one genus of small-sized beavers, *Euroxenomys*, which presents a cylindrical tail and apparently a less specialized skeleton, more similar to that of a muskrat (Daxner-Höck, 2004). However, this does not exclude an association with permanent water masses. In fact *Steneofiber esseri* also presents a quite generalized skeleton and a cylindrical tail coupled with other unequivocally aquatic adaptations, such as non-wettable fur (Hugueney & Escuillié, 1995; see also chapter 3). Given the fact that *Euroxenomys* is frequently associated to other larger-sized beaver species (usually *Chalicomys* in the sites considered), it may also have preferred similar environments.

Van Dam & Weltje (1999) assign a preference for wet environments to *Spermophilinus* on the basis of its cooccurrence with Pteromyinae and Eomyidae. The same authors assume that the ground squirrels of the tribe Xerini (which in the sites considered only include the genus *Heteroxerus*) indicate open environments and hence low humidity. This interpretation is based on the ecology of the living Xerini that inhabit dry savannas or arid mountainous environments. However, in the case of the Vallès-Penedès the peaks in the abundance of these two sciurid genera are correlated, thus suggesting that they did not have opposite ecological requirements (see fig. 6.1.). Assigning an environmental preference to these extinct fossil squirrels remains controversial.

We can only conjecture the values for mean temperature that fossil rodents preferred using data on paleobiogeography and life-history aspects of their living relatives as sources of information. Van Dam & Weltje (1999) considered the Gliridae II (a group supposedly including arboreal dormice), the Sciuridae II (another group that included the Marmotini, such as *Spermophilinus*, and the Sciurini), the Eomyidae and the Pteromyinae preferred temperate climates mainly because their diversity and abundance is lower in Spain than in northern regions during the Middle and Late Miocene. Considering the Gliridae II (*sensu* Van Dam & Weltje (1999)) the higher levels of diversity in the European Miocene are recorded during the Middle Miocene (MN 5) (Daams,1999; Hartenberger, 1994) coinciding in time with the Langhian thermal optimum (Wright *et al.*, 1992). As in the Late Miocene, the dormice are less abundant (but not less diverse) in Spain by this time, although this fact may be related to the presence of dryer and more seasonal environments in the Iberian Peninsula at this moment. Palynological data (Bessedik & Cabrera, 1985; Jiménez Moreno & Suc, in press) and macrofloral remains (Sanz de Siria, 1994) show the existence of warm environments with wet-dry seasonality in the Vallès-Penedès and in broad areas of Spain. In contrast, seasonality and dryness would have been lower in Central Europe (Kovar-Eder, 2003). It should be noted that most of the Vallesian dormice have an Early

Miocene (even Oligocene in the case of *Microdyromys*) origin and may have preferred the warm, less seasonal climates of the Early Miocene, most of them becoming extinct during the Late Vallesian and the Turolian. A preference for similar environments is proposed for the Pteromyinae. Nowadays the flying squirrels are specially successful and diverse in the subtropical forests of South-Eastern Asia, although some representatives live in temperate deciduous forests and present a weak hibernation.

The "cricetids" are a very diverse group including forms presumably adapted to different kinds of habitats. The larger-sized "cricetids" in the considered sites belong to the genus *Hispanomys*, which is characterized by molars presenting medium hypsodonty and may have included hard plant parts in its diet (De Bruijn & Ünay, 1996). Medium to small-sized "cricetids", such as *Eumyarion*, *Democricetodon*, *Cricetulodon* and *Megacricetodon* are brachyodont and bunodont "cricetids" which could have fed on a wide variety of plants and seeds. A preference for dry and open environments has been postulated for larger-sized *Megacricetodon* species (such as *M. ibericus*) (Daams & Freudenthal, 1988b), but in our opinion the evidences are not conclusive and this genus, as well as *Cricetulodon* may have been ubiquistic. *Eumyarion* presents a very complex pattern including long transverse ridges as well as additional connections between the main cusps. Many recent American sigmodontines and also some Malagasy nesomyines present teeth morphologies closely resembling that of *Eumyarion*. These rodents with complex plicident molars are primarily forests dwellers (Hershkovitz, 1967). Although this question needs more investigation, tentatively this genus may have had similar dietary habits and may have lived in similar environments. *Rotundomys* is a descendant of the Early Vallesian brachyodont *Cricetulodon* that developed moderately hypsodont molars and shows a tendency towards lophodont occlusal pattern (Mein, 1966). This dental morphology resembles that of early arvicolids and the "microtoid cricetids" (*sensu* Schaub, 1934), and may be an adaptation to diets containing fibrous plant parts.

The murids assumed the role of the "cricetids" as the dominant rodents in the Late Vallesian assemblages. This occurred immediately after their arrival into the Iberian Peninsula at 9.7 Ma (Agustí *et al*., 1997; Garcés *et al*., 1996). Van Dam (1997) and Van Dam & Weltje (1999) have related the success of the murids to the competitive advantage gained by their extremely reproduction-oriented "way of life" as a result of environmental change. For these authors this aspect would make murids competitively superior to "cricetids" (which present moderate reproduction rates) in low predictability wet-dry seasonal climates, such as the Mediterranean climate.

6.4.4. The environment associated to the different Rodent Paleocommunity Types

In this section we will summarize all the evidence presented in order to relate the different RPTs to broad environmental pictures. All the RPTs (except RPT3) include localities from different basins that are plotted in close positions in the CA because they share a similar rodent composition and a similar community structure. Nevertheless, we must keep in mind that the sites (and their associated paleoenvironment) are similar, not identical (if they were they all would plot at the same point in the CA). There are some differences between the localities included in the same group, and this differences use to

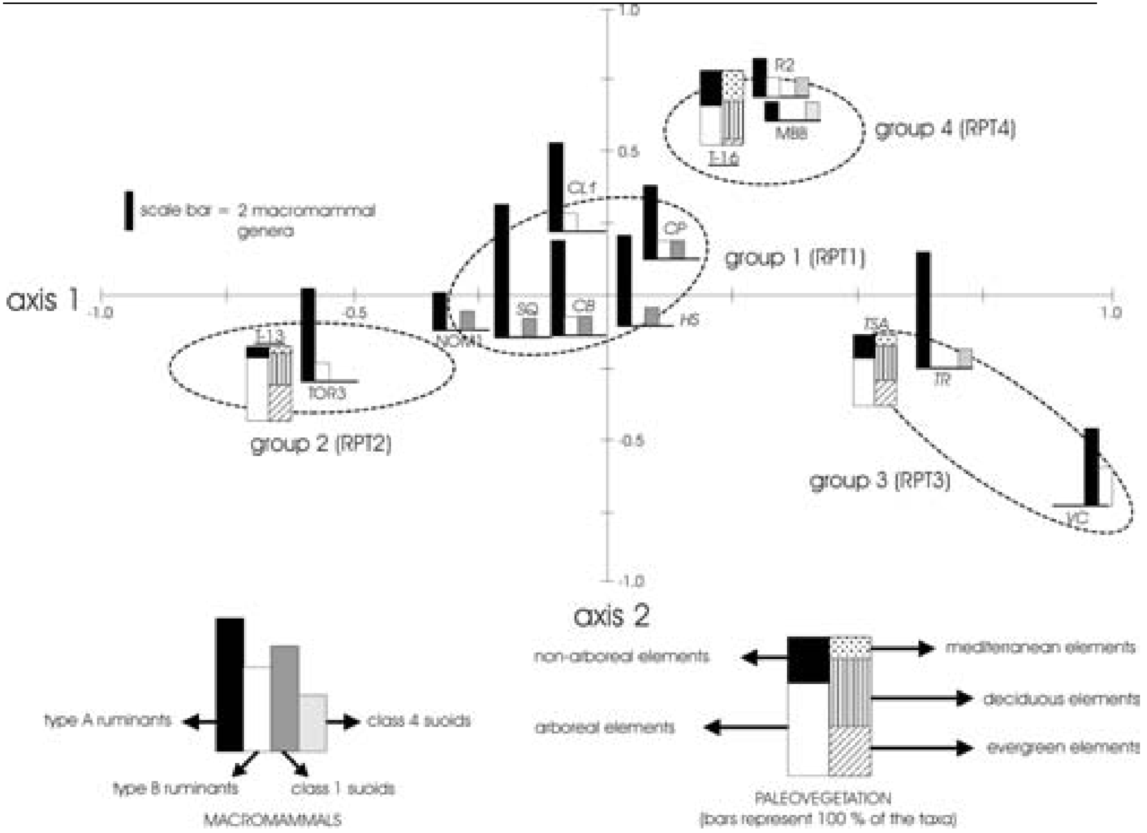


Figure 6.4. Additional information available for some sites (or approximately time-equivalent localities) plotted in the space defined by the two first axes of the CA (see text for details). Paleobotanical data refer to leaf assemblages or palynological data depending on the site. The palynological data from the Torremormojón section in the Duero Basin include the sites T-13 and T-16, which are approximately time equivalent to Torremormojón 5 and Ampudia 1, respectively (García Moreno, 1987). The leaf assemblage from Tal·lús Sud Autopista 2 (TSA2), in the Vallès-Penedès Basin, occurs in the same fossiliferous level that has delivered the micromammal remains (Agustí et al., 2003). The paleobotanical information from T-13 and T-16 is plotted in the position of the micromammal localities that are closer in age. The floral remains have been classified in categories: arboreal elements and non-arboreal elements; in their turn arboreal elements are classified as Mediterranean, deciduous and evergreen. The percent of taxa in each one of these categories is represented in a bar-chart (where the full bar is 100 %) for each site. The species richness of certain ecomorphological groups of ruminants and suoidea is also represented as a bar-chart for sites where abundant macromammal remains have been recovered (see table 6.5. and text for details).

be greater when we consider sites from different basins, a fact that may indicate the existence of slightly different paleoenvironments in the basins compared. In this way, we have performed ANOSIM over the different RPTs in order to test if there are significant differences according to the geographic position of the sites. We will also focus in this point at the end of the discussion of the environment associated to each RPT.

RPT1

Unfortunately the paleobotanic information for localities (or for equivalent sites) of group 1 (RPT1) is very scarce. This is restricted to Can Llobateres 1, in the Vallès-Penedès Basin, which has delivered some remains of *Sabal major*, abundant fruits of *Ficus* sp., *Pteris* sp. and *Cassia* sp. The presence of megathermal taxa evidences the existence of a warm temperate environment (Sanz de Siria, 1994) (climatic classification after Walter, 1970; see discussion in chapter 5). The limited paleobotanic information contrasts with the rich macromammal sites. Type A ruminants are very diverse (4 to 7 genera), while type B ruminants are only represented by the giraffid

Palaeotragus (CB, CP and CL1). Similarly, class 1 suoids are present in all the sites, where they are represented by one or two species. Class 4 suoids are absent (fig.6.4.). The rhinoceroses are usually very diverse, and forms that may have inhabited wet forest environments (*Alicornops*, *Brachypotherium*) are abundant. Other forest-dwellers such as chalicotheres, tapirids, pliopithecids and great apes are also present in some localities from this group. The chalicotheres are only recorded in the Vallès-Penedès, where they are represented by *Chalicotherium*. The presence of tapirids, pliopithecids and great apes (*Pierolapithecus* and *Dryopithecus*) is restricted to some sites of the Vallès-Penedès. *Tapirus* is found in CL1 and CP, while great apes are reported from BCV1, SQA, CB, CP and CL1 (Moyà-Solà *et al.*, 1990; Moyà-Solà *et al.*, 2004; see also chapter 2). Pliopithecids are reported from CB. Concerning the rodents, a set of genera that are classically considered to be forest-dwellers, such as the Pteromyinae and most of the Gliridae, are specially diverse in RPT1, although they are never major components. Amongst the Gliridae, the mouse-like dormice are more abundant in the sites of Calatayud-Teruel, while they are not recorded in the Vallès-Penedès, thus indicating higher moisture in this latter basin. The arboreal dormice are more diverse in the Vallès-Penedès thought they are not abundant. The Pteromyinae have been sporadically recorded in Calatayud-Teruel (CAL, Early Vallesian) and they are usually represented by a few teeth in the sites of the Vallès-Penedès. The Castoridae are abundant in some sites of the Vallès-Penedès (CB, CL1; where they are not only represented by *Euroxenomys* but also by the larger-sized *Chalicomys*) and are also recorded in the Early Vallesian of Calatayud-Teruel (PE2A). The ground squirrels of the genus *Spermophilinus* are common in several Vallès-Penedès sites. The “cricetids”, are the major components of the rodent assemblages and include the genus *Hispanomys*, very common in all the sites, plus *Megacricetodon* or *Cricetulodon*, which may be even more abundant. *Eumyarion* is very abundant in some sites of the Vallès-Penedès (in BCV1 is the most abundant rodent and in SQA, CB and CL1 it is very common). The evidence provided by macromammals and, to some degree, by floral remains strongly points to the presence of warm temperate evergreen forest environments associated to RPT1. Amongst the rodents, the forest-dwellers are very diverse, although they are only common in some sites. The ubiquists (the “cricetids” *Megacricetodon* and *Cricetulodon*) and forms that may have preferred open environments (*Hispanomys* and probably the ground squirrels) are very abundant in the assemblages. This fact may indicate the presence of an heterogeneous environment including forest as well as relatively more open areas. The results of the ANOSIM (see table 6.6.) show that the localities of Calatayud-Teruel and the Vallès-Penedès included in RPT1 are different at a significance level of $p = 0.05$. This result is also observed among the large mammal faunas. Therefore, the differences between the sites from the Vallès-Penedès and NOM1 from Calatayud-Teruel appear evident. Chalicotheres, tapirids, great apes and pliopithecids have never been recorded in this last basin, which may indicate the existence of a drier biotope in that area. As discussed above the rodent assemblage is similar, but many forest-dwellers are absent in Calatayud-Teruel reinforcing this interpretation.

Table 6.6. Results of the ANOSIM (using Bray-Curtis distance and bootstrapping by 5000) performed over groups of localities recognized by the CA to explore differences within RPTs according to geographic position. Bold indicates significant values. In RPT1 the sites from the Vallès-Penedès are compared to those of Calatayud-Teruel, while in RPT4 the sites of Calatayud-Teruel are compared to those of the Duero Basin. In RPT2 sites of all three basins are considered (see text for details).

	RPT1	RPT2	RPT4
mean rank within groups	31.72	17.67	11
mean rank between groups	46.17	34.38	25
R	0.3704	0.6078	1
p (same)	**0.01**	**$1.4 \cdot 10^{-3}$**	0.13

RPT2

The paleobotanical data associated to RPT2 refer to the T-13 pollen assemblage (Duero Basin). The palynological spectrum is dominated by arboreal elements and the proportion of deciduous and evergreen taxa is approximately equal (42 % and 48 %, respectively) (fig. 6.4.). Mediterranean elements are very rare (9 %). This assemblage, that includes a significant percentage of deciduous trees altogether with a "hard core" of evergreen elements, has been interpreted as a warm temperate forest (Rivas-Carballo & Valle, 1986). The macromammal fauna from Toril 3 is the only one in group 2 (RPT2). It shows a high diversity of type A ruminants (5 genera) (fig. 6.4.). The bovid *Samotragus* is the only representative of type B ruminants. The rhinoceros *Brachypotherium* is also present. This macromammal composition is similar to that of NOM1 and differs from the one of temporally close Vallès-Penedès sites (SQA, CB) by the absence of chalicotheres, tapirids, pliopithecids, great apes and class 1 suoids. The environment may have been similar to that of NOM1. The rodent assemblage is very similar to RPT1, although some dormice (*Bransatoglis*, *Glirudinus*, *Paraglirulus*, *Glirulus*), the eomyids, the flying squirrels and the "cricetid" *Eumyarion* are absent. From a quantitative point of view it differs from RPT1 by the overwhelming dominance of larger-sized *Megacricetodon* species. Considering our discussion on the environmental preferences of these taxa, RPT2 may be characteristic of dryer and/or more seasonal environments than RPT1. Nevertheless, the ground squirrels and the "cricetid" *Hispanomys* are less common than in RPT1, partly contradicting this interpretation. In the case of the localities of the Duero Basin, the high abundance of the endemic dormouse *Ramys* is very characteristic. As we did for RPT1, we have explored the differences between the localities in RPT2 according to the basin where they are placed. ANOSIM shows that there are significant differences at $p = 0.05$ (see table 6.6), and we must conclude that, as in the case of RPT1, group 2 is not a uniform group and some differences between the sites of different basins may exist.

RPT3

The leaf assemblage of TSA2 consists mainly in arboreal elements, where deciduous taxa are very important (48 %). The abundance of evergreen taxa is moderately lower (35 %) while Mediterranean taxa are minoritary (16 %) (fig. 6.4.). This assemblage, may be interpreted as a warm temperate forest similar to that associated to RPT2 (Agustí *et al*., 2003). There are two sites for which macromammal information is available: Viladecavalls (VC) and Terrassa (TR). The diversity of type A ruminants is moderately lower (3-4 genera) than in most of the sites from group 1 (RPT1), while type B ruminants include *Palaeotragus* and *Gazella* (fig. 6.4.). These sites also differ from group 1 ones by the absence of class 1 suoidea, tapirids and great apes. The last record of great apes in the Vallès-Penedès comes from the Late Vallesian site of La Tarumba 1 (near the city of Terrassa), which is only slightly younger than

RT7. The pliopithecids are represented in TR by *Egarapithecus narcisoi*, which was adapted to a folivorous diet, in contrast to other great apes and pliopithecids which are supposed to have been mainly frugivores (Moyà-Solà *et al.*, 2001). In TR this primate coexists with *Microstonyx*, which is placed in class 4 suoidea, thus reflecting relatively open environments. The presence of *Chalicotherium*, and of the rhinoceroses *Alicornops* and *Aceratherium* has been reported from VC and TR. Amongst the rodents, the dominance of a single taxon, the "cricetid" *Rotundomys*, characterizes RPT3. The high abundance of *Rotundomys* may indicate the presence of open environments maybe associated to grasses. Notwithstanding, this interpretation is in contrast with the paleobotanical and many of the paleomastological data available. The leaf assemblages of TSA2 suggest the presence of a warm temperate forest (Agustí *et al.*, 2003) instead of a more open landscape. The presence of some supposed forest-dwellers (*Miopetaurista*, *Myoglis*, *Glirulus*, *Muscardinus*, *Eomyops*) reinforces this interpretation. However, these rodents are not so abundant as the ones that may have preferred somewhat open environments (*Hispanomys*, *Spermophilinus* and *Progonomys*). Taking all into account, the available evidence points to the existence of forested environments associated to RPT3, similar to the case of RPT1, although some opening of the canopy seems to have occurred. Furthermore the absence of some forms such as tapirids or great apes may be related to lower temperatures or greater seasonality. Since all the sites in RPT3 are placed in the Vallès-Penedès Basin we have not tested the existence of significant differences according to their geographic position.

RPT4

As in previous cases the paleobotanical information refers to a single locality, the pollen assemblage of T-16 (Duero Basin), which is outstanding because of the abundance of non-arboreal elements (47 %) and Mediterranean taxa (42 %) (fig. 4). This composition has been interpreted as a dry temperate steppe-forest[33] with many Mediterranean taxa (Rivas-Carballo & Valle, 1986). The macromammal faunas which may have coexisted with the rodent assemblages of RPT4 are only represented by MBB and R2 from the Calatayud-Teruel Basin. The diversity is lower than in other sites, and consist in only 9 genera. These include *Microstonyx* (class 4 suoidea), the giraffid *Decennatherium* and the bovid *Tragoportax* (both type A ruminants), the bovid *Aragoral* (type B ruminant) plus the rhinos *Aceratherium* and *Alicornops* (fig. 6.4.). Most of the genera are still linked to forested environments, although the presence of *Microstonyx* and *Aragoral* indicate the existence of open areas. RPT4 is characterized by the abundance of a single murid species: *Progonomys hispanicus*. The success of murids may be related to the existence of open, wet-dry seasonal climates with a low predictability, an environmental picture that is congruent with the pollen spectrum of T-16. Furthermore, forest-dwelling rodents are very rare in RPT4, being only represented by a few dormice species (*Muscardinus*, *Microdyromys*) that are relatively common in some sites. The following genera in abundance (*Hispanomys*, *Myomimus* and *Tempestia*) probably inhabited open areas. Thus the composition of RPT4 contrasts with that of RPT3 and represents a rodent paleocommunity type adapted to more open and wet-dry seasonal environments. In the case of RPT4 ANOSIM shows that equality between the localities of different basins cannot be rejected at $p = 0.05$ ($R = 1$; $p = 0.13$; see table 6.6.). Thus, RPT4 appears to be more uniform than RPT1 and RPT2.

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[33] According to Walter (1970) steppes are typical landscapes of dry temperate climates. The seasonal contrasts in temperature and particularly in rainfall (with a long dry season of several months) characterize this climatic regime. The vegetation is largely dominated by herbaceous plants, including grasses.

All the non-rodent evidence exposed in the previous sub-sections points to the existence of different environments associated to the various RPTs. RPT1, RPT2 and RPT3 represent rodent paleocommunity types that preferred relatively forested environments. However, the nature of the forest cover may have been different in each group. High proportions of deciduous trees (close to 40 %) and about the same percentages of evergreen taxa, are recorded in pollen and leaf assemblages equivalent to certain localities of RPT2 and RPT3 (see fig. 6.4.). Nevertheless, in the case of RPT3 a certain proportion of Mediterranean elements is also present. Limited paleobotanical evidence is available for the background associated to RPT1, but the presence of megathermal taxa in at least one site (CL1) is a fact. The rich mammal assemblages, point to the existence of wet, warm forest environments in this case. The Calatayud-Teruel sites of this group appear to have been drier and less densely forested than the Vallès-Penedès ones. RPT4 appears to have been linked to more open environments. We must note that the environmental interpretation based on macromammals and paleovegetation data is highly congruent with what we would expect considering rodent assemblages alone.

6.5. Paleocommunity stability and ecogeographical patterns

6.5.1. Temporal stability of the RPTs

The composition of the different RPTs in a considered area and at a given moment may be the result of the influence of three main factors: temporal distribution of the genera considered, paleoenvironmental variables and geographic distribution of rodent genera. The temporal distribution of the taxa conforming an RPT can be a significant factor as to whether there is a mechanism that provides stability to the community through time, despite environmental changes.

Stasis at the level of entire faunas, punctuated by abrupt turnover events that lead to the replacement of the preexisting biota, has been documented for example in the case of the Devonian Hamilton fauna (Brett & Baird, 1995). Two different models have been devised in order to describe the nature of both stasis and turnover events: the causal theory term “turnover pulses” (Vrba, 1985) and the more theory-neutral term “coordinated stasis” (Brett & Baird, 1995). The two models advocate for the existence of punctuational trends and may be viewed as an extension of the punctuated equilibria model to the level of ecosystems or species aggregates (Gould, 2002). Brett & Baird (1995) examined several Devonian invertebrate lineages of the Hamilton fauna throughout a 70-million-years interval. They documented 13 successive faunas that exhibited considerable stability in species richness, composition and abundances pattern. Each fauna persists for 2-8 million years since it is rapidly replaced by a markedly distinct fauna which only retains 20 per cent or less of species from the previous one. Vrba (1985) described a similar pattern for Pliocene East African land mammal faunas, relating faunal replacements to important decreases in mean global temperatures (Vrba, 1985). This author generalized these observations and formulated the “turnover pulse hypothesis”, which emphasizes the role of environmental breakups. Vrba (1985) proposed two mechanisms in order to explain turnover pulses as recorded in East African ecosystems: habitat tracking and ecologically induced genealogical events. Habitat tracking simply implies the expansion of the geographic ranges of pre-existing species. Otherwise climatic change may cause increased speciation because of habitat fragmentation. Speciation does not occur in response to new empty niches, but due to fragmentation of species population.

The coordinated stasis and turnover pulses models propose the existence of long-lasting stasis periods followed by punctuated replacement of related species aggregates. Nevertheless, they differ in the proposed mechanism for this common trend. Brett & Baird (1995) also attribute the abrupt changes to important environmental changes but they tend to see stability as a consequence (at least in great part) of the ecological dynamic within the community. For these authors the new faunas derive from the migration of new elements from other regions instead of *in situ* local speciation as proposed by Vrba (1985). In the turnover pulse hypothesis interspecific interactions deserve a secondary role in the stability of the fauna, which mainly results of the basic expectation of punctuated equilibria for individual species.

