Nous primats de l'Eocè de la Península Ibèrica: implicacions filogenètiques i paleobiogeogràfiques

Judit Marigó Cortés

TESI DOCTORAL
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Memòria presentada per Judit Marigó Cortés per optar al títol de Doctor en Biologia, programa de doctorat en Biodiversitat del Departament de Biologia Animal, de Biologia Vegetal i d'Ecologia de la Universitat Autònoma de Barcelona, dirigida per:

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L’Elionor tenia
catorze anys i tres hores
quan va posar-se a treballar.
Aquestes coses queden
enregistrades a la sang per sempre.
Duia trenes encara
i deia: “sí, senyor” i “bones tardes”.
La gent se l’estimava,
l’Elionor, tan tendra,
i ella cantava mentre
feia córrer l’escombra.
Els anys, però, a dins la fàbrica
es dilueixen en l’opaca
grisor de les finestres,
i al cap de poc l’Elionor no hauria
pas sabut dir d’on li venien
les ganes de plorar
ni aquella irreprimible
sensació de solitud.
Les dones deien que el que li passava
era que es feia gran i que aquells mals
es curaven casant-se i tenint criatures.
L’Elionor, d’acord amb la molt sàvia
predicció de les dones,
va créixer, es va casar i va tenir fills.
El gran, que era una noia,
feia tot just tres hores
que havia complert els catorze anys
quan va posar-se a treballar.
Encara duia trenes
i deia: “sí, senyor” i “bones tardes”.

Miquel Martí i Pol. *La fàbrica* (1972).

Als meus pares

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RESUM / ABSTRACT

RESUM

Restes de primats de l'Eocè han estat recuperades de diferents jaciments de la Península Ibèrica des de la dècada de 1960, tot i que el seu estudi ha estat escàs des d'aleshores. Aquesta tesi doctoral inclou, d'una banda, una revisió bibliogràfica exhaustiva del registre de primats del Cenozòic de la Península Ibèrica, que representa una actualitació essencial després de les noves troballes fetes durant les últimes dècades i, d'altra banda, la descripció, comparació i determinació taxonòmica de noves restes dentàries de primats (Plesiadapiformes, Adapoïdeus i Omomioïdeus) de diferents jaciments de l'Eocè de la Península Ibèrica: Masia de l'Hereuet i Sossís (Lleida), Sant Jaume de Frontanyà (Barcelona) i Mazaterón (Sòria), emmagatzemades a les col·leccions de l'Institut Català de Paleontologia Miquel Crusafont. Aquests estudis han permès en alguns casos la definició de nous tàxons.

Concretament, s'ha descrit l'únic material de plesiadapiforme trobat a Espanya fins ara, procedent del jaciment de Masia de l'Hereuet (Eocè Inferior, Conca Sudpirinenca Central), i s'ha atribuït al gènere *Arcius*, l'únic gènere de la família Paromomyidae trobat a Europa, encara que l'escassedat de material no ha permès realitzar una determinació a nivell d'espècie.

Del jaciment de Sant Jaume de Frontanyà (Eocè Mitjà, Conca Sudpirinenca Oriental) s'han definit dues espècies noves, l'adapoïdeu *Anchomomys frontanyensis* i l'omomioïdeu *Pseudoloris pyrenaicus*. La troballa d'*A. frontanyensis*, que va existir als Pirineus simultàniament amb l'espècie *A. gaillardi* a França, revela l'existència d'un altre llinatge d'aquest gènere a Europa. La descripció del material de *P. pyrenaicus* revela que les espècies *P. saalae*-*P. isabenae*-*P. pyrenaicus*-*P. parvulus* constitueixen un llinatge que va evolucionar durant l'Eocè Mitjà-Superior a Europa.

També s'han definit un nou gènere i espècie, l'adapoïdeu *Mazateronodon endemicus*, i una nova espècie, l'omomioïdeu *Pseudoloris cuestai*, del jaciment de Mazaterón (Eocè Mitjà, Conca del Duero), que presenten diferències en la dentició amb els representants dels seus respectius grups a les conques pirinenques i a la resta d'Europa. Això reforça el caràcter endèmic de les faunes de la Bioprovíncia Occidental Ibèrica, que havia estat observat prèviament en altres grups de mamífers, causat per l'aïllament d'aquesta regió de la resta d'Europa durant l'Eocè, com a conseqüència de la transgressió marina que

connectà els mars Cantàbric i Mediterrani. A més a més, *Mazateronodon* representa la mostra més rica d'un primat de l'Eocè d'aquesta bioprovíncia.