Our results have shown the existence of at least four RPTs recognized by the recurrence of rodent species, usually with a characteristic pattern of relative abundances. This stability frequently extends to the basin level for relatively long time intervals. However, these RPTs are not completely stable, and some differences in taxonomic membership and the pattern of species abundance are recorded within the RPTs. Thus, our results only partly fit these models. Yet, major restructuring of the rodent paleocommunities seem to occur by the same time in all the basins, and in very short intervals.

6.5.2. Ecogeographical patterns and climatic differentiation within the Iberian Peninsula during the Late Miocene

RPT1 differs of the remaining RPTs by its higher species richness and its more equitative pattern of species abundances. On the basis of paleomastological and paleobotanical data this RPT is considered to be associated to predominantly warm temperate evergreen forest environments. This kind of environments were present by the Early Vallesian in Calatayud-Teruel and in the Vallès-Penedès, although in this latter basin they also existed during the Late Aragonian. The Late Aragonian RPTs of the Duero and Calatayud-Teruel are dominated by a single species of the “cricetid” *Megacricetodon* (RPT2), a fact which may indicate a different environmental picture. Accordingly, the paleobotanical data for the Duero Basin have shown that warm temperate mixed forests were present in the area. Within RPT1 important differences are observed between the Vallès-Penedès and Calatayud-Teruel, and are interpreted as the consequence of dryer conditions in the latter basin. The Duero Basin is characterized by a low species richness throughout all the time interval considered, and the rodent assemblages are always dominated by a single (or two) species.

By the Early/Late Vallesian boundary the structure and composition of the rodent paleocommunities changed markedly in all the areas. In Calatayud-Teruel and the Vallès-Penedès RPT1 was replaced by RPT4 and RPT3, respectively. In the Duero, RPT2 was replaced by RPT4. This breakup coincides with the Vallesian Crisis (Agustí & Moyà-Solà, 1990). The Vallesian Crisis (also cited as “Mid Vallesian Crisis” or “Late Vallesian Crisis”) was recognized for the first time in the Vallès - Penedès (Agustí &

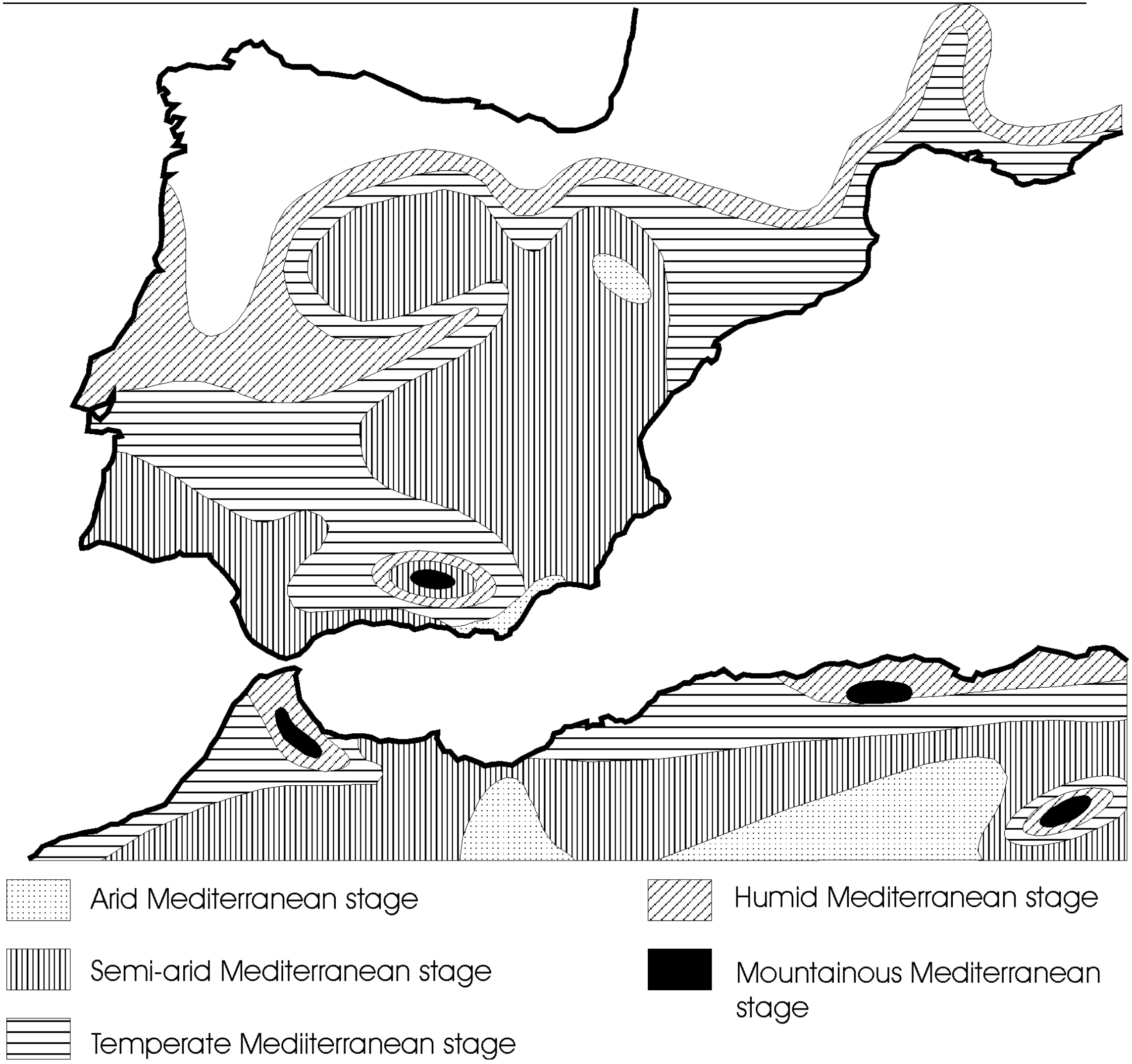

Figure 6.5. Bioclimatic zonation of the Mediterranean climate in the Iberian Peninsula and Northern Africa (modified after Emberger, 1933). Note that the inner Spanish basins belong to the semi-arid or even to the arid Mediterranean stage. In contrast, Catalan basins are situated in the temperate Mediterranean stage. The northwestern third of the Iberian Peninsula presents an Atlantic climate.

Moyà-Solà, 1990) and is known to have affected several mammal taxa of Middle Miocene origin. Recent reviews have considered the Vallesian Crisis a well documented major Eurasian mammal event with continent-wide effects (Agustí *et al.*, 1999; Fortelius and Hokkanen, 2001). However, other works suggest that the geographic extension of this event needs more investigation and that it may have been restricted only to the Iberian Peninsula (see chapter 7). Our results confirm the existence of the Vallesian Crisis and show that besides the disappearance of several rodent genera it implied a change towards dominance-controlled communities with a lower species richness. Some authors have related the Vallesian Crisis to an increase in seasonality and dryness in Western Europe (Agustí *et al.*, 1999; Fortelius *et al.*, 2002). Van Dam (1997) and Van Dam & Weltje (1999) note a shift from humid, temperate, cool/warm seasonal and predictable environments towards dryer, warmer, wet-dry seasonal and unpredictable ones in the Teruel Basin coinciding with the Vallesian Crisis. The mean hypsodonty maps of Fortelius *et al.* (2002) (where mean hypsodonty is used as a proxy of mean annual rainfall) as well as the mean annual paleoprecipitation maps of Van Dam (2006) (where paleoprecipitation values are based in the composition and structure of the small mammal community), also show increased aridification of Southwestern

Europe, although it is recorded somewhat later, by the Early Turolian. This scenario of increased aridification as a cause of the Vallesian Crisis is congruent with our results in the case of the Duero and Calatayud-Teruel Basins. The evidence provided by pollen data, macromammal faunas and the interpretations based on rodents point to the presence of open environments with a certain seasonality in humidity in those areas during the Late Vallesian. The more presence of a clear rainfall seasonality in Central Iberian basins would have favored the widespread of murids in this area.

The most interesting result of this study is that, although general trends can be recognized in the studied areas, the environmental response to the same global climatic signal seems to have been different in Inner Peninsula and coastal basins. The fact that global climate change manifests itself differently in specific regions is an expected result, but it is surprising to find markedly different climatic regimes and mammal faunas in such a small geographic area as the Iberian Peninsula. The different environmental response is especially evident in the Late Vallesian, when strongly different RPTs develop in Inner and Northeastern Spain. This fact points to the existence of different climatic regimes in both areas and a different climatic evolution that is congruent with the pattern seen today. Nowadays Catalan coastal basins and those of the Inner Peninsula present a Mediterranean climate, but belong to different bioclimatic units (Emberger, 1933; Allué Andrade, 1990; Quézel & Médail, 2003). The northeastern margin of the Iberian Peninsula belongs to the temperate Mediterranean stage while the interior basins are placed in the semiarid Mediterranean stage (see figure 6.5.). Some areas, such as the central Ebro Basin, and the Cabo de Gata, are particularly arid and belong to the arid Mediterranean stage that also includes areas of the southern Atlas. The Northwestern part of the Iberian Peninsula is dominated by Atlantic climate. Palynological data for the latest Miocene and Pliocene (Suc, 1984; Suc *et al.*, 1999) have shown the existence of a true Mediterranean climate during the Pliocene, and have revealed that the subdivision of this climate that we see today already existed. It seems that present-day situation started to take form by the Late Vallesian, although some regional climatic differentiation existed much earlier.

Chapter 7

The geography of a faunal turnover: tracking the Vallesian Crisis

7.1. The Vallesian Crisis and the Late Miocene faunal turnover

Abrupt faunal turnovers, along with the interplay between extinction, speciation and biogeographic change, all within the context of demonstrable physical environmental change, deserve a great deal of attention in paleobiology. As already emphasized by Elredge "There is today no more important topic in the general realm of "macroevolution" than these large-scale faunal turnovers, with their ecological and evolutionary components" (Elredge, 1996: 49).

The influence of climatic change and its relation to major ecological and evolutionary transitions on fossil mammal faunas has been a subject extensively studied during the past decades. Comprehensive studies have revealed the links between the changes in species composition to climatic events (see for example Vrba, 1985 and 1995; Van der Meulen & Daams, 1992; Fortelius *et al.*, 1996b; Agustí *et al.*, 1999; Bobe & Eck, 2001). However, as Alroy *et al.* (2000) have shown in the particular case of North American mammals, ecological and evolutionary changes are sometimes correlated to climatic shifts, whilst often other similar transitions occur at time of minor global climatic change. The patent effects of global climatic change upon mammal communities seems to be clear, even though the particular environmental conditions of the affected areas should still be empasized. Considering distribution of landmasses and past ecosystems can provide us with a better understanding of the mechanisms involved in faunal turnovers and why from time to time they occur at moments of moderate climatic shifts.

Within the Neogene the Late Miocene is a complex moment which appears punctuated by several climatic and phisiographic events. This period is characterized by a number of cooling episodes that predates the onset of the significant changes that will characterize the Pliocene epoch (with the onset of the glacial-interglacial dynamics in the Northern Hemisphere) (Zachos *et al.*, 2001). Furthermore, the progressive closure of eastern Mediterranean gateway during the late Serravallian – early Tortonian (Rögl, 1999; Popov *et al.*, 2004) and the uplift of the Tibetan plateau (Amano & Taira, 1992) led to a restructuring of atmospheric and marine circulation. These events resulted in the onset or intensification of monsoonal circulation in Asia as well as the appearance of a characteristic dry season in circum-Mediterranean regions (Kutzbach *et al.*, 1993).

In the terrestrial realm, these events must have influenced the patterns of dispersal and turnover among the mammalian faunas. In fact, the Late Miocene, that is the period covered by continental mammal stages Vallesian and Turolian, coincides with several faunal dispersals, induced by either climatic events, intercontinental relationships or by an interplay between both causes. Particularly, the Vallesian stage (between 11.1 Ma and 8 Ma) is characterized by the overall dispersal at 11.1 Ma of t hipparionine horses, which entered Eurasia from North America via the Bering Strait (Garcés *et al.*, 1997a; see also chapter 2). This event was possible due to an important sea level fall of about 100 m (Haq *et al.*, 1987; Miller *et al.*, 2005) coinciding with a major shift in δ^{18} O (Mi 5) (Miller *et al.*, 1991; Zachos *et al.*, 2001) which indicates general cooling. However, this climatic episode seems to have had few effects over land mammal communities, and in fact diversity increased continuously during the Early Vallesian (at least in Spain, see Agustí *et al.*, 1999).

This scenario changed abruptly at 9.7 Ma, when a significant mammal turnover, known as the Vallesian Crisis, profoundly altered the composition of the Western European terrestrial ecosystems. This point marks the boundary between the early and late Vallesian at 9.7 Ma (Garcés *et al.*, 1996). The Vallesian Crisis (sometimes referred to as Mid or Late Vallesian Crisis) was proposed on the basis of the rich mammal succession from the Vallès-Penedès Basin (northeastern Spain) and involved the disappearance of most of the Middle Miocene faunal elements adapted to wet subtropical environments (Agustí & Moyà-Solà, 1990; Moyà-Solà & Agustí, 1990; Agustí *et al.*, 1999). It has also been suggested that the Vallesian Crisis extended to the Central European mammal faunas (Fortelius *et al.*, 1996b; Franzen & Storch, 1999). The effects of the crisis in that area seem to have been less noticeable, and thus some Middle Miocene relics persisted in Germany, Austria and Hungary during the late Vallesian. On the other hand the Vallesian Crisis is not observed in the Rhône Valley (Mein, 1999b), while in southeastern Europe it seems to coincide with an increase in diversity and turnover. At 9.7 Ma a minor isotopic event is recorded, Mi 7 (Miller *et al.*, 1991; Zachos *et al.*, 2001), although it is even weaker than previous Mi 6 on this occasion the shift in δ^{18} O is accompanied by a noticeable lowering of the sea level (Haq *et al.*, 1987; Miller *et al.*, 2005). The Vallesian Crisis has been related to this climatic event (Agustí *et al.*, 1999), which would have implied the onset of a late Miocene glaciation in the Arctic zones (Zubakov & Borzemkova, 1990). This scenario of high latitude cooling and low latitude drying would have continued during the Turolian, a stage which records the progressive extension to the west of the bovid- and giraffid-dominated faunas that characterized Anatolian communities (Fortelius *et al.*, 1996b; Koufos, 2003).

As exposed above, after decades of study, a general picture of the climatic changes taking place during the late Miocene as well as their effect over European mammal is emerging. However, problems arise when focusing in concrete events, areas, or time spans. For example, the effects of the Vallesian Crisis and the existence of such event in some areas are still debated. The absence of a reasonably complete record in many countries may obscure the effects of the crisis in these areas, or it simply indicates thatthe crisis did not occur in there. There seems to be a loss of diversity in Spain and Central Europe, but in Anatolia diversity increased during the crisis as result of the entry of new taxa. The main aim of the present chapter is to shed new light into these important issues.

7.2. Material and methods

7.2.1. The database

The study area comprises the western part of the Old World, covering a latitudinal range from 35 to 55 degrees and from –10 to 40 degrees of longitude. Northern Africa and the British Islands are not included. We have selected a time span covering nearly all the late Miocene, ranging from the Late Aragonian (Middle Miocene) until the end of the epoch (13.8-4.9 Ma, numerical ages after Agustí *et al.*, 2001). This time span covers seven MN zones ("Mammal Neogene" biozones). See table 7.1. for boundary ages and duration of the zones.

The data source for this chapter is the version of the NOW (Neogene Old World) database (available at http://www.helsinki.fi/science/now/data.html) released in July

2003, which has been updated and expanded with data from many Spanish localities. We have included localities dated to at least the MN zone level of resolution and discarded those inaccurately positioned. Finally a genera occurrence by localities database has been written using the data compiled. For this second database we have selected only the localities from the first one that included at least five genera. If more than one species of the same genus is present in the locality the genus is counted only once. Taxa identified to a suprageneric level are counted as an additional genus only if there are no identified genera of the same suprageneric level. For instance, if in a locality the genus *Deinotherium* is present and we have also recorded Proboscidea indet., we only count one genus: *Deinotherium*. If in another site only Proboscidea indet. is recorded, it counts as a genus in our database. Macromammals and micromammals have been recorded in separate databases because they are recovered using different field methods. As a result we have obtained a database that includes a total of 299 sites: 111 macromammal sites and 188 micromammal sites (many sites include both macromammals and micromammals and are counted twice). A total of 443 taxa are recorded in the studied time span: 254 macromammals and 189 micromammals. In order to study the geographic trends in mammal assemblages through time we have divided the western Old World in 40 squares of the same area. These squares are defined by the intersection of latitude and longitude lines. Those are equally spaced so the side of each square is 5 °. Each site is assigned to one square numbered from 1 to 40 (see fig. 7.1. and table 7.2.). Some squares will obviously include land and sea, and the ratio land to sea will not always be the same. Although we consider that this fact will not affect the results a great deal, it should not be overlooked. The appendix 7.1. shows the localities included in the correspondence analyses of figs 7.3 to 7.9. as well as the square in which each one is included.

Land Mammal Ages	MN Zones	lower boundary age (Ma)	upper boundary age (Ma)	duration (My)
Turolian	MN 13	6.8	4.9	1.9
	MN 12	7.5	6.8	0.7
	MN 11	8.7	7.5	1.2
Vallesian	MN 10	9.7	8.7	1
	MN 9	11.1	9.7	1.4
Aragonian	MN 7+8	12.5	11.1	1.4
	MN 6	13.8	12.5	1.3

Table 7.1. MN zones comprised within the time span studied. For each MN zone we have indicated the numerical age of their top and bottom boundaries as well as its duration. Numerical ages after Agustí *et al.* (2001).

7.2.2. Provinciality

For each MN zone we have constructed two different taxa-occurrence-by-locality matrices, since macromammals and micromammals are considered separately. Correspondence Analysis (CA) has been performed on each matrix using the program PAST 1.65 (see chapter 6 for a brief description of the method)[34].

However, there is an important drawback in our provinciality analysis: the sites included in an MN zone do not have the same age. This would not be a significant problem if the MN zones consisted in relatively short time spans, but some zones, such as MN 7+8 and MN 9 last nearly 1.5 Ma. Unfortunately, more accurate calibrations are

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[34] In an earlier version of this chapter (Casanovas-Vilar *et al.*, 2005) cluster analysis was used. However, as pointed in the discussion of section 6.2.3. Correspondence Analysis or other ordination techniques such as Global Non-Metric Multidimensional Scaling may be a better approach to this kind of biogeographical and paleoecological studies.

not available for most of the sites, so an analysis at a finer level than an MN zone as a whole is not possible considering our data set. Thus in some cases the differences expressed by the CA may result from the fact that the localities compared are not contemporary. We faced similar problems in chapter 6, and as in that case this kind of situations will be discussed *a posteriori*.

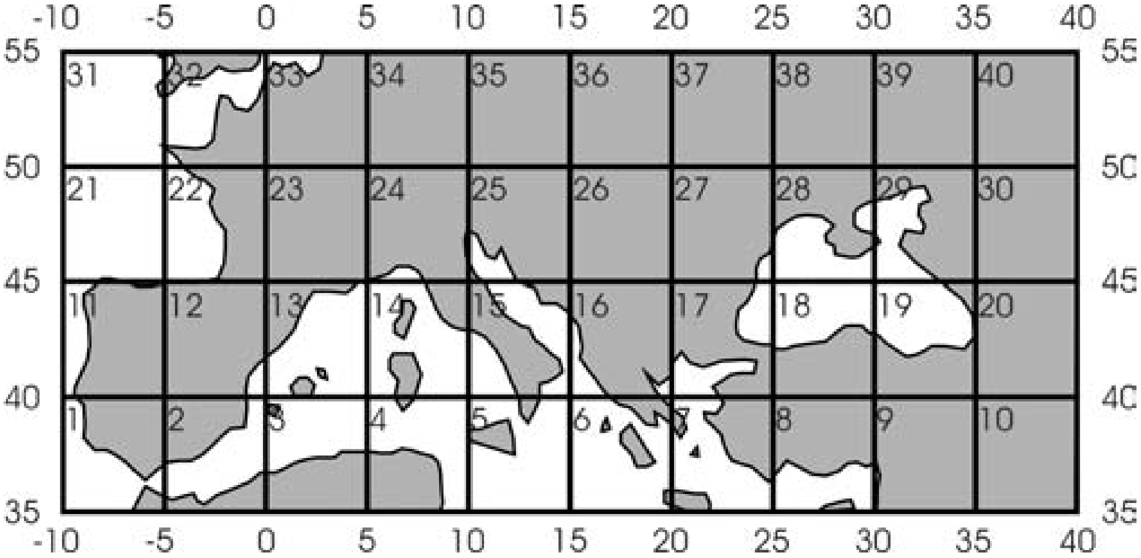


Figure 7.1. Map of the study area. The western Old World is divided in 40 squares of the same area defined by the intersection of latitude and longitude lines, each one equally separated 5 ° from their nearest neighbors. Each square is numbered from 1 until 40.

7.2.3. Taxonomic diversity

We have calculated taxonomic diversity for each MN zone for the whole study area and for each square (see fig. 7.1.) in order to explore geographic trends in diversity throughout time. We have calculated total diversity in each interval (N_{tot}) as:

$$N_{tot} = N_{FL} + N_{bL} + N_{Ft} + N_{bt}$$

Where N_{FL} is the number of genera confined to the interval (singletons *sensu* Foote, 2000); N_{bL} is the number that cross the bottom boundary only; N_{Ft} is the number that cross the top boundary only; and N_{bt} is the number that cross both boundaries. N_{bt} also includes taxa known before and after the time span but not during (see fig. 7.2.). These parameters are also calculated for each square, taking into account only the

	MACROMAMMALS (% of total number of localities in each MN)							MICROMAMMALS (% of total number of localities in each MN)						
square	**MN 6**	**MN 7 + 8**	**MN 9**	**MN 10**	**MN 11**	**MN 12**	**MN 13**	**MN 6**	**MN 7 + 8**	**MN 9**	**MN 10**	**MN 11**	**MN 12**	**MN 13**
1	0	0	0	0	0	0	0	8	0	0	7	0	0	0
2	0	0	0	0	7	7	11	0	0	0	0	4	4	15
3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	5	0	0	0	0	0	0	0
7	0	0	0	0	0	10	0	0	4	0	0	0	0	0
8	0	6	3	0	14	13	0	0	4	0	0	0	0	0
9	11	6	0	6	7	3	0	4	4	0	0	0	0	0
10	0	0	0	0	0	0	0	0	4	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	3	0	0	4
12	22	0	7	18	21	27	37	50	23	43	64	46	81	56
13	17	56	31	24	7	3	5	4	35	26	18	12	0	7
14	0	0	0	0	0	3	0	0	0	0	0	0	4	4
15	0	0	0	0	0	10	16	0	0	0	0	4	4	7
16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	6	0	0	24	21	0	21	0	4	0	0	4	0	7
18	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	7	3	0	0	0	0	0	0	4	0
20	0	0	0	6	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	5	8	0	0
24	11	6	31	6	7	0	0	17	8	4	5	15	0	0
25	11	13	3	0	0	0	0	4	4	0	0	0	0	0
26	17	0	7	0	7	0	5	4	4	9	3	8	0	0
27	0	6	0	0	0	0	0	0	4	4	0	0	0	0
28	0	0	17	18	0	13	0	0	0	9	0	0	4	0
29	0	0	0	0	0	3	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	6	0	0	0	0	0	0	8	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	0	6	0	0	0	0	0	0	4	0	0	0	0	0
37	0	0	0	0	0	0	0	0	0	4	0	0	0	0
38	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	0	0	0	0	0	3	0	0	0	0	0	0	0	0

Table 7.2. (previous page) Per-square percent of the total number of macromammal and micromammal sites recorded in each MN zone. The higher proportion of both micro and macromammal localities comes from central and northeastern Spain, so it is expected that Spanish results will clearly bias calculations when Europe is considered as a whole.

genera present in this single square and discarding those present in adjacent ones. N_{tot} is the total number of taxa that existed during the interval. This diversity measure is strongly affected by the duration of the time span considered: the longer time interval the higher the number of N_{FL}. Diversity measures that estimate standing diversity at a point in time express better the number of taxa susceptible to origination or extinction at an instant in time (Van Valen, 1984). One of this kind of diversity measure is the estimated mean standing diversity (N_{st}):

$$N_{st} = (N_b + N_t) / 2$$

Where,

$$N_b = N_{bL} + N_{bt}$$

and similarly,

$$N_t = N_{Ft} + N_{bt}$$

N_b and N_t are the bottom-boundary and top-boundary crossers respectively. Thus, N_{st} estimates the diversity as their average. Due to its definition N_{st} cannot be calculated for our first and last intervals (i. e. MN 6 and MN 13). Foote (2000) has shown the advantages and drawbacks of this and other diversity measures. Modeling shows that this measure becomes progressively worse as the length of the interval increases, thus overestimating mean standing diversity if origination rate is different to extinction rate. The advantage of this measure is that singletons are simply irrelevant. Singletons are especially sensitive to variation in preservation and interval length, so basing diversity measures in the estimated number of taxa partly removes these undesirable effects. Unfortunately there is not any measure of absolute diversity independent of temporal variation in preservation and interval length.

We have also estimated changes in diversity using the ratio (Foote, 2000):

$$\ln (N_t / N_b)$$

Normalized by interval length (Δt), which gives the proportional change in diversity throughout an interval. This measure is directly derived from the difference between origination and extinction rates (see below) and is particularly useful because all differences in species richness that may exist between areas (many of them resulting from the quality of their record) are leveled of. The proportional change in diversity is calculated for the study area as a whole as well as for the selected squares. As for the standing diversity, it cannot be calculated for the first and the last interval in the studied time span.

7.2.4. Origination and extinction rates

We have calculated estimated per-capita origination ($\hat{p}$) and extinction ($\hat{q}$) rates (Foote, 2000) for the study area as a whole as well as for the selected squares:

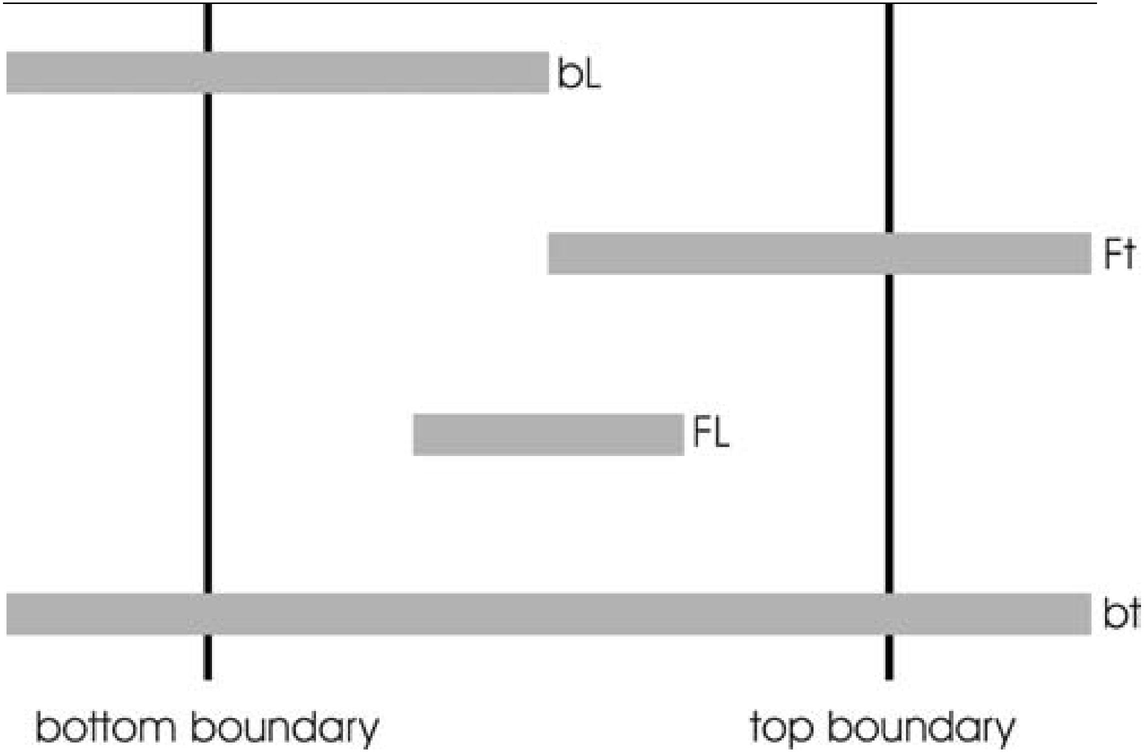


Figure 7.2. Illustration of the four fundamental classes of taxa present during a stratigraphic interval. FL are the taxa confined to the interval, the so-called singletons; bL are the taxa that cross the bottom boundary only; Ft are the taxa that cross the top boundary only; and bt are the taxa that cross both boundaries, the range-through taxa.

$$\hat{p} = -\ln (N_{bt} / N_t) / \Delta t$$

$$\hat{q} = -\ln (N_{bt} / N_b) / \Delta t$$

As modeling has shown (Foote, 2000) these estimates are unaffected by interval length. The ratios N_{bt} / N_t and N_{bt} / N_b decay exponentially with time if rates are constant within the interval; thus the logarithm of each ratio declines linearly with time. Even if true origination and extinction rates (p and q respectively) are not constant, $\hat{p}$ and $\hat{q}$ provide unbiased estimates of the mean rate within an interval. In contrast to other rate measures, these rates do not rely on counting events within the interval and normalizing by a diversity measure. Thus $\hat{p}$ is not affected by extinction rate, while $\hat{q}$ is unaffected by origination rate. Singletons are irrelevant, so these rates are expected to be less sensitive to variation in preservation rates. The ratio ln (N_t / N_b) used here to estimate relative changes in diversity derives from subtracting $\hat{q}$ from $\hat{p}$. These measures were intended for analyzing the entire fossil record of animal groups, rather than for studying small areas and concrete time intervals. So in our case it is accurate to refer to $\hat{p}$ and $\hat{q}$ as per-capita entry and exit rates respectively because true origination and extinction may have taken place outside the area considered. Then $\hat{p}$ and $\hat{q}$ include not only true originations and extinctions but also immigration and regional disappearance of taxa.

7.2.5. Distinguishing variation in origination and extinction rates from variation in the rates of preservation

A singular increase in preservation rate in one interval will cause an increase in both rates in this interval (see Foote, 2000; his figure 15). The number of genera that would have made their last appearance in preceding intervals is reduced because they now appear last in the interval with better preservation. The same is true for first appearances in succeeding intervals. Metrics underestimate extinction before the pulse in preservation, and underestimate origination afterwards. The measures are also affected by a singular decrease in preservation in an opposite way. In contrast, a pulse in extinction will not affect origination, and likewise a pulse in origination will not affect extinction (see Foote, 2000; his figure 12). We will the have to analyze the variation in apparent taxonomic rates that is potentially attributable to variation in preservation rates.

Preservation probability (R_i) can be estimated as:

$$R_i = X_{bt,\ samp} / X_{bt}$$

Where X_{bt} is the number of genera known both before and after the interval and $X_{bt,\ samp}$ is the number of these genera actually sampled during the interval. Preservation rate r_i is estimated as (Foote, 2000):

$$r_i = -\ln (1 - R_i) / \Delta t$$

If variations in apparent taxonomic rates were dominated by variation in preservation rates, then the correlation between both kinds of rates would be large and positive. We will calculate r_i for the study area as a whole as well as for selected squares. We will test for correlation between both variables by calculating Kendall's τ (see Hammer & Harper, 2006 for a brief description of this non-parametric correlation method). As in previous calculations, by definition preservation rates cannot be calculated for our first and last time intervals.

7.3. Results

7.3.1. Provinciality

The results of the correspondence analyses performed on our dataset are displayed in figures 7.3 to 7.9. In most cases the names of the localities are not indicated in order to avoid confusion, since in many graphs several points cluster in a small portion of the multivariate space (see for example 7.6b or 7.8b). We have divided the study area into seven broad geographic regions: Iberian Peninsula, France, Italy, Central Europe, Eastern Europe, Eastern Mediterranean and Anatolia (the countries included in each region are indicated in table 7.3.). These regions do not correspond to *a priori* defined or "expected" biogeographic regions, and this distinction has been just performed in order to facilitate the interpretation of the graphs.

The correspondence analyses (figs. 7.3.-7.9.) evidence the existence of a high degree of provinciality although there are some minor incongruities (see for example

Table 7.3. The study area is divided in seven geographic regions in order to facilitate its interpretation. The countries included in each one of these regions are listed below. The countries that were not represented by any locality in our database are not considered.

Region	Included countries
Iberian Peninsula	Spain, Portugal
France	France
Italy	Italy
Central Europe	Germany, Switzerland, Austria, Hungary, Poland, Slovakia
Eastern Europe	Romany, Ukraine, Moldova
Eastern Mediterranean	Greece, Serbia
Anatolia	Turkey

fig. 7.4.b.). The same broad bioprovinces can be recognized considering micro- and macromammals. Furthermore, the results show the maintenance of these bioprovinces during most of the considered time span. In a broad view these bioprovinces include: an eastern province (comprising Anatolia, the Eastern Mediterranean and in some time intervals Eastern Europe) and a western one, including Central Europe and the Western Mediterranean. The existence of two distinct provinces occurring synchronously in the Late Miocene was first recognized by Tobien (1967) and has been confirmed by subsequent studies (see for example Bernor, 1984; Fortelius *et al.*, 1996b). This well-known eastern bioprovince is also called the “sub-Paratethyan” (Bernor, 1984) or “Greek-Iranian” province (De Bonis *et al.*, 1992). However, our analyses indicate that the western province is not very uniform and may be divided into three distinct provinces (or subprovinces) during most or the entire time-span in consideration: a Central European province, an Iberian province (possibly including southern France during most of its existence) and finally an Italian province during the Turolian. Crusafont (1954, 1958) had already emphasized the endemic character of the Iberian faunas. Later on Hartenberger *et al.* (1966) recognized a zoogeographic unit, the Ibero-Occitanian province, comprising the whole Iberian Peninsula plus southern France. Finally Agustí (1981, 1990) proposed that the Iberian Peninsula also comprises two different biogeographic provinces, Ibero-Central and Ibero-Levant, which show significant differences during most of the Miocene. The Tusco-Sardinian bioprovince is well-known by its distinct, bizarre insular faunas (for recent synthesis see Rook *et al.*, 1999; Moyà-Solà *et al.*, 1999a; Bernor *et al.* 2001).

In MN 6 (fig.7.3.) the localities cluster together in three main groups. When the macromammals are considered separately (fig. 7.3.a) these include a group defined by Central European sites, another including French and Iberian sites, and a last group which only includes two sites: Çandir (Turkey) and Prebreza (Serbia) (ÇA and PREZ). In the case of micromammals (fig. 7.3.b) the Central European and French sites appear together and the Iberian sites are weakly separated from these localities. The micromammal fauna from Çandir (Turkey) appears isolated. In summary three main provinces can be recognized: the Greek-Iranian one, the Central European province and the Iberian province. However, the distinction between a Central European and an Iberian province is still diffuse, so in the case of macromammals the Iberian sites appear very close to French ones. On the contrary, when only micromammals are considered the French sites seem closer to the Central European ones. The French and Central European localities are characterized by a high diversity of insectivores, dormice and “cricetids”. Three Swiss sites (Rümikon, Wiesholz and Schwamendingen) cluster apart, due to a higher diversity of flying squirrels and eomyids. The single micromammal

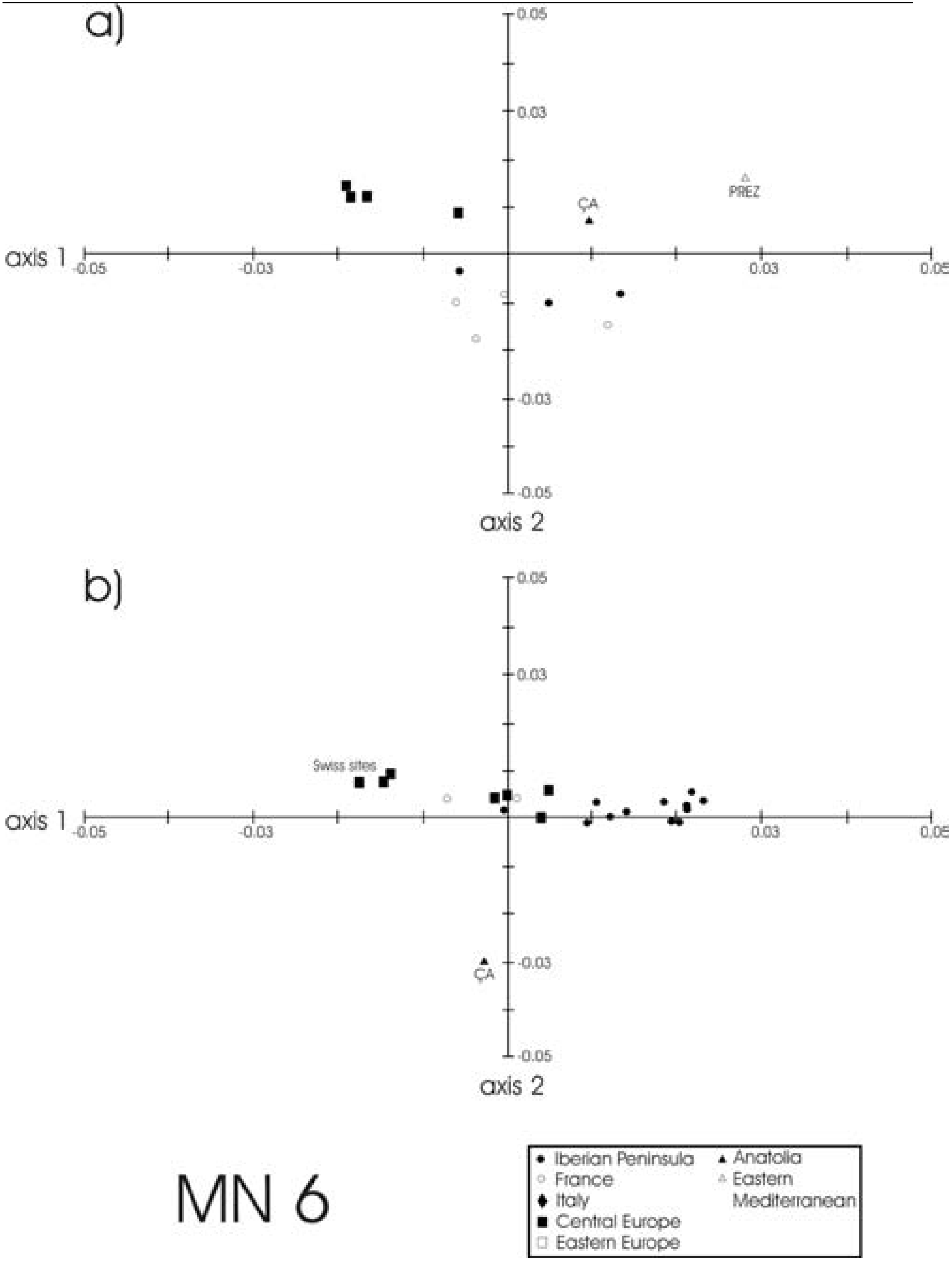


Figure 7.3. Correspondence analyses for MN 6 micro and macromammal sites. The exact position of the different sites in the multivariate space is given in the appendix 7.1.

fauna from the Greek-Iranian province (Çandir, Turkey) also appears isolated from the rest of the sites. This fauna is characterized by the absence of many western "cricetid" genera, and by the presence of spalacids. When considering the macromammals, the eastern faunas (Turkey, Serbia) are clearly separated from western ones. The former are characterized by a higher bovid diversity including many exclusively eastern genera, although some reached Central Europe (*Turkoceras*, *Hypsodontus*). Central European faunas are characterized by the presence of the rhinos *Alicornops*, *Plesiaceratherium* and *Hoploaceratherium*, along with a higher diversity of Suidae and Cervidae.

Macromammal faunas of Spain included less Cervidae genera and appear somewhat different from the Central European ones.

In MN 7+8 the situation is very similar (fig. 7.4.), the Greek-Iranian province is clearly distinguished, but the Iberian sites often appear altogether with the Central European ones. When considering the micromammals (fig. 7.4.b), the Greek-Iranian province is clearly recognized, being characterized by a relatively low diversity of dormice and squirrels. The "cricetids" are also distinct, thus different forms lived in the East and the West of Europe. An illustrative example is the different lineages of hypsodont Cricetodontini which are represented by the genus *Byzantinia* in the East and *Hispanomys* in the West. Both genera arose from *Cricetodon* (although from different species) and followed a parallel evolution during the late Miocene (for a review of the evolutionary history of the Cricetodontini see De Bruijn *et al.*, 1993; and De Bruijn & Ünay, 1996). However, there are two Eastern Mediterranean sites which are plotted within the group defined by Central European and Iberian ones: Plakia (Greece) and Comanesti 1 (Romania) (PLAK and COM1). This apparent incongruence emerges from the fact that the small mammal fauna from both sites is not very rich, and, particularly in the case of Comanesti 1, includes several dormice that are common in Central European sites. The Central European, French and Iberian sites appear to be arranged in a latitudinal continuum following axis 2 (fig. 7.4.b), whilst the sites from inner Spanish basins taking the lower values. This differentiation is due to the presence of rodent assemblages in Central Spain which are dominated by a few species of "cricetids" and present a much lower diversity of dormice genera (see chapter 6). Other Spanish sites, situated in the northeastern margin of the peninsula (Castell de Barberà, CB; Sant Quirze, SQ; or Barranc de Can Vila 1, BCV1; all from the Vallès-Penedès Basin), cluster with Central European sites due to their more diverse rodent faunas including many dormice genera and also some beavers, flying squirrels and eomyids, which are very rare in the inner Peninsula. An important bovid radiation occurred in the Eastern Mediterranean at this time, evidenced by the presence of more than six bovid species in Turkish sites. The occurrence of these elements explains why these sites appear so different from the rest of the European ones in the macromammal CA (fig. 7.4.a). The Central European and Iberian localities cluster all together, being characterized by their less diverse bovid fauna as well as by the presence of certain rhinos (*Dicerorhinus steinheimensis*), suids (*Albanohyus*) and primates. Overall, the similarity between the Central European and Iberian provinces seems to have increased as compared to MN 6 (see also fig. 7.10.a).

The MN 9 recorded the dispersal of hipparionine horses in the Old World. Some other taxa extended their range from the East and accompanied the "hipparions" in their dispersal into Western Europe (the sabertoothed cat *Machairodus* for instance, while the hyaenid *Thalassictis* and the giraffid *Palaeotragus* form part of an older migration wave by the end of MN 7+8). This event coincided with a rhino turnover in Eastern Europe (appearance of *Ceratotherium* and *Chilotherium*) while bovid diversity continued rising. There seems to be an absence of turnover in macromammal faunas in central and southwestern Europe, and the new immigrants are simply incorporated to the pre-existing faunas. When considering the macromammals, the Spanish sites appear together with German, Swiss and Hungarian ones showing a few differences between them (fig. 7.5.a). The locality of Los Valles de Fuentidueña (Spain) (VFÑ) is plotted

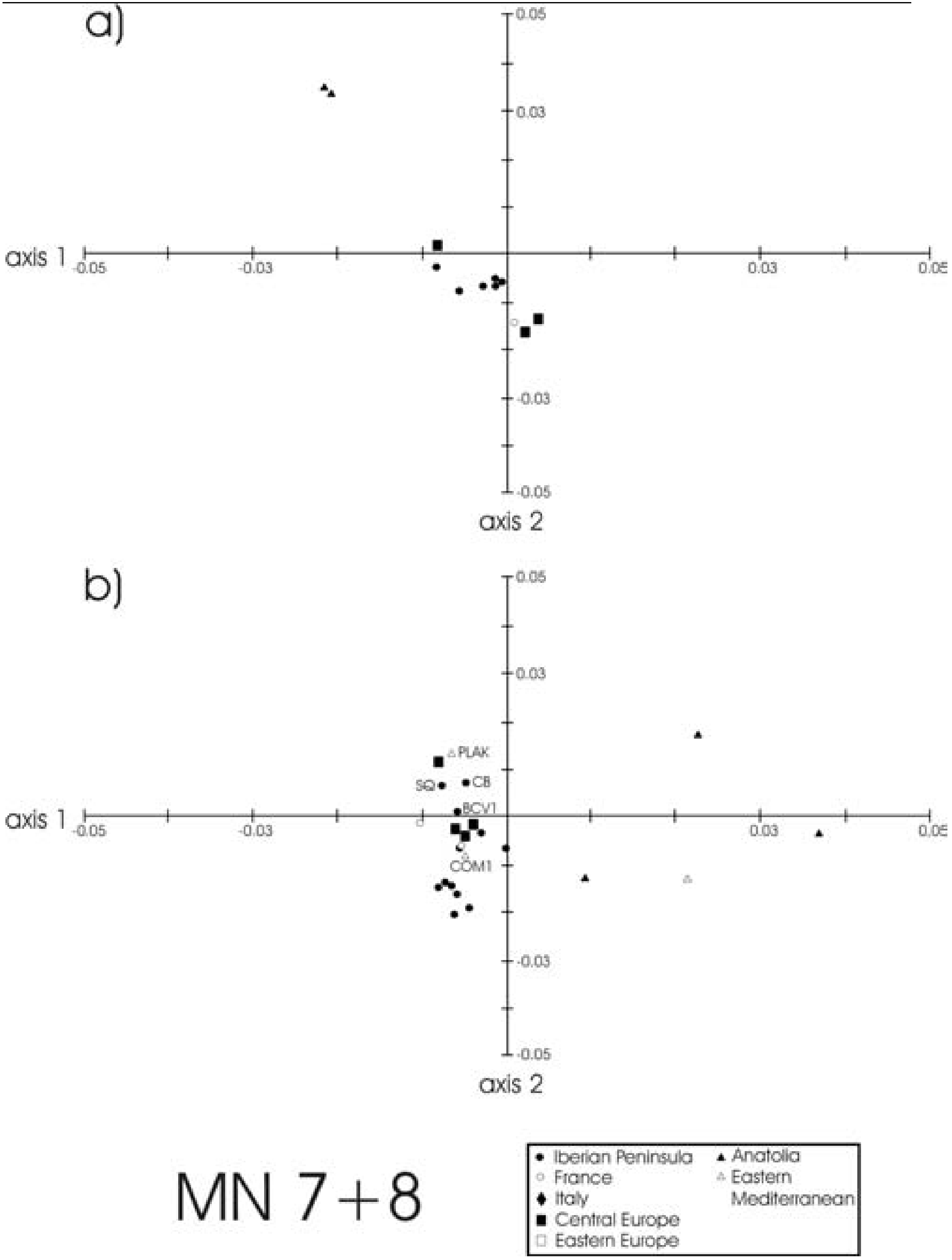


Figure 7.4. Correspondence analyses for MN 7+8 micro and macromammal sites. The exact position of the different sites in the multivariate space is given in the appendix 7.1.

closer to Moldavian sites (Buzhor 1, BUZ1; and Kalfa, KF), certainly because of its poorer macromammal fauna if compared to other Spanish sites such as Can Llobateres and Can Ponsic. The Moldavian sites are clearly different from European ones, thus belonging to the Greek-Iranian province, although they also differ from the Turkish site Esme Akçaköy (EAKY) because bovid diversity in Moldova appears to have been lower. The analysis based on micromammals shows the three main provinces (fig. 7.5.b). The Greek-Iranian province (represented only by Moldovan sites) is completely split from a great group including Central Europe and the Iberian Peninsula. These later provinces are more dissimilar than they were in previous analyses. Southwestern Europe (Iberian Peninsula and Southern France) is characterized by "cricetid"-dominated assemblages, while the rest of rodent families are less diverse. The genus *Cricetulodon* appears in Spain at the beginning of the Vallesian and will be a major component of the MN 9 rodent faunas (see chapter 6). This genus is an eastern immigrant (recorded in the Turkish MN 7+8 site Bayraktepe 1), which is absent from Central European sites. Another eastern immigrant is the ground dormouse *Myomimus*, which is very common in the faunas of the inner Spanish basins (see chapter 6). Central European faunas were similar to those of the MN 7+8, with high levels of diversity and several genera dormice, along with ground and flying squirrels as well as beavers. The Spanish localities of Can Llobateres (CLL1) and Can Ponsic (CP1) (Vallès-Penedès Basin), exhibit a very diverse rodent fauna (although still dominated by *Cricetulodon*) similar to that of Central European localities, so they plot closer to these sites.

During the Late Vallesian (MN 10) the differentiation amongst Central European and Iberian micromammal faunas appears to have been greater (fig. 7.6.b). The Central European province, which mainly includes French sites is characterized by the presence of a still diverse "cricetid" and glirid fauna. In contrast, the rodent faunas in the Iberian province are very poor and murids have assumed the role of "cricetids", thus becoming the most abundant rodents in most of the sites. The murids evolved during the Middle Miocene in Asia, and entered Europe by MN 9. The first occurrence of the murid *Progonomys* in Turkey is dated at 10.135 Ma (Kappelman *et al*. 2003), while in Spain it is recorded somewhat later, at 9.7 Ma in the Vallès-Penedès Basin (Garcés *et al*., 1996; see also chapter 2). The murids will characterize the Iberian rodent assemblages of the Late Vallesian and the Turolian. However, they will not become major components of the rodent assemblages from the Vallès-Penedès Basin, which are dominated by the "cricetid" *Rotundomys* and still show some affinities with the Central European sites, since eomyids, arboreal dormice and flying squirrels are recorded at some sites (see chapter 6). As far as the macromammals are concerned, two bioprovinces are clearly distinguished, an eastern and a western one, although three Greek sites (Pentalophos, Ravin de la Pluie and Ravin des Zouaves 1) plot very near to those in the west (fig. 7.6.a). The rest of eastern sites include Moldovan and Turkish localities characterized by a high diversity of open-country Bovidae and Giraffidae. Furthermore, during the Late Vallesian a process of vicariant evolution affected the hipparionine horses leading to the origin of *Cremohipparion* in the Eastern Mediterranean, and to *Hipparion* s. s. in the West (Bernor & Armour-Chelu, 1999). Western faunas include less Bovoidea and a higher diversity of Cervidae, Suidae and Tragulidae besides some eastern immigrants such as the hyaena *Adcrocuta* and the Boselaphini *Tragoportax*. The clustering of Greek localities closer to western ones reflects the diachronous dispersal of open-country eastern herbivores, since many genera are recorded in Moldovan and Turkish sites but not in Greek ones (such as *Oioceros*, *Nisidorcas* or *Palaeoryx*).

Similarity between Greek and Turkish macromammal assemblages increased during MN 11 (fig. 7.7.a) with the entry into Greece of open-country Bovoidea and Giraffidae. The cercopithecid monkeys (*Mesopithecus*) and the proboscidean *Choerolophodon* followed these artyodactyls in their dispersal. These open-country faunas will be characteristic of the Greek-Iranian province during the whole Turolian.

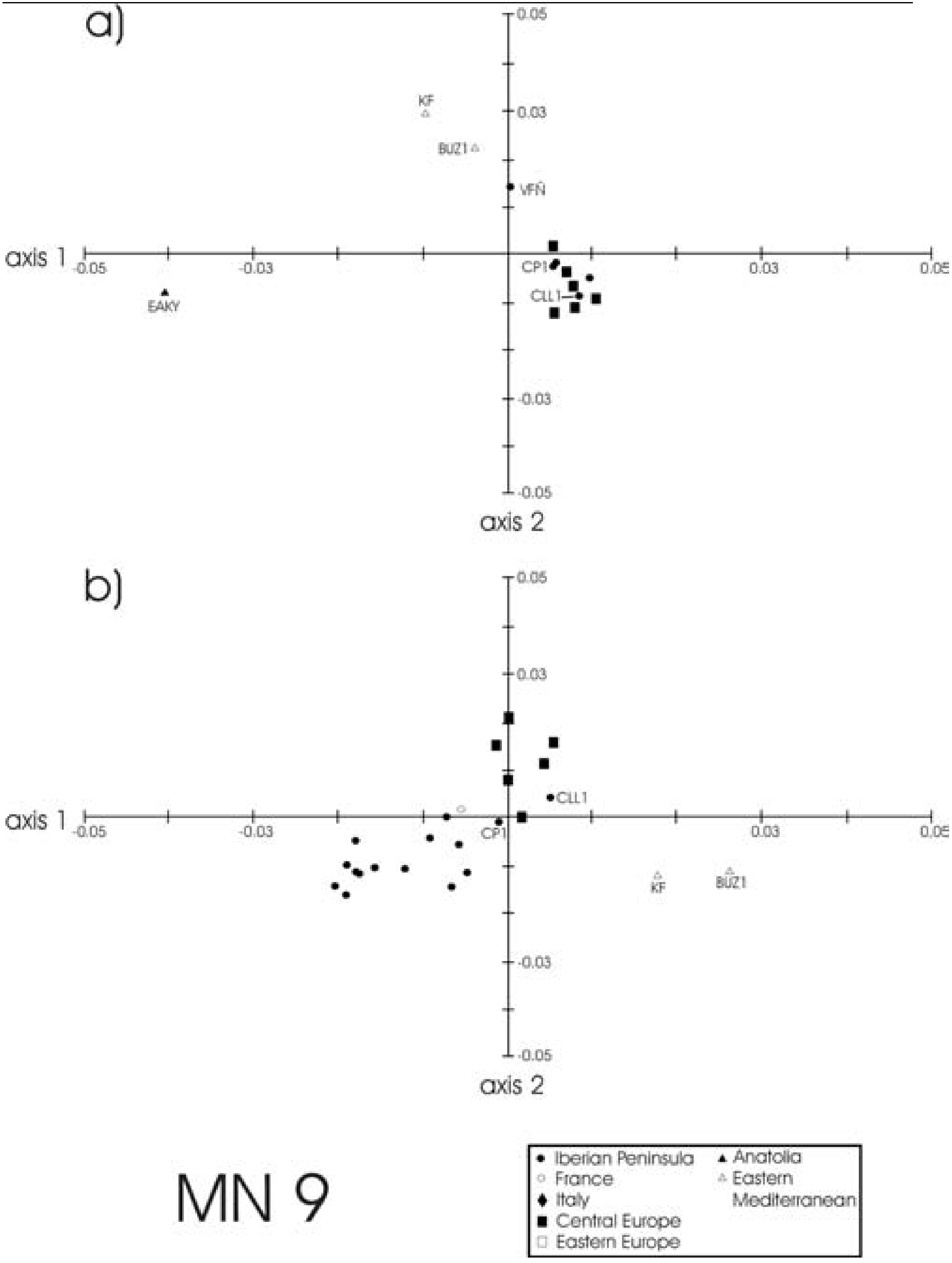


Figure 7.5. Correspondence analyses for MN 9 micro and macromammal sites. The exact position of the different sites in the multivariate space is given in the appendix 7.1.

The analysis also distinguishes an Iberian province with impoverished macromammal faunas. There is a third province which is very different from the remaining ones: the Central European province. The persistence of many forest-adapted families (tragulids, tapirids) and the absence of open-country Bovoidea is the main criterion for its distinction. When considering micromammals, the Greek-Iranian province is

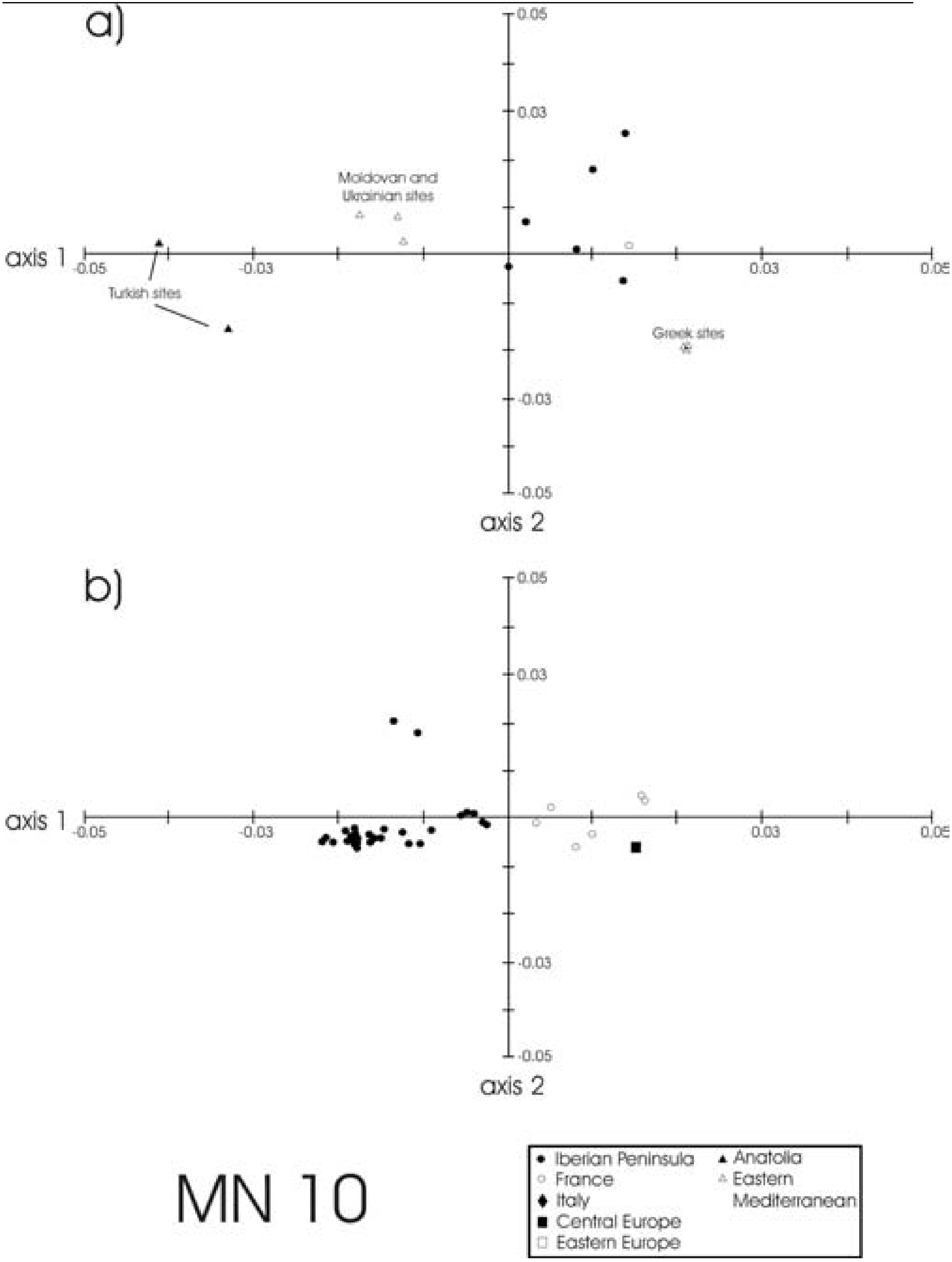


Figure 7.6. Correspondence analyses for MN 10 micro and macromammal sites. The exact position of the different sites in the multivariate space is given in the appendix 7.1.

represented by the poor fauna of Lefkon (LK; fig. 7.7.b) that clusters near to the French sites due to the presence of certain rodent (*Kowalskia*, *Pliopetaurista*, *Progonomys*) and insectivore (*Desmanella*) genera. The faunas of Central Europe also appear as clearly different from the Iberian ones and are characterized by a fauna still diverse including several arboreal dormice and squirrels, plus some mice, beavers and "microtoid

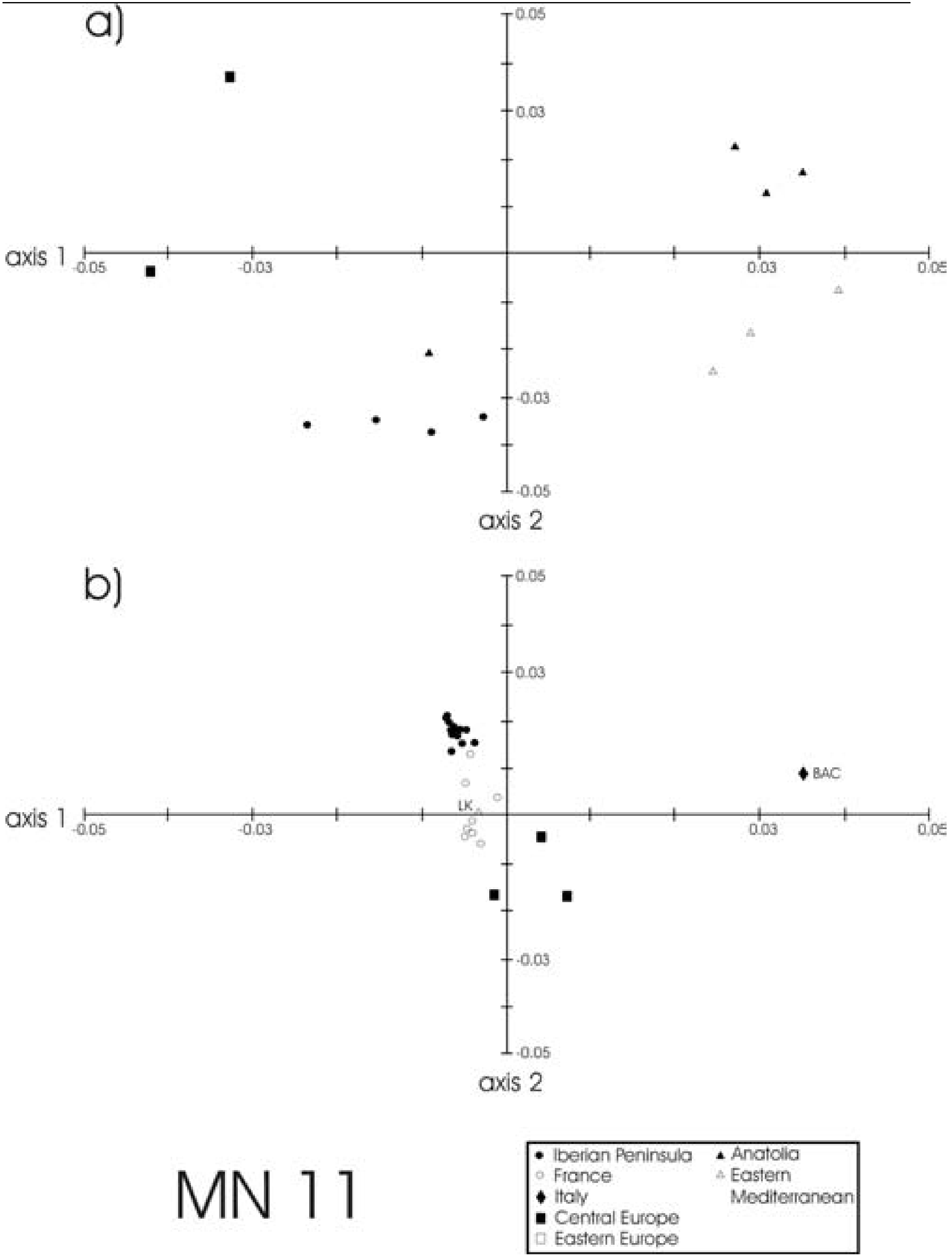


Figure 7.7. Correspondence analyses for MN 11 micro and macromammal sites. The exact position of the different sites in the multivariate space is given in the appendix 7.1.

cricetids" (sensu Schaub, 1934). The rodent faunas of the Iberian province are very poor and characterized by the murids *Parapodemus*, *Occitanomys* and *Huerzelerimys*. Minor components of the fauna include the Cricetinae *Kowalskia* and the Cricetodontini *Hispanomys*. A new fourth group appears in the micromammal CA, the Tusco-Sardinian province, which only includes one site: Baccinello V0 (BAC). This is an insular fauna characterized by its low generic richness as well as by the presence of some endemic genera such as the dormouse *Anthracoglis* or the lagomorph *Paludotona*.

The highest degree of similarity in between macromammal sites is recorded at MN 12 (fig. 7.8.a), when eastern faunas attain their maximum range. The macromamamal localities appear arranged in a longitudinal continuum along axis 2, with the localities from the Iberian Peninsula taking the lower values. This is due to the fact that bovid diversity in Western Europe is much lower. The insular fauna from the Tusco-Sardinian province continued evolving in isolation from the continent, and therefore it is clearly distinguished. The high degree of similarity evidenced by the macromammal CA is not recorded by the micromammal faunas (fig. 7.8.b). The Iberian rodent faunas are still very poor, and lack certain taxa characteristic of the East. The Central European record disappears at MN 11, so the persistence of a Central European province cannot be confirmed (see also fig. 7.10.b).

The Messinian (MN 13) records another increase in provinciality, with further separation between Iberian and Eastern sites (see also fig. 7.10.c). The Iberian province is characterized by its low macromammal diversity, except in the case of the locality of Venta del Moro (VMOR) which is slightly differenced from the others (fig. 7.9.a). This site records the dispersal into Spain of the canids of the genus *Nyctereutes* and camelids (*Paracamelus*) from North America. The relatively poor fauna from Gravitelli (Italy) (GRA) may account for its closeness to Spanish sites. The Greek-Iranian province is only represented by Greek sites with a diverse bovid and giraffid fauna inherited from the Turolian.

Certain Italian faunas (Brisighella, BRI; Casino, CAS; and Baccinello V3, BACV3) appear rather different from those of the remaining sites (fig. 7.9.a). Given the fact that the Tusco-Sardinian province, together with its bizarre insular faunas disappeared when Italy became part of the main land during the Messinian, the differences observed are not an insularity effect. This supposed new Italian province shows a clear Central European influence, since these sites include many taxa present in Central Europe during MN 11, but which are absent from the rest of the provinces since MN 10 (*Tapirus*, *Euprox*, Moschidae), as well as the exclusively Central European proboscidean *Zygolophodon*. The macromammal community is completed with few immigrants from other areas such as *Mesopithecus* and elements that are going to characterize the Pliocene (*Parabos*, *Korynochoerus* (= *Propotamochoerus*), *Nyctereutes*). The presence of many MN 11 relicts may support the existence of a Central European province extending at least until the end of the Miocene. Many genera from Central Europe would have arrived into Italy when it became part of main land. But when considering the micromammal faunas the existence of this Italian province seems less clear, with some localities such as Brisighella appearing as clearly distinct while others such as Baccinello V3 or Ciabot Cagna (CIACG) do not (fig. 7.9.b). Brisighella is clearly distinguished due to its rich chiropter fauna, which contrasts with the remaining sites. In the case of the other Italian sites the micromammal fauna resembles that of the Iberian localities, however, some endemic taxa such as *Anthracoglis* are still recorded.

By MN 13 the rabbits and hares (Leporidae) appear in all micromammal faunas of Europe. The Leporidae evolved in North America and dispersed into Eurasia during the Messinian, but they did not replace the Ochotonidae (the Lagomorph family

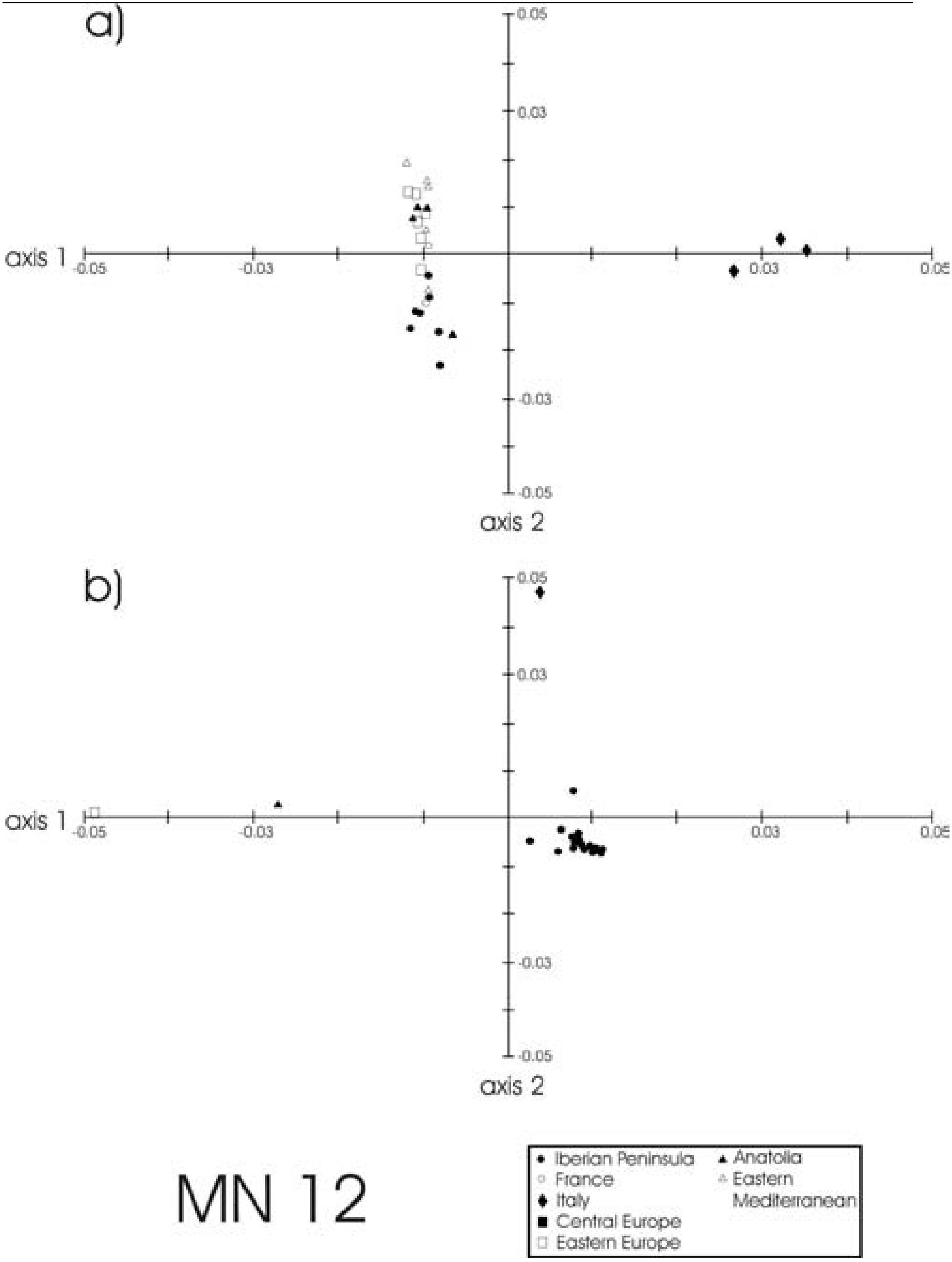


Figure 7.8. Correspondence analyses for MN 12 micro and macromammal sites. The exact position of the different sites in the multivariate space is given in the appendix 7.1.

including pikas) since the Pleistocene. The French micromammal fauna of Lissieu (LIS) includes a considerable diversity of "microtoid cricetids", murids, eomyids, zapodids and dormice, in contrast with the poor fauna of the Iberian sites. The Iberian bioprovince is characterized by a diverse mice-dominated fauna (including the genera *Castillomys*, *Stephanomys*, *Apodemus*, *Occitanomys* and *Castromys*) and by the hypsodont endemic Cricetodontini genus *Ruscinomys*. In some localities of the eastern

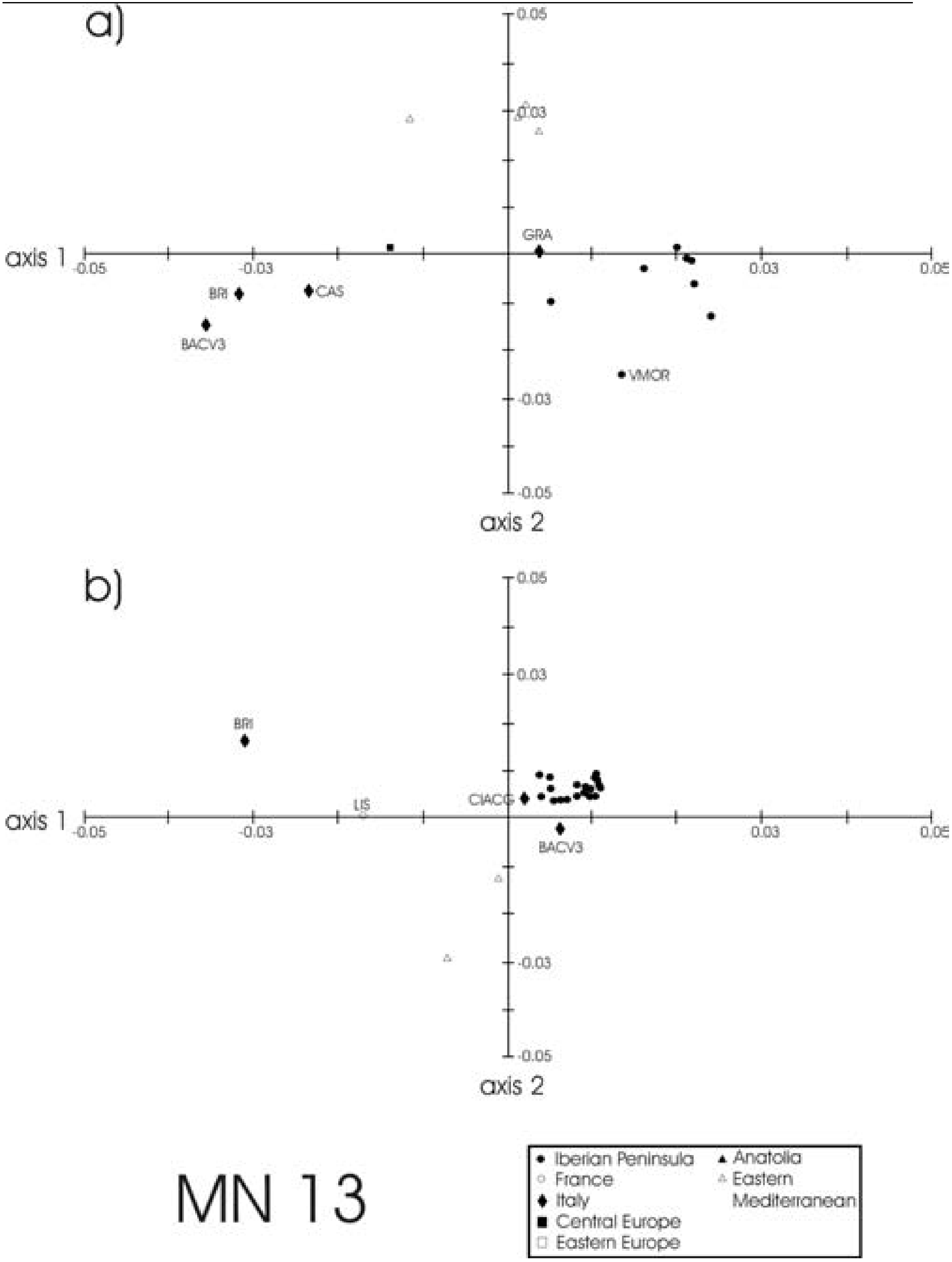
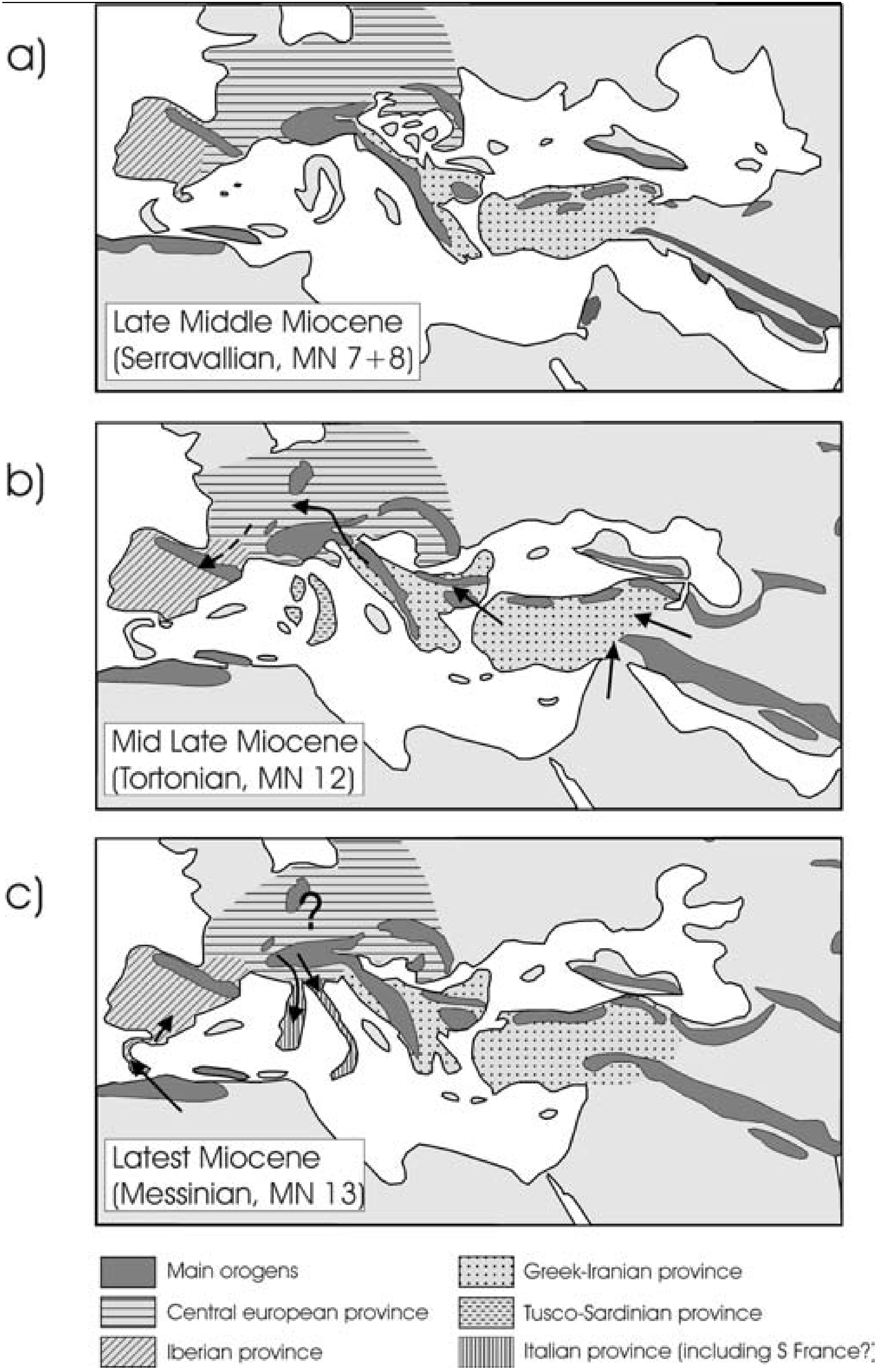


Figure 7.9. Correspondence analyses for MN 13 micro and macromammal sites. The exact position of the different sites in the multivariate space is given in the appendix 7.1.

Figure 7.10. (next page) Paleogeographical maps for the Serravallian, Tortonian and Messinian (after Popov *et al.*, 2004 and Rögl, 1999; modified) showing evolution of the Mediterranean Basin during the studied time-span. Distribution of main orogens, the area covered by identified bioprovinces and possible dispersal paths are also shown (see text for details).


a)
Late Middle Miocene
(Serravallian, MN 7+8)
b)
Mid Late Miocene
(Tortonian, MN 12)
c)
?
Latest Miocene
(Messinian, MN 13)
Main orogens
Central european province
Iberian province
Greek-Iranian province
Tusco-Sardinian province
Italian province (including S France?)

margin of the Iberian Peninsula (such as Venta del Moro and Casablanca M) the rodent fauna is more diverse and includes dormice, squirrels and gerbils. However, according to our results the two subprovinces (Ibero-central and Ibero-levant) are not clearly distinguished during this MN as proposed by Agustí (1981, 1990). A Greek-Iranian province is also recognized in our analysis, which is characterized by the absence of some Western mice genera and by the presence of gerbils, beavers, ground and flying squirrels, absent in most of the western sites.

7.3.2. Taxonomic diversity

We have estimated diversity as well as origination and extinction rates for the whole study area and for selected squares. We have only selected squares containing a moderately rich mammal record covering at least five MN zones without temporal gaps in the range. Only three squares suit the criteria (see fig. 7.1. and table 7.2.): 12, 13 and 24. Thus we could only consider Northern Spain plus Southern France and Central Europe. In order to include SE Europe we have added together squares 8 and 9 to obtain a moderately rich macromammal record ranging from MN 6 to MN 12. However, we would rather compare areas of approximately the same surface, so if we take two squares for SE Europe we will also have to take two squares for the other areas to be compared. Therefore, we have summed squares 12 and 13 and obtained a continuous record covering the whole time span, including both macro- and micromammals. It should be noted that squares 12 and 13 include most of European localities in every MN zone. We have also considered square 24, and added the adjacent square 25, resulting in a rather complete Central European micro- and macromammal record that lasts until the MN 11.

The total number of genera (N_{TOT}) in Europe is shown in fig. 7.11.a. Macromammals show two diversity peaks: MN 9 and MN 12. These peaks are also associated with an abrupt increase in the number of singletons (N_{FL}), especially in the case of the MN 12. MN 13 shows a moderate decrease even though N_{FL} keeps increasing. The lowest values of diversity are attained at MN 6 and MN 10 representing the loss of about 30 genera. MN 10 minimum coincides with a decrease in N_{FL}, whereas this is not the case in the MN 6 minimum. Micromammals increase diversity until their optimum at MN 7+8, although a decrease in diversity starts to take place afterwards. This loss is moderate until MN 11 but at MN 12 N_{TOT} falls abruptly to its minimum values. Micromammals would have lost close to 30 genera from MN 7+8 to MN 12. A moderate recovery takes place at MN 13, when N_{TOT} reaches values similar to those of MN 11. Decrease in N_{TOT} coincides with a progressive decrease in N_{FL} and the abrupt fall observed in MN 12 is associated with the absence of singletons in this zone. The apparent recovery in MN 13 coincides with a spectacular increase in $N_{FL.}$ If we exclude singletons from our calculations and estimate mean standing diversity, the situation changes considerably (see fig. 7.11.b). The apparent diversity crisis that affected macromammals at MN 10 disappears, and their diversity gradually increases until its peak in MN 11. Afterwards N_{ST} remains approximately the same. The loss of genera concerning to micromammals appears less marked, but it still exists. Micromammal diversity reaches its maximum at MN 9–MN 10, and afterwards decreases until MN 12. Thus, a diversity crisis seems to have affected micromammal genera in Europe although it occurred in the Turolian rather than in the Vallesian. Nevertheless, as we have seen, Spanish sites represent most of the European micromammal record, so we find it necessary to consider to what extent these results are affected by this fact.

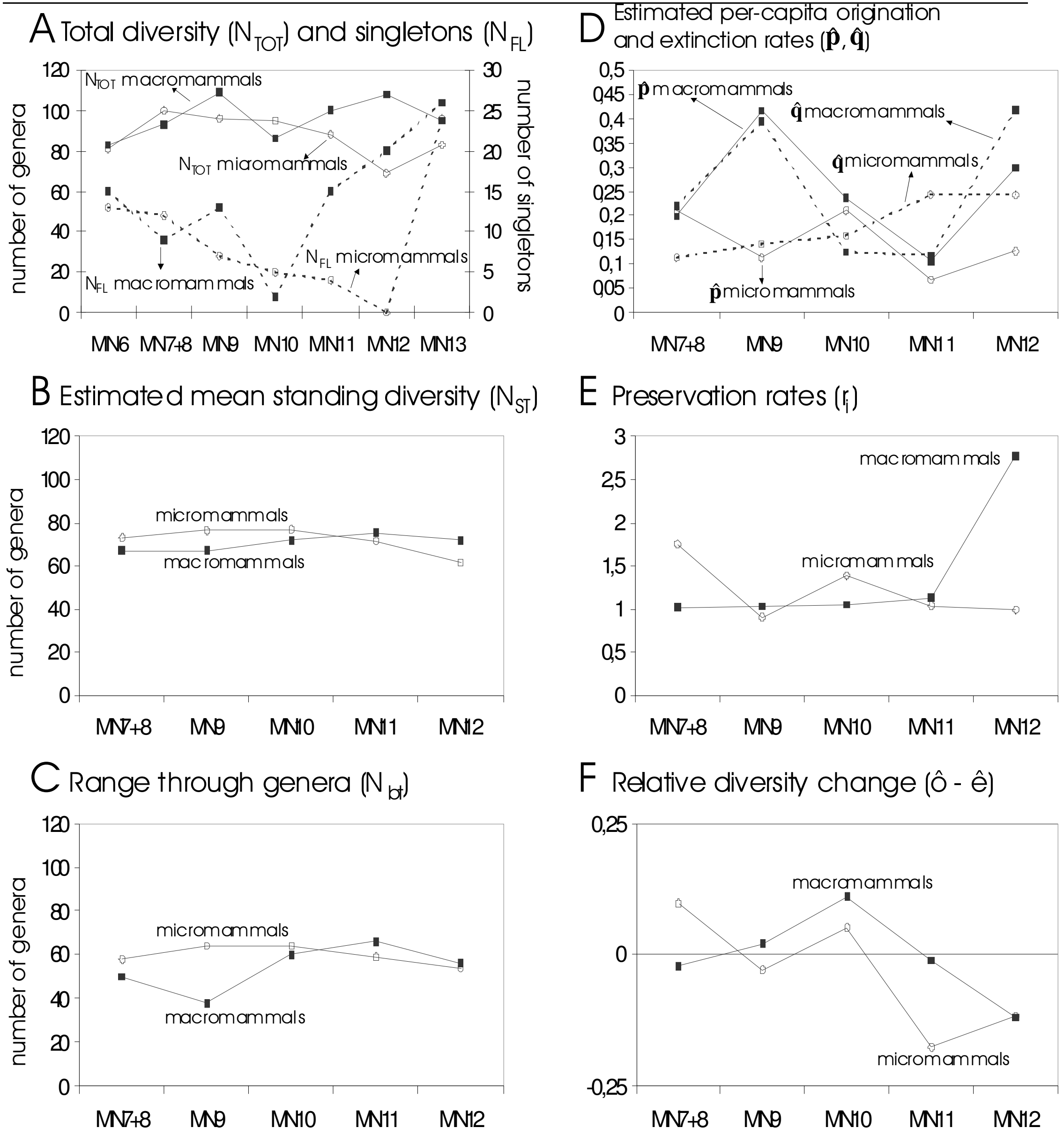


Figure 7.11. Diversity and taxonomic and preservation rates plots for the whole study area (see text for details). a) Total diversity (N_{TOT}) and singletons (N_{FL}); b) Estimated mean standing diversity (N_{ST}); c) Range through genera (N_{bt}); d) Estimated per-capita origination and extinction rates ($\hat{p}$, $\hat{q}$); e) Preservation rates (r_i);f) Relative diversity change ($\hat{p}$ minus $\hat{q}$). Plots display results for macromammals and micromammals. For results of correlation test between N_{ST}, $\hat{p}$, $\hat{q}$ and r_i see table 7.4.

Fig. 7.12.a shows N_{TOT} and N_{FL} of macromammals and micromammals respectively for the selected squares 8+9 (labeled as Turkey), 12+13 (labeled as SW Europe), and 24+25 (labeled as Central Europe). In SW Europe, N_{TOT} of micro and macromammals has its higher values at MN 7+8 and MN 9 respectively. In the case of macrommals diversity starts a moderate decrease afterwards, while micromammals loose genera faster. Macromammal N_{TOT} keeps falling until MN 13 with a slight recovery at MN 12. Although micromammals had lost about 30 genera since MN 7+8, but an important recovery takes place at MN 13 and N_{TOT} attained values similar to those of MN 9. Increases in N_{TOT} in micromammals are associated with increases in the number of singletons, while in the case of macromammals this pattern is not so clear and only the extreme low values of N_{TOT} at MN 11 coincide with extreme low values of N_{FL}. The whole picture changes only slightly if we consider N_{ST} in SW Europe (see fig. 7.12.b). Macromammals loose diversity gradually from MN 7+8 until they reach a

minimum at MN 10, afterwards there is a slight recovery at MN 11 followed by a new decrease during MN 12. Micromammals were very diverse at MN 9, but afterwards diversity decreased gradually throughout the entire time span at higher rate than macromammals. The existence of a diversity crisis starting at MN 10 (or maybe earlier in the case of macromammals) seems clear in SW Europe. This crisis affected all land mammal communities but its effects were probably more severe on micromammals. Central Europe and Turkey show lower values of diversity than SW Europe, but this is almost certainly an effect of the quality of the record, which is clearly more complete in SW Europe. The Central European record unfortunately disappears at MN 11, but if the Vallesian Crisis at MN 10 affected the whole of Europe it should still be detected. This crisis is apparent, and N_{TOT} of macromammals shows an abrupt decrease in MN 10, while micromammals reduced their diversity earlier, at MN 9 (see fig. 7.12.a). In both cases there is a quick recovery afterwards. Changes in N_{TOT} are clearly associated with changes in N_{FL} during the same zones. Moreover the decrease in the number of singletons observed at MN 9 and MN 10 is related to a decrease in the number of localities relative to previous time spans. Thus, these apparent falls are most probably an effect of completeness and should be removed if singletons are excluded from the analysis. This is what we have done by computing N_{ST} (see fig. 7.12.b), and our results evidence these undesirable effects of such a poor record. Macromammal diversity remains more or less stable, while micromammals even increase their diversity during MN 10, showing opposite trends than in SW Europe. Only macromammals can be considered in the case of Turkey, but the trends observed in this area are very different from those seen in SW and Central Europe. N_{TOT} has high values at MN 6 but falls abruptly to its minimum at MN 7+8, and later on diversity gradually recovers until a new maximum at MN 12. Note that the trends shown by N_{TOT} clearly follow those of N_{FL} (fig. 7.12.a) but in this case they are not associated with a significant decrease in the number of sites. By removing the singletons we obtain the same pattern: diversity in Turkey is low during MN 7+8 and MN 9, and it increases gradually thereafter. A diversity crisis might have occurred in Turkey, but it would taken place about 3 million years earlier than in SW Europe, during the latest Middle Miocene.

We have tested for correlation between N_{ST} and preservation rate (r_i) in Europe and the selected areas (see figs. 7.11.e and 7.13.c respectively) using Kendall's τ (see table 7.4.). The existence of a correlation between both parameters could only be rejected in the case of micromammal N_{ST} in Central Europe.

7.3.3. Origination and Extinction rates

Figure 7.11.c shows the number of genera that range throughout each entire MN zone (N_{bt}) for all Europe. Macromammal N_{bt} is surprisingly low during MN 9, but quickly recovers afterwards. Micromammal N_{bt} decays gradually from MN 10 onwards. This fact points to the existence of an important macromammal turnover at MN 9, as opposed to a more gradual micromammal turnover starting at MN 10. Fig. 7.11.d displays origination and extinction rates for Europe. In the case of macromammals both rates increase spectacularly during MN 9. An important decrease in both rates follows thereafter until they rise again in MN 12, although in this occasion extinctions outnumber originations reaching their higher values. Micromammal originations reach their maximum values at MN 7+8 and MN 10, but there is a first minimum at MN 9. Afterwards extinctions gradually increased until MN 11, when an abrupt rise associated with a decrease in originations is recorded. In MN 12 extinctions stopped their increase and the origination rate rose. We have tested for correlation between rates and r_i (see fig. 7.11.e and table 7.4.) in each situation and results show that both variables are not

correlated in any case. For macromammals in both cases Kendall's τ is 0, so variables are totally uncorrelated. However, these surprisingly good results are probably an effect of the few points included in the calculations: the fewer points the test finds perfect no correlation if the two variables are not very correlated. On the contrary if variables are strongly correlated, a few data points will result on perfect positive or negative correlations and an absolute value of 1 for τ. In our particular situation we assume that our variables are nearly uncorrelated. In the case of micromammals there is no statistically significant correlation between $\hat{p}$ and r_i but results are not very good and probably the origination peaks of MN 7+8 and MN 10 are partly due to an increase in r_i. In the case of micromammal $\hat{q}$ correlation is negative ($\tau = -0.2$). If variation in $\hat{q}$ was dominated by changes in r_i, τ should be large and positive, so in this last situation we also conclude that micromammal preservation and extinction rates are nearly uncorrelated.

In the case of macromammals, the maximum in origination rates is at MN 10 for SW Europe and Turkey (see fig. 7.13.a), while the minimum values are recorded at MN 11. A moderate increase in the rates is also observed in SW Europe during MN 12. Central Europe shows a peak in originations at MN 9 coinciding with the peak we have already seen when considering Europe as a whole, which otherwise is not evident in Turkey and SW Europe. The global European record also shows a peak in macromammal $\hat{p}$ at the MN 9 that may be due to the existence of high rates in Central Europe plus moderately high rates in Turkey and SW Europe (see fig. 7.11.d). On the other hand, the decrease recorded in the European macromammal record at MN 11, is mostly due to the decay in $\hat{p}$ observed in these two areas during this MN zone. Micromammal $\hat{p}$ reached its maximum values at MN 7+8 in SW Europe, and decreased significantly during MN 9 (see fig. 7.13.a). Finally a moderate recovery is observed at MN 10. Central Europe shows the same trends than the lower latitudes although the increase in originations in MN 10 appears to have been more noticeable. The Central European record disappears at MN 11 while in Spain the data show that $\hat{p}$ decreased during the following intervals. The pulse in macromammal $\hat{p}$ seen in Europe in MN 9 (fig. 7.11.d) is associated with a pulse in $\hat{q}$. As fig. 7.13.b shows, this pulse in $\hat{q}$ only occurred in Central Europe, while only a moderate increase in $\hat{q}$ took place in SW Europe and, on the contrary, $\hat{q}$ decreased in Turkey. However, the values of this rate were rather high in all regions, so they result in a peak when the whole European record is considered. $\hat{q}$ reached 0 in Turkey and in Central Europe during MN 10, whilst in SW Europe there was only a slight decrease. In SW Europe $\hat{q}$ show their minimum value at MN 11, when Turkish macromammal $\hat{q}$ increase again. In MN 12 $\hat{q}$ increased abruptly in Spain reaching a maximum of 0.65. Note that most of macromammal data from MN 12 and MN 13 are from central Spain, so the increase in $\hat{q}$ seen in Europe in MN 12 partly results from the local increase in $\hat{q}$ in Spain during this interval. In the case of micromammals (fig. 7.13b) the plot representing $\hat{q}$ for Central Europe is

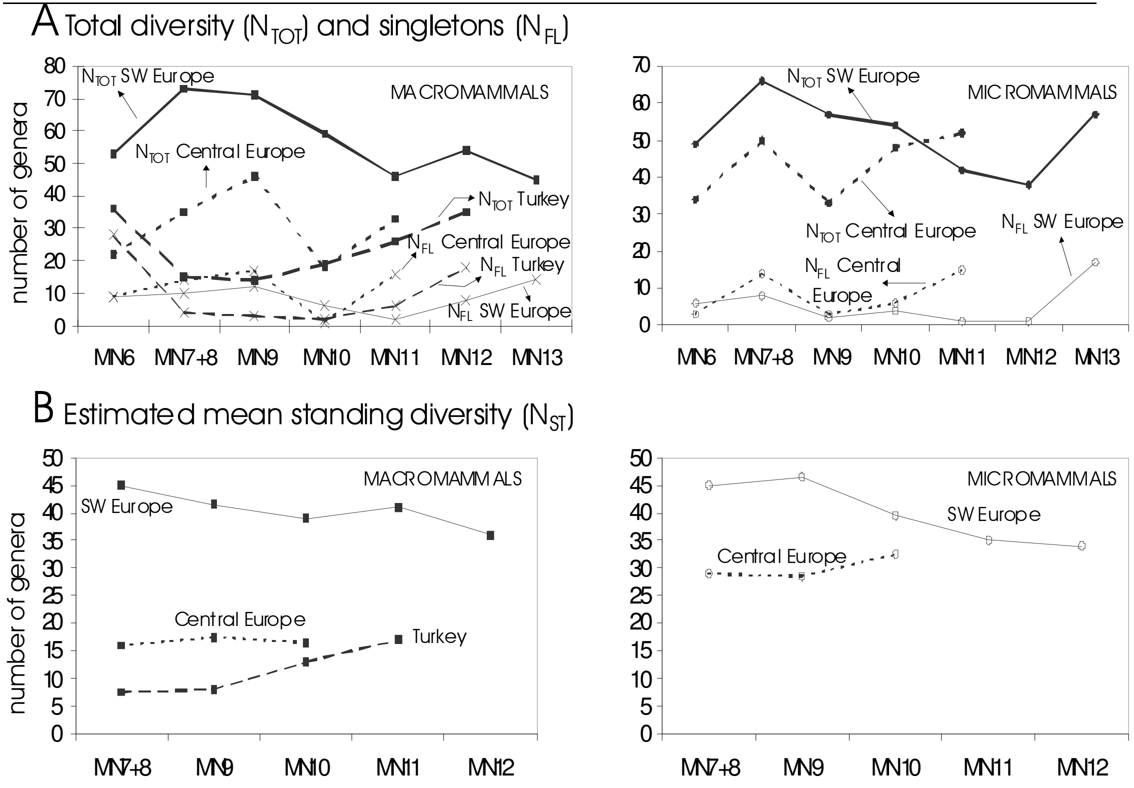


Figure 7.12. Diversity calculated for selected squares: SW Europe (squares 12 + 13), Central Europe (squares 24 + 25) and Turkey (squares 8 + 9) (see text for details). a) Total diversity (N_{TOT}) and singletons (N_{FL}); b) Estimated mean standing diversity (N_{ST}). Plots display results for macromammals and micromammals. For results of correlation test between N_{ST} and r_i see table 7.4..

Table 7.4. Results of correlation test between standing diversity (N_{ST}), origination ($\hat{p}$) and extinction ($\hat{q}$) rates to preservation rate (r_i). Kendall's τ and probability of being uncorrelated is given for macromammals and micromammals in each area and the whole continent. Significant values are in bold.

Area		N_{ST}		$\hat{p}$		$\hat{q}$	
		τ	p(unc.)	τ	p(unc.)	τ	p(unc.)
Europe	macromammals	0.67	0.10	**0.00**	**1.00**	**0.00**	**1.00**
	micromammals	0.10	0.79	0.60	0.14	-0.20	0.62
SW Europe	macromammals	-0.20	0.62	0.20	0.62	0.40	0.33
	micromammals	-0.20	0.62	0.60	0.14	**0.00**	**1.00**
Central Europe	macromammals	-0.33	0.60	0.33	0.60	0.33	0.60
	micromammals	**0.00**	**1.00**	0.33	0.60	1.00	0.00
Turkey	macromammals	0.18	0.71	-1.00	0.04	0.33	0.50

depressed at MN 9, while in MN 10 it increases until reaching values very close to those recorded at MN 7+8. In SW Europe there was an abrupt increase in $\hat{q}$ in MN 10 and a decrease immediately afterwards. The increase in $\hat{q}$ seen in Europe during MN 11 and MN 12 (see fig. 7.11.d) may be attributable to the absence of more micromammal records in other areas apart from SW Europe.

As in previous calculations we have tested for correlation between $\hat{p}$, $\hat{q}$ and r_i using Kendall's τ (see table 7.4.). The existence of correlation between the taxonomic and preservation rates could be rejected in the case of macromammals in the whole of

Europe and in the case of micromammal $\hat{q}$ in Southwestern Europe. In the case of macromammal $\hat{p}$ in Turkey the correlation is negative ($\tau = -1$), and if we presume that changes in these parameters where related to variations in r_i we would expect these values to be high and positive, thus the existence of a significant correlation between both variables has to be ruled out. On the contrary, there is a clear positive correlation between $\hat{q}$ and r_i in the micromammal record of Central Europe.

7.4. Discussion: biogeographical stability and the Late Miocene mammal turnover

The Spanish record is the most complete mammal record for the Late Miocene of Europe (Alba *et al.*, 2001, calculated the completeness of the Spanish Neogene mammal record in the means of Foote & Raup (1996) and showed that completeness was even higher than in some marine records), so this fact will surely influence the European record when it is taken as a whole. The graphs for diversity as well as $\hat{p}$, $\hat{q}$ and r_i rates in Europe (see fig. 7.11.) resemble those of southwestern Europe (see figs. 7.12. to 7.13.), especially in the case of micromammals. Thus, events taking place only in the Iberian Peninsula are also expressed when all the European record is considered.

There are three main bioprovinces maintained during most of the time span: Iberian (including southern France in certain intervals), Central European and Greek-Iranian (see figs. 7.3. to 7.9.). During the Middle Miocene the two western provinces were not very different and they even may even constitute a single province characterized by a high diversity of forest-adapted mammals. The levels of diversity during MN 7+8 (see fig. 7.12.b) are the highest of the considered period (the differences in this parameter between central and southwestern Europe are probably an artifact of completeness). In contrast the faunas from Turkey exhibit low levels of diversity (fig. 7.12.b). The Iberian province is hardly distinguished from the Central European one, especially when only macromammals are considered (see figs. 7.3 and 7.4.), further suggesting that a similar environment might had been present in both areas. During the late Middle Miocene the Central European paleovegetation record shows a progressive decrease in evergreen woody taxa and an increase in deciduous ones, resulting in associations comparable to modern mixed mesophytic forests (Kovar-Eder, 2003). Previously, in southwestern Europe the progressive cooling during the early Middle Miocene had led to the disappearance of megathermic taxa as well as the existing *Avicennia* mangrooves (Bessedik *et al.*, 1984).

The palynological data from the Duero Basin (Spain) assigned to the MN 7+8 (after García-Moreno, 1987) indicate the presence of a forest environment including wet areas with many hydrophile elements (*Typha*, *Sparganium*, *Magnolia*) (Rivas-Carballo & Valle, 1986; see also chapter 6). The vegetation of the Greek-Iranian province included many sclerophyllous taxa together with some evergreen genera already present in Central Europe in preceding periods (*Platanus neptuni*, *Calocedrus*) (Kover-Eder, 2003). On the other hand, Fortelius *et al.* (2002) calculated mean hypsodonty for several Eurasian macromammal sites and used it as a proxy for mean annual precipitation. Whilst present-day relations between small mammal community structure and rainfall

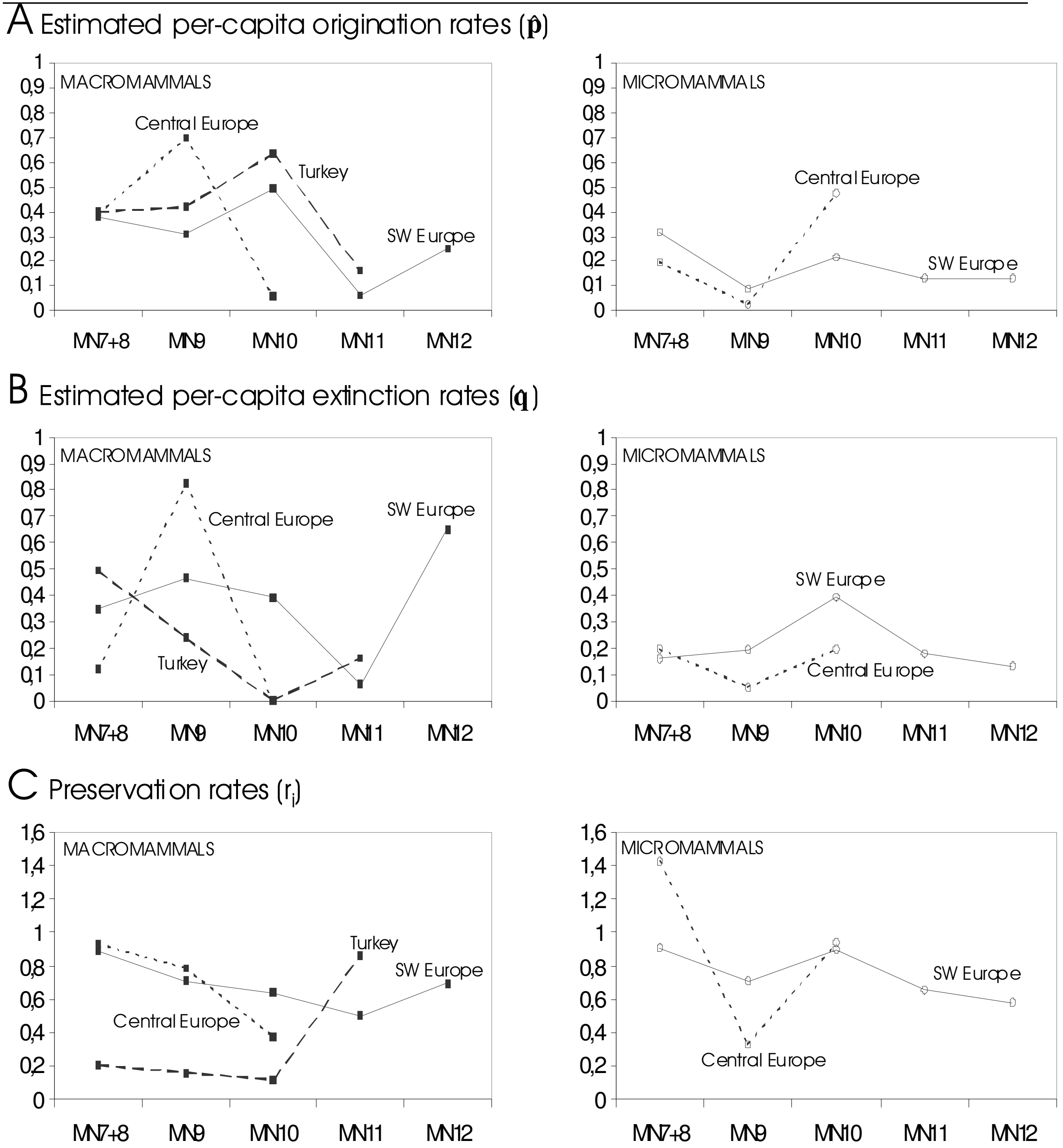


Figure 7.13. Taxonomic and preservation rates calculated for selected squares: SW Europe (squares 12+13), Central Europe (squares 24+25) and Turkey (squares 8+9) (see text for details). A) Estimated per-capita origination rate ($\hat{p}$); B) Estimated per-capita extinction rate ($\hat{q}$); C) Preservation rates (r_i). Plots display results for macromammals and micromammals. For results of correlation test between $\hat{p}$, $\hat{q}$ and r_i see table 7.4.

were applied to small mammal fossil assemblages by Van Dam (2006) to predict the Late Neogene paleoprecipitation patterns in Europe. Their maps for the Middle Miocene show the existence of two areas of different mean precipitation values corresponding to the two well known Greek-Iranian and Western European province. The Greek-Iranian province would be characterized by moderately lower paleoprecipitation levels. In the Iberian Peninsula paleoprecipitation is slightly lower than in both France and Central Europe, which are referred to the so-called European Temperate Wet Zone (ETWZ) by Van Dam (2006). During MN 7+8 taxonomic rates were moderate in Western Europe ($\hat{q}$ in Central Europe is very low, see fig. 7.13.b). However, originations exceeded extinctions resulting in an increase in diversity (fig. 7.12.b). In contrast, the

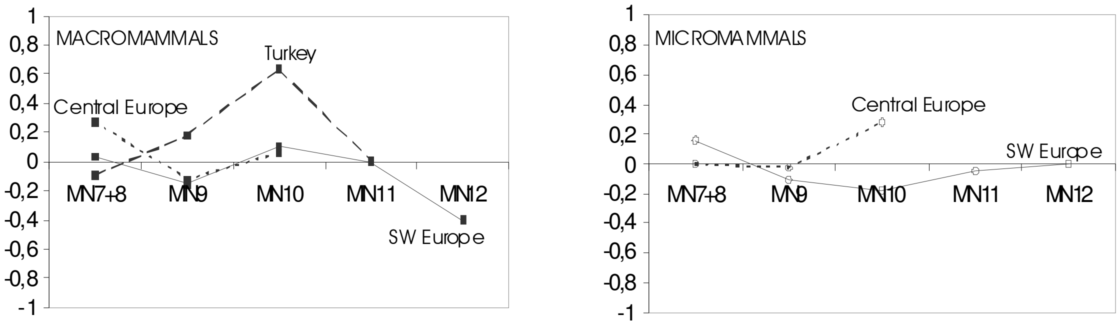


Figure 7.14. Relative diversity change ($\hat{p} - \hat{q}$) calculated for selected squares: SW Europe (squares 12 + 13), Central Europe (squares 24 + 25) and Turkey (squares 8 + 9) (see text for details).

macromammal extinction rates in Turkey are considerably high (fig. 7.13.b), while originations (fig. 7.13.a) reach similar values than in the remaining areas. This fact explains the relatively low diversity recorded in the province, and may reflect some opening of the mid-Miocene forests, which led to an important turnover in herbivore faunas.

The beginning of the Vallesian coincides with a major isotopic event (Mi 5, *ca.*11 Ma) (Miller *et al.*, 1991; also recorded in the Mediterranean by Turco *et al.*, 2001) and a sea level fall of nearly 100 m (Haq *et al.*, 1987; Miller *et al.*, 2005) which is contemporary to a phase of expansion of the eastern Antarctic Ice Sheet (Zachos *et al.*, 2001). These global changes allowed the dispersal of hipparionine horses through Beringia. In Central Europe (northern Danube Basin, Slovakia) the arrival of the "hipparion faunas" coincided with the clear appearance of a clear cool/warm seasonality in the area (Kováč *et al.*, 2006). The Early Vallesian (MN 9) is characterized by a progressive decrease in the $\hat{p}$ rates in all the provinces (except for macromammals in Central Europe, see fig. 7.13.a), while extinctions increased in central and southwestern Europe (fig. 7.13.b). The moderate decrease in $\hat{p}$ and the increase in $\hat{q}$ in southwestern Europe (mainly Spain) resulted in a decline in macromammal diversity. This did not occur in the case of micromammals, which maintained their diversity (although extinctions were also quite high). The macrofloral remains recovered some Catalan coastal basins (Spain) evidence the appearance of broad-leafed deciduous taxa such as *Acer tricuspidatum* and *Platanus leucophylla* (Sanz de Siria, 1993,1994). However some subtropical genera (*Ficus*, *Sabal*) survived in the same area during the latest MN 9 (see also chapter 6). The environment in Spain may have been less forested than in Central Europe during the lowermost Vallesian as already noted by Fortelius *et al.* (1996b). Nevertheless, the Early/Late Vallesian boundary seems to have coincided with a particularly humid phase in the Spanish basins, clearly associated to the existence of a dense forest cover (Van der Meulen & Daams, 1992; see also chapter 6). Consequently, diverse micro- and macromammal assemblages characterize the Early Vallesian Spanish sites, especially those of the Vallès-Penedès Basin. In Turkey extinction rates kept lowering while originations remain stable. Bovid diversity continued increasing with both browsing and grazing adaptations being represented, and indicating the beginning of the break-up of the forest environments in the region (Bernor *et al.*, 1996). This is further supported by palynological data from lacustrine sediments at Samos Island in the eastern Mediterranean, dated to 11.2 Ma, which are interpreted as representing closed to open woodlands with conifers on nearby uplands (Ioakim & Solounias, 1985). However, two of these samples include a low proportion of grass pollen (less than 10 %), therefore although the ground cover included grasses amongst other herbaceous plants, they were not a significant component of the vegetation.

The Vallesian Crisis is thought to coincide with Early/Late Vallesian boundary (or the MN 9/MN 10 boundary), that is at 9.7 Ma (Agustí *et al*., 2001). Our results (fig. 7.12.b) are not consistent with a decrease in diversity in all areas during this time span. In fact, diversity only decreased in the Iberian province, especially in the case of the small mammals. In Central Europe it remained stable (with an slight increase in the case of micromammals) and in Turkey diversity began to rise at higher rates. In southwestern Europe an important micromammal turnover implied a rising in both $\hat{p}$ and $\hat{q}$, although the increase in the number of extinctions was higher (fig. 7.13.a and 7.13.b). The per-capita macromammal origination rates in this region increased following the pattern seen in Turkey, and therefore large mammal diversity stopped declining. The Vallesian Crisis also coincides with an isotopic event (Mi 7; Miller *et al*., 1991), although it is not as marked as the preceding Mi 5 and Mi 6. However, during the late Vallesian the global temperatures kept decreasing while the changes in atmospheric circulation due to the Tibetan uplift resulted in the intensification of Asian monsoons and, at low latitudes, in an increment of wet/dry seasonality (Kutzbach *et al*., 1993). It has been proposed that this increase in rainfall seasonality would have favored the replacement of "cricetids" by murids in the inner Peninsula (Van Dam, 1997; see also chapter 6). However, in the northern basins this seasonality in humidity may have been accompanied by an increase in the seasonality in temperature. The Late Vallesian macrofloral remains from the Vallès-Penedès Basin (NE Spain) indicate the presence of a warm temperate forest (Agustí *et al*., 2003), although the presence of a 15 % of dry sclerophyllous Mediterranean elements (*Quercus ilex*, *Quercus praecursor*) also suggest the existence of a dry season. This fact would explain the conspicuously different rodent assemblages from the Vallès-Penedès Basin, which were overwhelmingly dominated by the hypsodont cricetine *Rotundomys*, as compared to other contemporary Spanish sites (see also chapter 6). The palynological record of the Duero Basin (NW Spain) is consistent with the existence of more open, probably steppe environments (Rivas-Carballo & Valle, 1986). This type of open environments would probably extend to other inner Spanish basins, which present very similar rodent assemblages (see chapter 6). It seems very likely that the previously existing Middle Miocene warm temperate forests were reduced as a result of climatic changes, being replaced by open woodlands in inner Spain. In contrast, more dense forest environments seem to have characterized the Vallès-Penedès Basin, although probably the proportion of deciduous trees was higher than in previous times. The mammal taxa adapted to the mid-Miocene forest environments would have been greatly affected, and ultimately becoming locally extinct when the size of the "patches" of their habitat became too small to allow the maintenance of their populations. The effects would have been greater on the small mammals populations, because of their generally reduced migration capability, while many large mammals most likely migrated to more suitable environments. The fauna of Dorn Dürkheim (MN 11, Germany) includes a number of forest-adapted forms that migrated from the Greek-Iranian and the Iberian provinces (Franzen & Storch, 1999) The graphs in figures 7.12.b and 7.14 show a sharp decrease in micromammal diversity and a moderate decrease and recovery in the case of macromammals. Certain macromammals, unable to tolerate a marked seasonality in temperature or rainfall would have disappeared from the Iberian Peninsula during the so-called Vallesian Crisis. This is the case of the hominoid primate *Dryopithecus*. These primates needed whole-year availability of fruits, so they could not migrate to higher latitudes and were trapped in the "patches" of southern forests (Andrews, 1992; Fortelius & Hokkanen, 2001; Agustí *et al*., 2003). The combined effects of the increasing reduction of those environments and the progressive substitution of evergreen by deciduous trees brought hominoids to the extinction in Europe. The survival of the hominoid *Oreopithecus* *bambolii* in the Turolian faunas of Tuscany and Sardinia is derived from the insular conditions of this geographic area during that time. The peculiar trophic adaptations of this primate, a consequence of the peculiar selective pressures of insular ecosystems, allowed this hominoid to tolerate the effect on vegetation trophic resources of seasonality (Köhler & Moyà-Solà, 1996; Moyà-Solà *et al.*, 1999b; Köhler & Moyà-Solà, 2003).

The same global events that presumably caused the Vallesian Crisis in southwestern Europe affected extensive areas of the Old World too. The palyonological record from western Turkey documents and increase in conifers and herbaceous taxa (including Poaceae) in the Late Miocene (Benda, 1971). Nevertheless, the effects of such environmental change on land mammal communities were completely different. In Turkey diversity started increasing as a result of a minimum in extinction rates (fig. 7.13.b) and a maximum in originations (fig. 7.13.a). This fact reflects the radiation of open-country bovids and giraffids that later become so characteristic of the Turolian faunas of this province. Apparently the reduction of forest in southeastern Europe, had the opposite effects than in Spain, allowing the migration of many taxa of Asian or African origin. Migrations of some large mammals into each of the European regions, such as the hipparionine horses or the bovid *Tragoportax*, were quick events taking no more than 1 million years in length. In contrast, many eastern open-country mammal taxa failed to disperse into Western Europe (Koufos, 2003). Extensive areas of southwestern and Eastern Europe appear to have been covered by open woodlands, therefore why would the same open-country mammals not be found in both areas? One working hypothesis may emphasize the role of certain mountain ranges, such as the Alps or the Pyrenees, as effective barriers for migration. Nevertheless, some eastern genera managed to cross these mountain ranges, especially during the Middle Turolian (MN 12). Our preferred hypothesis implies the persistence of humid and forested environments in Central Europe (as shown by the hypsodonty maps by Fortelius *et al.*, 2002; and Van Dam, 2006) that may have acted as an ecological filter, and therefore only certain taxa (for instance *Tragoportax*, *Microstonyx*) could cross these natural barriers and successfully arrive at the Iberian Peninsula. This situation would have persisted during the Turolian.

During the Turolian, mammal diversity kept declining in the Iberian province (see figs. 7.12. and 7.14.), this was initially caused by a decay in $\hat{p}$ and $\hat{q}$, whereas in MN 12 extinctions exceeded originations (figs. 7.13.a and 7.13.b). As already suggested, this fact may result from the impossibility of eastern faunas to disperse into southwestern Europe (only a few taxa reached the Iberian Peninsula during the Turolian, for example sivatherine giraffids, some species of *Gazella* and *Protoryx*), as well as from the extinction of the last forest-dwelling relicts (*Dorcatherium*, *Micromeryx*, *Lucentia*). However, in the case of micromammals there was a different situation, which resulted in the development of a characteristic fauna of mice and hypsodont "cricetids" in the inner basins (although it was not very diverse). The macromammal based correspondence analyses from figures 7.7. and 7.8. show an increasing degree of similarity between the Iberian and the Greek-Iranian province during the Turolian (culminating by MN 12) which indicates the westward extension of open-country herbivore faunas. This point may indicate some opening of the canopy in certain areas of central and south-central Europe, which, according to the hypothesis exposed above, would have allowed the dispersal of more eastern herbivores than in preceding periods. Cerling *et al.* (1997) have provided impressive isotopic evidence of a global vegetation change starting at 8-7 Ma (thus coinciding with the Turolian) and caused by the transition from C_3 to C_4 vegetation. However, the isotopic record of

Europe throughout the Miocene indicates a predominance of C_3 vegetation (Jacobs *et al.*, 1999). Therefore, it appears that the expansion of grass-dominated ecosystems apparently did not occur in Europe. Consequently, the dispersal of the eastern herbivores is not related to the C_3/C_4 shift. Although a classical interpretation of the Turolian environments of Turkey and Greece is open grassland, the herbivore fauna from these areas includes both browsers and grazers, so the fauna as a whole does not reflect such a pure grassland (Jacobs *et al.*, 1999). Solounias *et al.* (1995) suggested that the environment included forest and bushy country.

The northeastern movement of the African plate during the Late Miocene led to a restriction of the gateway between the western Mediterranean and the Atlantic Ocean during the Late Turolian (MN 13 and its marine equivalent, the Messinian). This time period witnessed a restoration of the level of provincial diversity (see fig. 7.9.)and an important recovery of the environmental conditions in the Mediterranean. Three bioprovinces are recognized: the Iberian, the Greek-Iranian and, once more, an Italian one. Italy was a small archipelago during the Early and the Middle Turolian inhabited by bizarre insular faunas. The connection to main land during the MN 13 led to the extinction of these faunas, and allowed the migration of faunas showing some Central European affinities into the new peninsula (see previous section). The floras from the lower part of the Komnina Formation (Ptolemais Basin, Greece) generally indicate humid and warm continuous climatic conditions (Kloosterboer-van Hoeve *et al.*, 2000). The pollen records for the Northwestern Mediterranean also indicate the existence of warm climatic conditions during the Messinian and Early Zanclean (Pliocene) (Fauquette *et al.*, 2006). However, the Iberian Peninsula is still characterized by a low diversity of macromammals (including few immigrants, such as *Paracamelus*), further suggesting that the Central European forest filter kept restricting migration until the Pliocene. Fortelius *et al.* (2002) and Van Dam (2006) have shown the persistence of a high mean annual precipitation zone in Central Europe during the Pliocene, which would explain the maintenance of the inferred forest filter.

By the end of the Turolian (at 5.6 Ma) the tectonic closure of the western Mediterranean connection ultimately led to the total drying up of the Mediterranean sea, an event known as the “Messinian Salinity Crisis” (Hsü *et al.*, 1973; Hsü *et al.*, 1978). However, during that crisis, the Iberian micromammal fauna was enriched with the entry of some immigrants of African origin, such as *Hexaprotodon* and *Macaca* (Agustí *et al.*, 2006).

Although open, savanna-like environments persisted in southeastern Europe, there are no new occurrences in Greek sites by MN 13. Furthermore, many of the taxa that characterized the Turolian in the province (the giraffids, *Adcrocuta*, *Choerolophodon*, *Microstonyx*, *Tragoportax* or *Prostrepsiceros*) would not cross the Miocene/Pliocene boundary and would be replaced by a new macromammal community including, amongst others, *Parabos*, *Sus*, *Paracamelus* and *Korynochoerus* (= *Propotamochoerus*) (Koufos, 2003).

7.5. Concluding remarks

The Late Miocene mammal turnover that affected European faunas seems to be the result of a complex interplay between climatic and physiographic events. Climatic fluctuations, as well as tectonic events, do not progress gradually, but rather in a discontinuous way. Accordingly, a punctuated response of the ecosystems should be expected, with major turnovers being related to important shifts in these parameters. As already pointed out in the previous chapter, the response to the same climatic signal is different depending on the area considered, and it is not surprising that important extinction events, such as the Vallesian Crisis, coincide with origination pulses in other areas.

The original definition of the Vallesian Crisis (Agustí & Moyà-Solà, 1990) did not establish that its effects were continent-wide, and it was thought to occur only in Spain. As we have shown this crisis can only be recognized in the Iberian Peninsula, and was probably related to an intensification of seasonality both in precipitation and in temperature. The Crisis coincided with an increase in diversity in Turkey, with the entry of many open-country Bovoidea and Giraffidae, while in Central Europe macromammal assemblages remained stable and micromammals actually increased their diversity. Fortelius *et al.* (1996b) and Franzen & Storch (1999) recognized the Vallesian Crisis in Central Europe, however there is no evidence of this event when mean standing diversity is taken into account. Most probably the use of the total number of taxa in their calculations resulted in an apparent diversity crisis coinciding with the Late Vallesian (as we have shown, the number of records in Central European MN 10 is very low as compared to MN 9 and MN 11).

The increase in seasonality in the Iberian Peninsula resulted in an opening of the forest cover in the inner basins, while forested environments persisted in northeastern coastal ones, although including a significant proportion of deciduous trees. Thus, the environment in inner Spain may have been similar to that prevailing in the Greek-Iranian province during the Late Vallesian and the Turolian. However, the persistence of temperate forests in Central Europe acted as an ecological filter preventing the dispersal of eastern open-country herbivores, since only very few taxa of eastern origin reached the Iberian Peninsula. This situation, which persisted during most of the Turolian, may account for the low diversity of the Iberian mammal faunas during this time span. By the Middle Turolian a few more immigrants arrived into Spain, resulting in a moderate increase in genera richness.

According to the turnover pulse model (Vrba, 1985; see also chapter 6) the environmental fragmentation that occurred in the Iberian Peninsula as a result of the Vallesian Crisis may have led to a series of ecologically induced genealogical events. However, as a mater of fact this did not occur, and this area did not develop an autochthonous open-country herbivore fauna. Perhaps macromammal populations were not deeply fragmented thus precluding vicariant speciation. Furthermore, the migration of eastern forms (that is, “habitat tracking” after Vrba, 1985) was apparently stopped by the persistence of humid forest environments in Central Europe. So the final result was a continued impoverishment of the faunas.

Many forest-dwellers that inhabited the Iberian Peninsula, such as the great apes or the tapirids, were adapted to tropical to warm temperate climates. The Late Miocene global cooling (Zachos *et al.*, 2001) implied an important reduction of the evergreen component in Central Europe, leading to the development of deciduous forests by the end of this epoch (Kovar-Eder, 2003). Presumably, the existence of this unfavourable environment would have also acted as a barrier for the migration of those taxa adapted to warm forest environments that were ultimately confined to the Iberian Peninsula until they became extinct.

Appendix 7.1.

Localities included in the analyses. Most of the localities and their respective ages are taken from the NOW database. Each one of the sites is assigned to one of the squares from figure 7.1. The position of each site in the multivariate space of the correspondence analyses from figures 7.3.-7.9. is also indicated.

Locality	Country	Age	Square	CA1 macro.	CA2 macro.	CA1 micro.	CA2 micro.
Alcocer 2	Spain	MN7+8	12			-0,006	-0,020
Alfambra	Spain	MN11	12			-0,006	0,018
Aljezar B	Spain	MN12	12			0,010	-0,006
Ambérieu 1	France	MN11	23			-0,005	-0,004
Ambérieu 2A	France	MN10	23			0,010	-0,003
Ambérieu 2C	France	MN10	23			0,008	-0,006
Ambérieu 3	France	MN11	23			-0,003	-0,006
Ampudia 1	Spain	MN10	12			-0,011	0,018
Ampudia 9	Spain	MN9	12			-0,007	-0,014
Anwil	Switzerland	MN7+8	24	0,004	-0,013	-0,009	0,012
Arenas del Rey	Spain	MN13	2	0,005	-0,010	0,008	0,005
Armantes 7	Spain	MN6	12			0,010	0,004
Arquillo	Spain	MN13	12	0,022	-0,001		
Arquillo 1	Spain	MN13	12	0,021	-0,001	0,009	0,006
Arquillo 4	Spain	MN13	12			0,004	0,009
Arroyo del Val	Spain	MN6	12	0,013	-0,008		
Baccinello V0	Italy	MN11	15			0,035	0,009
Baccinello V2	Italy	MN12	15	0,044	0,001	0,004	0,048
Baccinello V3	Italy	MN13	15	-0,035	-0,015	0,006	-0,002
Bacochas 1	Spain	MN13	2			0,011	0,006
Baltavas	Hungary	MN13	26	-0,014	0,001		
Barranc de Can Vila 1	Spain	MN7+8	13			-0,007	0,000
Bayraktepe 1	Turkey	MN7+8	10			0,022	0,017
Belchatow A	Poland	MN9	37			-0,001	0,015
Belka	Ukraine	MN12	39	-0,007	0,012		
Bernardière	France	MN11	24			-0,005	-0,003
Bois de Raube 15	Switzerland	MN7+8	24			-0,006	-0,003
Borjas 1	Spain	MN6	12			0,019	-0,001
Brisighella	Italy	MN13	15	-0,032	-0,009	-0,031	0,016
Bunker de Valdecebro 4/5	Spain	MN13	12			0,004	0,008
Bunker de Valdecebro B	Spain	MN13	12			0,005	0,008
Buzhor 1	Moldova	MN9	28	-0,004	0,022	0,026	-0,011
Can Casablanques 2	Spain	MN10	13			-0,005	0,001
Can Feliu	Spain	MN7+8	13	-0,001	-0,006	-0,002	-0,006
Can Llobateres 1	Spain	MN9	13	0,008	-0,008	0,005	0,004
Can Missert	Spain	MN7+8	13	-0,001	-0,006	-0,005	-0,007
Can Ponsic 1	Spain	MN9	13	0,005	-0,002	-0,001	-0,001
Çandir	Turkey	MN6	9	0,010	0,007	-0,003	-0,030
Carrilanga 1	Spain	MN9	12			-0,019	-0,010
Casa del Acero	Spain	MN12	12			0,006	-0,003
Casablanca M	Spain	MN13	13			0,010	0,005
Casas Altas	Spain	MN9	12			-0,018	-0,011
Casino	Italy	MN13	15	-0,023	-0,008		
Casteani	Italy	MN12	15	0,041	0,003		
Castell de Barberà	Spain	MN7+8	13	-0,006	-0,007	-0,004	0,008
Castelnau-d'Arbieu	France	MN6	13	-0,006	-0,010		

Celadas 1	Spain	MN13	12			0,007	0,004
Celadas 2	Spain	MN13	12			0,008	0,007
Ceràmiques Viladecavalls	Spain	MN10	13	0,010	0,018	-0,004	0,001
Cerro de la Garita	Spain	MN12	12			0,002	-0,005
Charmoille	Switzerland	MN9	24	0,005	0,001		
Chimishlija	Moldova	MN12	28	-0,008	0,012	-0,049	0,000
Chobruchi	Moldova	MN12	28	-0,007	0,007		
Chomateres	Greece	MN12	7	-0,005	0,015		
Chrysavgi	Greece	MN7+8	17			0,021	-0,012
Ciabot Cagna	Italy	MN13	14			0,002	0,004
Çobanpinar	Turkey	MN12	19	-0,002	-0,017	-0,027	0,002
Comanesti 1	Romania	MN7+8	27			-0,005	-0,008
Concud	Spain	MN12	12	-0,007	-0,012	0,008	-0,005
Concud 2	Spain	MN12	12	-0,006	-0,012	0,010	-0,007
Concud 3	Spain	MN12	12			0,010	-0,007
Concud B	Spain	MN12	12			0,009	-0,006
Concud Barranco	Spain	MN12	12	-0,004	-0,016	0,008	-0,005
Çorak Yerler	Turkey	MN10	20	-0,041	0,003		
Creu Conill 20	Spain	MN9	13			-0,007	0,000
Creu Conill 22	Spain	MN9	13			-0,009	-0,004
Crevillente 15	Spain	MN12	2	-0,005	-0,009	0,008	0,005
Crevillente 16	Spain	MN12	2	-0,005	-0,004		
Crevillente 2	Spain	MN11	2	0,000	-0,022	-0,005	0,015
Csakvar	Hungary	MN11	26	-0,028	0,031	0,004	-0,004
Dionay	France	MN11	24			-0,004	-0,003
Dorn Dürkheim	Germany	MN11	24	-0,032	-0,002	0,007	-0,017
Douvre	France	MN10	24			0,016	0,005
Duredos 1	Spain	MN6	12			0,012	0,001
Dytiko 1	Greece	MN13	17	0,001	0,029		
Dytiko 2	Greece	MN13	17	0,002	0,031		
Dytiko 3	Greece	MN13	17	0,004	0,025		
Eppelsheim	Germany	MN9	24	0,008	-0,008		
Escobosa	Spain	MN7+8	13	0,051	0,021	-0,004	-0,019
Esme Akçaköy	Turkey	MN9	8	-0,041	-0,008		
Esselborn	Germany	MN9	24	0,005	-0,012		
Fiume Santo	Italy	MN12	15	0,035	-0,004		
Four	France	MN6	13			0,001	0,004
Freiria do Rio Maior	Portugal	MN10	11			-0,005	0,001
Garkin	Turkey	MN11	8	0,028	0,017		
Götzendorf	Austria	MN9	26			0,005	0,016
Gravitelli	Italy	MN13	6	0,004	0,000		
Gritsev	Ukraine	MN9	28			0,000	0,008
Grossulovo	Ukraine	MN10	28	-0,018	0,009		
Gülpinar	Turkey	MN10	9	-0,033	-0,015		
Gura-Galben	Moldova	MN12	28	-0,005	0,009		
Hambach 6C	Germany	MN6	34	-0,017	0,012		
Hammerschmiede	Germany	MN9	24			0,004	0,011
Hasznos	Hungary	MN7+8	26			-0,005	-0,004
Haulies	France	MN6	13	0,000	-0,008		
Hostalets de Pierola superior	Spain	MN9	13	0,006	-0,002	-0,006	-0,005
Isere	France	MN7+8	13			-0,006	-0,006
Jujurieux	France	MN9	14			-0,005	0,002
Kalfa	Moldova	MN9	28	-0,010	0,029	0,018	-0,012
Kayadibi	Turkey	MN11	8	0,017	0,015		

Kemiklitepe A-B	Turkey	MN12	8	-0,006	0,010		
Kemiklitepe D	Turkey	MN11	9	0,026	0,016		
Kinik	Turkey	MN12	9	-0,006	0,009		
Klein Hadersdorf	Austria	MN6	26	-0,006	0,009		
Kohfidisch	Austria	MN10	26			0,015	-0,006
Küçükçekmece	Turkey	MN11	19	0,004	-0,004		
La Cantera	Spain	MN11	12	0,008	0,001	-0,012	-0,005
La Cantera 2	Spain	MN10	12			-0,018	-0,004
La Gloria 1	Spain	MN13	11			0,005	0,006
La Gloria 10	Spain	MN11	12			-0,007	0,019
La Gloria 11	Spain	MN10	12			-0,010	-0,005
La Gloria 14A/B	Spain	MN10	12			-0,012	-0,003
La Gloria 5	Spain	MN13	11			0,011	0,008
La Gloria 6	Spain	MN13	11			0,008	0,007
La Grive St. Alban	France	MN7+8	13	0,001	-0,014	-0,010	-0,001
La Roma 1	Spain	MN10	12			-0,018	-0,003
La Roma 2	Spain	MN11	12	0,000	-0,002	-0,018	-0,005
La Salle	Spain	MN10	12			-0,019	-0,004
La Tarumba 1	Spain	MN10	13	0,014	0,025		
Las Casiones	Spain	MN13	12	0,024	-0,013	0,011	0,007
Las Casiones superior	Spain	MN13	12			0,010	0,009
Las Planas 5B	Spain	MN6	12			0,018	0,004
Las Planas 5H	Spain	MN7+8	12			-0,007	-0,014
Las Planas 5K	Spain	MN6	12			0,009	-0,001
Las Planas 5L	Spain	MN6	12			0,021	0,003
Lefkon	Greece	MN11	17			-0,003	0,001
Librilla	Spain	MN13	2			0,008	0,007
Lissieu	France	MN13	13			-0,017	0,000
Lo Fournas 1993	France	MN10	13			0,005	0,003
Lobrieu	France	MN11	13			-0,005	0,007
Los Aguanaces	Spain	MN11	12			-0,006	0,017
Los Aguanaces 1	Spain	MN11	12			-0,005	0,018
Los Aguanaces 5	Spain	MN11	12			-0,007	0,021
Los Aguanaces 5A	Spain	MN10	12			-0,015	-0,002
Los Mansuetos	Spain	MN12	12	-0,004	-0,023	0,006	-0,007
Los Mansuetos 2	Spain	MN12	12			0,008	-0,004
Mahmutgazi	Turkey	MN12	8	-0,007	0,007		
Manchones 1	Spain	MN6	12			0,020	-0,001
Maramena	Greece	MN13	17	-0,012	0,028	-0,007	-0,029
Masada del Valle 2	Spain	MN12	12			0,010	-0,007
Masada del Valle 3	Spain	MN12	12			0,009	-0,006
Masada del Valle 4	Spain	MN12	12			0,009	-0,006
Masada del Valle 5	Spain	MN12	12			0,010	-0,008
Masada del Valle 6	Spain	MN13	12			0,004	0,004
Masada del Valle 7	Spain	MN13	12			0,010	0,009
Masada Ruea	Spain	MN10	12			-0,015	-0,004
Masía de la Roma 11	Spain	MN10	12			-0,018	-0,005
Masía de la Roma 4B	Spain	MN10	12			-0,022	-0,004
Masía de la Roma 4C	Spain	MN10	12			-0,019	-0,002
Masía de la Roma 5	Spain	MN10	12			-0,018	-0,002
Masía de la Roma 6	Spain	MN10	12			-0,016	-0,003
Masía de la Roma 7	Spain	MN10	12			-0,018	-0,004
Masía de la Roma 8	Spain	MN10	12			-0,021	-0,004
Masía de la Roma 9	Spain	MN10	12			-0,018	-0,004

Masía del Barbo A	Spain	MN10	12			-0,018	-0,005
Masía del Barbo B	Spain	MN10	12	0,002	0,007	-0,018	-0,006
Masía la Roma 3	Spain	MN9	12			-0,018	-0,012
Milagros	Spain	MN13	12	0,016	-0,003		
Modorras	Spain	MN13	13			0,006	0,004
Molina de Aragón	Spain	MN9	12			-0,020	-0,014
Mollon	France	MN11	24			-0,004	-0,001
Monasteri	Greece	MN13	17			-0,001	-0,012
Montredon	France	MN10	13	0,021	-0,019	0,003	-0,001
Mt. Luberon	France	MN12	14	-0,005	-0,010	0,009	-0,007
Neudorf-Spalte	Slovakia	MN6	26			0,000	0,005
Nombrevilla	Spain	MN9	12	0,010	-0,005	-0,018	-0,005
Novaja Emetovka	Ukraine	MN12	29	-0,006	0,004		
Opole 2	Poland	MN7+8	36			-0,005	0,012
Paracuellos 3	Spain	MN6	12	0,005	-0,010		
Paracuellos 5	Spain	MN6	12	-0,006	-0,003		
Pedregueras 2A	Spain	MN9	12			-0,012	-0,011
Pedregueras 2C	Spain	MN9	12			-0,016	-0,010
Pentalophos	Greece	MN10	17	0,021	-0,019		
Peralejos 4	Spain	MN10	12			-0,021	-0,005
Peralejos 5	Spain	MN9	12			-0,019	-0,016
Peralejos A	Spain	MN10	12			-0,018	-0,003
Peralejos C	Spain	MN10	12			-0,016	-0,005
Peralejos D	Spain	MN11	12			-0,006	0,017
Pero Filho	Portugal	MN6	1			0,000	0,002
Piera	Spain	MN11	13	0,000	-0,018		
Pikermi-MNHN	Greece	MN12	7	-0,008	0,019		
Plakia	Greece	MN7+8	7			-0,007	0,013
Poksheshty	Moldova	MN10	28	-0,013	0,008		
Prebreza	Serbia	MN6	17	0,028	0,016		
Prochoma	Greece	MN11	17	0,021	-0,006		
Przeworno 2	Poland	MN7+8	36	-0,008	0,002		
Puente Minero	Spain	MN11	12	-0,012	-0,024	-0,006	0,019
Puente Minero 2	Spain	MN10	12			-0,016	-0,004
Puente Minero 3	Spain	MN11	12			-0,007	0,018
Puente Minero 5A/5B	Spain	MN11	12			-0,006	0,018
Puy Courny	France	MN12	13	-0,005	0,002		
Pyrgos Vassilissis	Greece	MN12	7	-0,005	0,014		
Rambla de Valcecebro 0	Spain	MN13	12	0,020	0,001		
Rambla de Valcecebro 3	Spain	MN13	12			0,009	0,006
Rambla de Valcecebro 6	Spain	MN13	12			0,010	0,009
Ravin de la Pluie	Greece	MN10	17	0,021	-0,019		
Ravin des Zouaves 1	Greece	MN10	17	0,021	-0,019		
Ravin des Zouaves 5	Greece	MN11	17	0,031	0,001		
Regajo 2	Spain	MN11	12			-0,004	0,015
Regajo 3	Spain	MN12	12			0,008	-0,007
Regajo 4	Spain	MN12	12			0,008	-0,006
Regajo 5	Spain	MN13	12			0,006	0,004
Respopeny	Moldova	MN10	28	-0,012	0,003		
Rubí-Terrassa 7	Spain	MN10	13			-0,005	0,001
Rudabánya	Hungary	MN9	27	0,007	-0,004	0,000	0,021
Rümikon	Switzerland	MN6	24			-0,017	0,007
Saint Bauzille	France	MN11	13			-0,001	0,004
Samos Main Bone Beds	Greece	MN12	8	-0,005	-0,008		

Samos White Sands	Greece	MN12	8	-0,005	0,005		
Sansan	France	MN6	12	-0,004	-0,018	-0,007	0,004
Sant Quirze	Spain	MN7+8	13	-0,003	-0,006	-0,008	0,005
Santiga	Spain	MN9	13				
Schwamendingen	Switzerland	MN6	24			-0,015	0,008
Simancas 2	Spain	MN6	12			0,014	0,001
Simorre	France	MN6	13	0,012	-0,015		
Soblay	France	MN10	24	0,014	0,002	0,016	0,004
Sofça	Turkey	MN7+8	9	-0,021	0,034	0,009	-0,013
Solera	Spain	MN7+8	12			-0,006	-0,016
Stätzling	Germany	MN6	25	-0,019	0,012		
Steinberg	Germany	MN6	34			0,005	0,006
Steinheim	Germany	MN7+8	25	0,002	-0,015	-0,005	-0,002
Sümeg	Hungary	MN11	26			-0,002	-0,016
Tal·lús Sud Autopista 2	Spain	MN10	13			-0,009	-0,002
Thannhausen	Germany	MN6	25	-0,019	0,014		
Toril	Spain	MN7+8	12			-0,008	-0,015
Torremormojón 1	Spain	MN10	12			-0,013	0,020
Torremormojón 4	Spain	MN9	12			-0,005	-0,012
Torremormojón 5	Spain	MN7+8	12			-0,001	-0,006
Torrent de Febulines	Spain	MN10	13	0,014	-0,005		
Torrent de Febulines 3	Spain	MN10	13			-0,003	-0,001
Tortajada	Spain	MN12	12			0,009	-0,006
Tortajada A	Spain	MN11	12			-0,007	0,021
Tortajada B	Spain	MN12	12			0,008	-0,004
Tortajada D	Spain	MN12	12			0,010	-0,007
Tudorovo	Moldova	MN12	28	-0,006	-0,003		
Unterneul	Germany	MN6	25			0,004	0,000
Valalto 1	Spain	MN6	12			0,021	0,002
Valalto 2B	Spain	MN6	12			0,023	0,004
Valalto 2C	Spain	MN6	12			0,022	0,006
Valdecebro 5	Spain	MN12	12	-0,007	-0,016		
Valles de Fuentidueña	Spain	MN9	12	0,000	0,014		
Valréas	France	MN11	13			-0,004	0,013
Vathylakkos	Greece	MN11	17	0,023	-0,009		
Venta del Moro	Spain	MN13	2	0,013	-0,025	0,009	0,005
Vilafeliche 9	Spain	MN7+8	12			-0,007	-0,014
Villalba Baja 2/2C	Spain	MN12	12			0,009	-0,007
Villastar	Spain	MN13	12	0,022	-0,006	0,010	0,004
Vivero de Pinos	Spain	MN11	12	-0,018	-0,026	-0,007	0,014
Vösendorf	Austria	MN9	26			0,002	0,000
Wartenberg	Germany	MN9	25	0,010	-0,009		
Westhofen	Germany	MN9	24	0,008	-0,011		
Wiesholz	Switzerland	MN6	24			-0,014	0,009
Xirochori 1	Greece	MN10	17	0,021	-0,019		
Yeni Eskihisar 1	Turkey	MN7+8	8	-0,022	0,035	0,037	-0,003
Zeglingen	Switzerland	MN6	24			-0,002	0,004

Epilogue

Summary and conclusions

Chapters 1 and 2

The Vallès-Penedès Basin, in the North-Eastern margin of the Iberian Peninsula, is a classical area for the study of the Miocene mammalian succession in Europe, and still presents itself as one of the most suitable areas to calibrate the set of events that punctuated the Middle and the Late Miocene in the continent. Recently the number of mammal sites known has increased spectacularly as the result of the magnetostratigraphic survey of the Vallès Occidental area, and more importantly by the field work at the Abocador de Can Mata (ACM) series, near els Hostalets de Pierola (l'Anoia, Catalonia). A thick and continuous section (300 m) covering part of the Late Aragonian (MN 7+8 and in all probability also MN 6) an (in the near future) the Early Vallesian is being sampled and for the moment being has delivered nearly 100 new mammal sites. The preparation and study of the material are still in course, however, preliminary results allows us to suggest a new biozonation for the Late Aragonian of the Vallès-Penedès Basin that may be also applied to the successions of Calatayud-Daroca Basin (Inner Spain) and the La Grive fissure fillings (France). Further field work, and the study of the material will refine these preliminary conclusions.

Chapter 3

The first castorid remains from the area of els Hostalets de Pierola are described. These fossil remains include a virtually complete hemimandible, two maxillary fragments and several isolated teeth from the ACM locality C4-C2 (Late Aragonian, MN 7+8), as well as an almost complete femur from stratigraphically close locality C3-Ak. A new species, *Chalicomys* (= *Palaeomys*) n. sp., is erected on the basis of the C4-C2 material. The femur from C3-Ak is also tentatively included within the hypodigm of the newly described species, being compared to another femur form Sant Quirze (Vallès-Penedès Basin, Late Aragonian, MN 7+8) which is attributed to *Chalicomys catalaunicus* comb. nov. *Chalicomys* n. sp. is a medium-sized *Chalicomys* species characterized by the presence of pronounced secondary enamel folds on cheek teeth. Its size and degree of hypsodonty appears to be intermediate between *C. catalaunicus* and *C. jaegeri*. Taxonomic and nomenclatural issues regarding the genus *Chalicomys* are discussed, and on the basis of the Principle of the First Reviser, it is concluded that *Chalicomys* must be preferred over *Palaeomys*. An emended diagnosis of this genus is provided. On the basis of femoral anatomy it is concluded that, like living *Castor*, these extinct beavers were efficient swimmers highly committed to aquatic locomotion, which propelled mainly by means of hind feet paddling. The presence of an extinct beaver with *Castor*-like aquatic adaptations in this are permits to infer more humid conditions than previously thought for the area of els Hostalets de Pierola; at least for a restricted to a short time interval given the rarity of castorid remains elsewhere in the ACM stratigraphic series.

Chapter 4

The area of els Hostalets de Pierola is well known amongst paleoprimatologists because of the discovery of a few hominoid dentognathic remains (currently attributed to *Dryopithecus laietanus*) during the first half of the 20th century. Soon after the beginning of the extension works of the ACM, in fall 2002, the excavations marginally affected a ravine close to the farm house of Can Vila (the so-called "Barranc de Can Vila"). The machines unearthed some mammal remains including a remarkably complete partial skull of a great ape. Systematic paleontological excavations at the Barranc de Can Vila 1 site (BCV1) were finally undertaken during May-June 2003, providing as much as 83 bones or identifiable bone fragments from a single primate individual which would define the base for the erection of a new genus and species: *Pierolapithecus catalaunicus*. In addition to *P. catalaunicus*, BCV1 has delivered remains of eight species of macromammals besides an abundant sample of micromammal cheek teeth including insectivores, a few lagomorphs and mostly rodents.

The rodent fauna from BCV1 is described. It includes eleven rodent species distributed amongst sciurids (2), glirids (4) and "cricetids" (5). The sciurids include the ground squirrel *Spermophilinus bredai*, which is fairly abundant, besides a few teeth attributed to the flying squirrel *Miopetaurista* cf. *crusafonti*. The glirids are nearly as diverse as the "cricetids" but much less abundant. The "cricetids" represent more than 80 % of the recovered cheek teeth, while the glirids are less than the 5 %. *Glirudinus undosus* is the most abundant dormice (Gliridae), being represented by only eight teeth. The remaining Gliridae species include *Muscardinus sansaniensis* and *Microdyromys complicatus*, which are here reported for the first time from the Vallès-Penedès Basin. The fourth dormice identified is *Bransatoglis* sp., which is represented by just one M^3. Concerning the "cricetids", *Eumyarion leemani*, which–represents 40 % of the assemblage, is by far the most abundant rodent in the sample. The *Eumyarion* material from other Late Aragonian sites of the Vallès-Penedès Basin (Sant Quirze, Castell de Barberà) is ascribed to *E. leemani*. The remaining identified "cricetid" species are: *Democricetodon larteti*; *Democricetodon brevis brevis*, which is here quoted for the first time in the Vallès-Penedès Basin; *Megacricetodon minor minor*; and the numerically rare *Hispanomys* sp.

The composition of the rodent assemblage indicates an early MN 7+8 age for the fauna. Further biochronological resolution may be achieved by a close comparison of the *Democricetodon larteti* population from BCV1 with those from several sites from the Calatayud-Daroca Basin, which have been magnetostratigraphically calibrated. The size and morphology of *D. larteti* from BCV1 indicates that this is a derived population, clearly younger than the youngest populations of this species in the Calatayud-Daroca Basin (Toril 3B). Accordingly, the age of BCV1 is inferred to lie between 12.5 and 12 Ma, being half a million of years younger than the age previously proposed by Moyà-Solà *et al.* (2004). This site is also clearly older than other MN 7+8 "classical" sites from the Vallès-Penedès Basin, such as Sant Quirze or Castell de Barberà. Therefore BCV1 records the first occurrence of the hominoid primates in basin.

Chapter 5

The taphonomical study of the micro- and macrovertebrates from BCV1 allows us to recognize different the taphonomical agents involved in the origin of the accumulation. All the remains of *Pierolapithecus catalaunicus* are attributable to a single individual. Moreover, they are spatially associated and randomly oriented, suggesting little transport. Given the fact that carnivore marks are present in some of the primate bones, predation is proposed as the main accumulation agent. In contrast, predation marks are mostly absent in other macromammal remains. These seem to derive from isolated bones scattered around the alluvial plain, next to the burial area. Concerning the small mammals, the accumulation does not seem to be predator-derived, given the fact that digestion traces on bone and teeth are very rare. All the remains would have been buried by a low energy muddy current flow and soon afterwards underwent some early diagenetic modifications related to its shallow burial in the alluvial deposits

The small mammal fauna from BCV1 indicates the presence of considerably humid warm-temperate forest environments. The composition of the small mammal fauna from BCV1 and from other Late Aragonian sites from the Vallès-Penedès area shows similarities with those from France and Central Europe. It is clearly distinct from that of the basins of inner Spain, where the environment appears to have been dryer, thus precluding the dispersal of hominoids in that area.

Chapter 6

The composition and structure of rodent taxocenosis from three Iberian basins (Calatayud-Teruel, Duero and Vallès-Penedès) with a reasonably complete record for the latest Aragonian and Vallesian is explored by the means of Correspondence Analysis (CA). CA classifies the assemblages in four great groups that are interpreted as rodent paleocomunity types (RPTs). On the basis of paleobotanical and paleomastological data available for some of the sites considered (or time-equivalent localities) each RPT is considered to be characteristic of certain environmental conditions.

Taxonomic membership and relative abundance patterns in the recognized RPTs are quite stable throughout relatively long time intervals in each basin, suggesting the existence of coordinated stasis. However, the predictions of the coordinated stasis model are only partly achieved, and important differences are shown to occur within certain RPTs. RPTs with a low species richness and dominated by one or two genera characterize the record of the Duero Basin. In the case of the Vallès-Penedès and Calatayud-Teruel more equitative RPTs with a high species richness are present during the Early Vallesian (and also during the latest Aragonian in the Vallès-Penedès). The Late Vallesian sites appear as clearly differentiated of the remaining ones and grouping is strongly influenced by geographic position. The environment seems to have been more open and wet-dry seasonal in the Late Vallesian sites of the Calatayud-Teruel and Duero basins. Instead in the Vallès-Penedès Basin it appears to have been more humid and cool-warm seasonal. This fact points to the existence of a zonation of the Iberian climate during the Late Vallesian that closely matches the pattern observed today.

Chapter 7

The Late Miocene is a complex moment which appears punctuated by several climatic and phisiographic events. In the terrestrial ecosystems, these events must have influenced the pattern of dispersal and turnover among the mammalian faunas. In fact, the Late Miocene, that is the period covered by continental mammal stages Vallesian and Turolian, coincides with several faunal dispersals, induced by either climatic events, intercontinental relationships or by an interplay between both causes. At about 9.7 Ma, a significant and abrupt mammal turnover, known as the Vallesian Crisis, profoundly altered the composition of the Western European terrestrial ecosystems from the Vallès-Penedès Basin. This event involved the disappearance of most of the Middle Miocene faunal elements adapted to wet subtropical environments. Certain authors have advocated for the extension of the Crisis to other areas of Eurasia. Nevertheless, the effects of the Vallesian Crisis and the existence of such event in other areas are still controversial.

In order to investigate and refine the chronologic and geographic limits of the Vallesian Crisis we explore a large data base defined by a series of European fossil mammal sites covering most of the middle and all the late Miocene (13.8 – 4.9 Ma). Temporal resolution in the age of the sites is at the level of the MN zone. Provinciality is studied by the means of successive CA for each MN unit. Results indicate the maintenance of three main bioprovinces (Greek-Iranian, Iberian and Central European) during most of the time span. Mean standing diversity and origination and extinction rates have been calculated for all Europe and for each main bioprovince by the methods devised by Van Valen (1984), for standing diversity, and Foote (2000), for taxonomic rates. The results show that diversity increased during the Late Vallesian and the Turolian in the Greek-Iranian bioprovince because of the development of open-country herbivore faunas while diversity remained stable in Central Europe. A decay in diversity started in the Iberian Peninsula by the Early Vallesian and genera richness kept descending during the Turolian. This diversity decline, which corresponds the Vallesian Crisis, is supposed to be related to the fragmentation or change in the pre-existing warm temperate forests. Therefore, the Vallesian Crisis appears to have been an exclusively Iberian event.

During the Turolian the environment was probably similar in the Greek-Iranian and the Iberian provinces; however, Turolian mammal faunas from the Iberian Peninsula are very poor and show few eastern immigrants. We suggest that the presence of mixed mesophytic forests, that then covered a great part of Central Europe, acted as an ecological filter, precluding the dispersal of open-country adapted taxa characteristic from the Greek-Iranian province. This model would account for the slow recovery of the diversity in the aftermath of the Vallesian Crisis, which would not occur until the end of the Miocene.

Epíleg

Resum i conclusions

Capítols 1 i 2

La conca del Vallès-Penedès, situada al marge nord-oriental de la Península Ibèrica és una àrea clàssica per a l'estudi de la successió de mamífers del Miocè europeu, i encara representa una de les àrees més adequades per a calibrar la sèrie d'esdeveniments que puntuaren el Miocè Mitjà i Superior al continent. Recentment el nombre conegut de jaciments amb mamífers fòssils ha incrementat espectacularment arrel de la prospecció magnetoestratigràfica de l'àrea del Vallès Occidental, i d'una manera més important degut als treballs de camp a la sèrie del Dipòsit Controlat de Can Mata (Abocador de Can Mata; ACM), situat al terme municipal dels Hostalets de Pierola (l'Anoia, Catalunya). S'està mostrejant una secció llarga (300 m) i continua que cobreix part de l'Aragonià Superior (MN 7+8 i molt probablement també MN 6) i (en un futur proper) el Vallesià Inferior i que fins a data d'avui ha lliurat prop de 100 nous jaciments. La preparació i estudi del material encara estan en progrés, no obstant els resultats preliminars permeten suggerir una nova biozonació per l'Aragonià Superior de la conca del Vallès-Penedès que també podria ser aplicable a les successions de la conca de Calataiud-Daroca (Saragossa, Aragó) i els rebliments càrstics de La Grive (França). Els futurs treballs de camp a l'àrea dels Hostalets de Pierola, així com l'estudi del material recuperat permetrà refinar aquestes conclusions preliminars.

Capítol 3

Es descriuen les primeres restes de castòrids de l'àrea dels Hostalets de Pierola. Les restes inclouen una hemimandíbula pràcticament completa, dos fragments de maxil·lar i unes poques dents aïllades provinents de la localitat C4-C2 de l'ACM (Aragonià Superior, MN 7+8), així com un fèmur gairebé complet provinent de la localitat C3-Ak de l'ACM, estratigràficament propera a l'anterior. S'erigeix una nova espècie, *Chalicomys* (= *Palaeomys* n. sp.), en base al material de C4-C2. El fèmur de C3-Ak també s'inclou de manera temptativa a l'hipodigma de la nova espècie i és comparat amb un altre fèmur provinent del jaciment Sant Quirze (conca del Vallès-Penedes, Aragonià Superior, MN 7+8) que s'atribueix a *Chalicomys catalaunicus* comb. nova. *Chalicomys* n. sp. és una espècie de *Chalicomys* de mida mitjana caracteritzada per la presència de replecs secundaris pronunciats en l'esmalt de les dents postcanines. La seva talla i grau d'hipsodòncia sembla intermedi entre *C. catalaunicus* i *C. jaegeri*. Es discuteixen problemes taxonòmics i nomenclaturals relacionats amb el gènere *Chalicomys*, i en base al Principi del Primer Revisor es conclou que el nomen *Chalicomys* ha de tenir preferència sobre *Palaeomys*. Es proposa una diagnosi esmenada per a aquest gènere. En base a l'anatomia del fèmur de *Chalicomys* es conclou que, al igual que l'actual *Castor*, aquests castors eren eficients nedadors estretament compromesos amb la locomoció aquàtica, els quals es propulsaven principalment per mitjà del impuls coordinat dels seus peus. La presència d'un castòrid extingint amb adaptacions aquàtiques similars a les de *Castor* permet inferir condicions més humides del que es creia per l'Aragonià Superior de l'àrea dels Hostalets de Pierola; almenys durant un període de temps restringit a curt, donada la raresa de les restes de castòrid en altres punts de la sèrie.

L'àrea dels Hostalets de Pierola és ben coneguda entre els paleoprimatòlegs degut a la descoberta d'unes poques restes dentognàtiques d'hominoïdeus (actualment atribuïdes a *Dryopithecus laietanus*) durant la primera meitat del segle XX. Poc després d'iniciar-se les obres d'ampliació de l'ACM, a la tardor de 2002, les excavacions afectaren de manera marginal un barranc proper a la masia de Can Vila. Les màquines excavadores van desenterrar algunes restes de mamífers incloent un crani parcial remarcablement complet d'un primat hominoïdeu. Durant, les excavacions paleontològiques sistemàtiques al jaciment de Barranc de Can Vila 1 (BCV1), que es portaren a terme entre el Maig i el Juny de 2003, es van recuperar fins a 83 ossos o fragments d'os identificables corresponents a un únic individu de primat que constituiria la base per a l'erecció d'un nou gènere i espècie: *Pierolapithecus catalaunicus*. A més de *P. catalaunicus*, BCV1 ha lliurat les restes de vuit espècies de macromamífers així com una abundant mostra de dents postcanines de micromamífers que inclou insectívors, escassos lagomorfs i sobretot rosegadors.

Es descriu la fauna de rosegadors de BCV1. Aquesta inclou fins a onze espècies distribuïdes entre esciúrids (2), glírids (4) i "cricètids" (5). Els esciúrids inclouen l'esquirol terrestre *Spermophilinus bredai*, que és prou abundant, a més d'algunes poques dents atribuïdes a l'esquirol volador *Miopetaurista* cf. *crusafonti*. Els glírids són pràcticament tan diversos com els "cricètids" encara que molt menys abundants. Els "cricètids" representen més del 80 % de les dents postcanines recuperades, mentre que els glírids defineixen menys d'un 5 % d'aquestes. *Glirudinus undosus* és el glírid més abundant, estant representat per vuit dents. La resta d'espècies de Gliridae inclouen *Muscardinus sansaniensis* i *Microdyromys complicatus*, que es citen per primer cop de la conca del Vallès-Penedès en aquest treball. El quart liró identificat és *Bransatoglis* sp., que està representat per sols una M^3. Pel que es refereix als "cricètids", *Eumyarion leemani*, que representa un 40 % de l'associació, és de llarg el rosegador més abundant a la mostra. El material d'*Eumyarion* d'altres localitats de l'Aragonià Superior de la conca del Vallès-Penedès (Sant Quirze, Castell de Barberà) és adscrit a *E. leemani*. Les altres espècies de "cricètids" identificades són: *Democricetodon larteti*; *Democricetodon brevis brevis*, que també es cita per primer cop de la conca del Vallès-Penedès; *Megacricetodon minor minor*; i el numèricament escàs *Hispanomys* sp.

La composició de l'associació de rosegadors indica que la fauna correspon a la part baixa de la MN 7+8. Es pot assolir una precisió biocronològica més acurada basant-se en la comparació de la població de *Democricetodon larteti* de BCV1 amb les de diversos jaciments de la conca de Calataiud-Daroca que s'han calibrat magnetoestratigràficament. La mida i la morfologia de *D. larteti* de BCV1 indiquen que es tracta d'una població avançada, clarament més jove que les poblacions més joves d'aquesta espècie de la conca de Calataiud Daroca (Toril 3B). En conseqüència s'infereix que l'edat de BCV1 es situa entre els 12.5 i els 12 Ma, essent mig milió d'anys més jove que la que prèviament havien proposat Moyà-Solà *et al.* (2004). Aquest jaciment també és clarament més antic que altres localitats "clàssiques" de la MN 7+8 de la conca del Vallès-Penedès, com Sant Quirze i Castell de Barbera. Per tant, BCV1 registra la primera aparició dels primats hominoïdeus a la conca.

Capítol 5

L'estudi tafonòmic dels micro- i macrovertebrats de BCV1 ens permet reconèixer els diferent agents tafonòmics involucrats en l'origen de l'acumulació. Totes les restes de *Pierolapithecus catalaunicus* són atribuïbles a un únic individu. A més, aquestes restes estan espacialment associades i orientades a l'atzar, fet que suggereix poc transport. Donat que alguns ossos de primat presenten marques fetes per carnívors es proposa que la predació és el principal agent d'acumulació en aquest cas. Per contra, la majoria de les restes d'altres macromamífers no presenta marques de predació. Aquestes restes sembla que deriven d'ossos escampats al llarg de la plana al·luvial, adjacents a l'àrea d'enterrament. Pel que es refereix als petits mamífers, l'acumulació no sembla derivar de la predació, donat que les traces de digestió en ossos i dents són molt rares. Totes les restes haurien estat enterrades per un corrent fangós de baixa energia i poc després van patir algunes modificacions diagenètiques relacionades amb el seu enterrament superficial en dipòsits al·luvials.

La fauna de petits mamífers de BCV1 ens indica la presència d'ambients forestals subtropicals i considerablement humits. La composició de la fauna de BCV1 i d'altres localitats de l'Aragonià Superior de l'àrea del Vallès-Penedès presenta semblances amb la de França i Europa Central. Aquesta és clarament diferent de la de les conques de l'interior d'Espanya, on l'ambient sembla haver estat més sec, impedint en conseqüència la dispersió dels hominoïds a aquella àrea.

Capítol 6

La composició i estructura de la taxocenosi de rosegadors de tres conques ibèriques (Calataiud-Terol, Duero i Vallès-Penedès) amb un registre raonablement complet per l'Aragonià terminal i el Vallesià és explorada mitjançant un Anàlisis de Correspondència (CA). El CA classifica les associacions en quatre grans grups que s'interpreten com a tipus de paleocomunitats de rosegadors (RPTs). En base a dades paleobotàniques i paleomastològiques cada RPT es considera característica de determinades condicions ambientals.

La composició taxonòmica i els patrons d'abundància relativa a les RPTs reconegudes es mantenen força estables al llarg d'intervals de temps relativament llargs a cada conca, suggerint l'existència d'estasi coordinada. No obstant, les prediccions del model de l'estasi coordinada tan sols s'assoleixen en part, i es mostra que existeixen importants diferències dins certes RPTs. RPTs amb una baixa riquesa específica i dominades per un o dos gèneres caracteritzen el registre de la conca del Duero. En el cas de la conca del Vallès-Penedes i Calataiud-Terol les RPTs són més equitatives i contenen una alta diversitat d'espècies durant el Vallesià Inferior (i també durant l'Aragonià terminal en el cas del Vallès-Penedès). Els jaciments del Vallesià Superior apareixen clarament diferenciats de la resta i en una agrupació fortament influenciada per la seva posició geogràfica. L'ambient sembla haver estat més obert i amb una estacionalitat en el règim pluvial a les localitats del Vallesià Superior de les conques de Calataiud-Daroca i el Duero. Per contra, a la conca del Vallès-Penedès sembla haver estat més humit i amb una estacionalitat alternant estacions fredes i càlides. Aquest fet apunta vers a l'existència d'una zonació del clima ibèric durant el Vallesià Superior que s'aproxima al patró existent avui en dia.

Capítol 7

El Miocè Superior és un moment complex que apareix puntuat per nombrosos esdeveniments climàtics i fisiogràfics. Als ecosistemes terrestres aquests esdeveniments necessàriament han d'haver influenciat els patrons de dispersió i recanvi faunístic entre les faunes de mamífers. De fet, el Miocè Superior, és a dir el període de temps representat pels estatges paleomastològics Vallesià i Turolià, coincideix amb nombroses dispersions faunístiques induïdes bé per esdeveniments climàtics, relacions intercontinentals o una interacció entre ambdues causes. Vers als 9.7 Ma, un important i abrupte recanvi en la fauna de mamífers, conegut com la Crisi Vallesiana, va alterar profundament la composició dels ecosistemes terrestres de la conca del Vallès-Penedès. Aquest esdeveniment implicà la desaparició de la majoria de mamífers amb un origen que es remunta al Miocè Mitjà i que estaven adaptats als ambients subtropicals humits. Alguns autors han proposat que la Crisi s'estengué a altres zones d'Euràsia. No obstant, els efectes de la Crisi Vallesiana i fins hi tot l'existència d'aquest esdeveniment a altres àrees és un tema controvertit.

A fi d'investigar i refinar els límits cronològics i geogràfics de la Crisi Vallesiana s'explora una gran base de dades de localitats amb mamífers fòssils europees que comprèn la majoria del Miocè Mitjà i tot el Superior (13.8 – 4.9 Ma). La resolució temporal en l'edat de les localitats és a nivell de biozona MN. La provincialitat s'estudia per mitjà de successius CA a cada unitat MN. Els resultats indiquen la permanència de tres bioprovíncies principals (greco-iraniana, ibèrica i centreuropea) durant la major part del lapse de temps. S'han calculat la diversitat mitjana permanent i les taxes d'originació i extinció per la totalitat d'Europa i per cada una de les bioprovíncies principals per mitjà dels mètodes proposats per Van Valen (1984), per la diversitat mitjana permanent, i Foote (2000), per les taxes taxonòmiques. Els resultats mostren que la diversitat va incrementar de manera contínua durant el Vallesià Superior i el Turolià a la província greco-iraniana degut al desenvolupament d'una fauna d'herbívors de camp obert, mentre que la diversitat es va mantenir estable a la província centreuropea. A la Península Ibèrica s'inicià un descens en la diversitat vers al Vallesià Inferior i la riquesa genèrica va continuar decreixent durant el Turolià. Aquesta davallada en la diversitat, que correspon a la Crisi Vallesiana, es suposa relacionada amb una fragmentació o canvi dels boscos subtropicals pre-existents. Per tant la Crisi Vallesiana sembla haver estat un fenomen exclusivament ibèric.

Durant el Turolià l'ambient era probablement similar a les províncies greco-iraniana i ibèrica, no obstant, les faunes de mamífers del Turolià de la Península Ibèrica són molt pobres i presenten pocs immigrants d'origen oriental. Es suggereix que la presència de boscos mixtes mesofítics, que llavors cobrien bona part d'Europa central, va actuar com un filtre ecològic, impedint la dispersió de les faunes adaptades al camp obert característiques de la província greco-iraniana. Aquest model explicaria la lenta recuperació de la diversitat en el període posterior a la Crisi Vallesiana, que no succeiria fins a finals del Miocè.

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