Del jaciment de Sossís (Eocè Superior, Conca Sudpirinenca Central) s'ha descrit un nou gènere i espècie, l'adapoïdeu *Nievesia sossissensis*, que ha ajudat a aclarir, juntament amb la resta d'adapoïdeus estudiats en aquest treball, tots pertanyents a la tribu Anchomomyini, les relacions filogenètiques entre els anchomomyins i amb la resta d'adapoïdeus i estrepsirins actuals. Els resultats indiquen que els nous gèneres *Nievesia* i *Mazateronodon* semblen estar més emparentats entre ells que no pas amb la resta d'anchomomyins, i tot indica que els anchomomyins no estarien més relacionats amb els estrepsirins corona que amb altres adapiformes, i que en canvi hi hauria una relació filogenètica més estreta entre els anchomomyins i els asiadapins i els sivaladàpids que amb altres adapiformes. Tot i això, aquests resultats s'han d'analitzar amb precaució, degut a que és necessària més informació sobre caràcters que ens són encara desconeguts.

ABSTRACT

Fossil remains of Eocene primates have been recovered from many sites in the Iberian Peninsula since the 1960's, although they have been poorly studied. This doctoral thesis includes, on the one hand, a thorough bibliographic revision of all the Cenozoic primate material from the Iberian Peninsula, which represents an essential updating after the new discoveries of the last decades. On the other hand, the description, comparison and taxonomic determination of new primate dental remains of Plesiadapiformes, Adapoidea and Omomyoidea from different Eocene fossil sites of the Iberian Peninsula: Masia de l'Hereuet and Sossís (Lleida), Sant Jaume de Frontanyà (Barcelona) and Mazaterón (Soria), stored in the collections of the Institut Català de Paleontologia Miquel Crusafont. These studies have allowed, in some cases, the definition of new taxa.

Specifically, the only material of a plesiadapiform found in Spain has been described, which was recovered from the fossil site of Masia de l'Hereuet (Early Eocene, Southern Pyrenean basins). The studied remains have been attributed to the genus *Arcius*, the only genus of the family Paromomyidae found in Europe, even though the scarcity of the material has not allowed a specific determination.

From the fossil site of Sant Jaume de Frontanyà (Middle Eocene, Southern Pyrenean basins) two new species have been erected, the adapoid *Anchomomys frontanyensis* and the omomyoid *Pseudoloris pyrenaicus*. The finding of *A. frontanyensis*, which existed in the Pyrenees simultaneously with the species *A. gaillardi* in France, reveals the existence of another lineage of this genus in Europe. The description of the *P. pyrenaicus* material reveals that the species *P. saalae*-*P. isabenae*-*P. pyrenaicus*-*P. parvulus* constitute a lineage that evolved during the Middle-Late Eocene in Europe.

Moreover, a new genus and species, the adapoid *Mazateronodon endemicus*, and a new species, the omomyoid *Pseudoloris cuestai*, have also been described from the locality of Mazaterón (Middle Eocene, Duero Basin). They both present traits in their dentition that differ from the representatives of their groups in the Pyrenean basins and the rest of Europe. This reinforces the endemic character of the faunas of the Western Iberian Bioprovince, which was previously observed in other groups of mammals, caused by the isolation of this region from the rest of Europe during the Eocene, as a consequence to the marine transgression that connected the Cantabric and

Mediterranean seas at that time. In addition, *Mazateronodon* represents the richest sample of an Eocene primate from this bioprovince.

From the Sossís fossil site (Late Eocene, Southern Pyrenean basins) a new genus and species has been described, the adapoid *Nievesia sossissensis*, which will help to clarify, together with the rest of the adapoids studied in this thesis, all belonging to the tribe Anchomomyini, the phylogenetic relationships among the anchomomyins and with the rest of adapoids and extant strepsirhines. The results indicate that the new genera *Nievesia* and *Mazateronodon* seem to be more related to each other than to other anchomomyins, and also that the anchomomyins would not be more related to crown strepsirhines than to other adapiforms, and that, on the contrary, there would be a closer phylogenetic relationship between anchomomyins, asiadapines and sivaladapids than to other adapiforms. Nevertheless, these results need to be taken with caution, since more information about still unknown characters is needed.

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INTRODUCCIÓ

Els primats constitueixen un ordre de mamífers de gran diversitat morfològica i adaptativa, amb una distribució geogràfica molt àmplia. El grup comprèn formes tan variades com els lèmurs, els ai-ais, els lorísids, els gàlags, els tarsers, els micos i els simis, amb els humans inclosos en aquesta última categoria.

Els primats actuals es divideixen en dos grans grups, el subordre Strepsirhini (estrepsirins o primats de nas humit) que inclouen els lèmus de Madagascar, els lorisiformes i els ai-ais, i el subordre Haplorhini (haplorins o primats de nas sec) que inclouen els tarsers i els simiformes (veure taula 1).

- Ordre **Primates** Linnaeus, 1758
  - Semiordre **Plesiadapiformes**† Simons i Tattersall, 1972 (in Simons, 1972)
    - Superfamília **Paromomyoidea**† Simpson, 1940
    - Superfamília Plesiadapoidea† Trouessart, 1897
  - Semiordre **Euprimates** Hoffstetter, 1977
    - Subordre **Strepsirhini** Geoffroy Saint-Hilaire, 1812
      - Infraordre **Adapiformes**† Hoffstetter, 1977
        - Superfamília **Adapoidea**† Trouessart, 1879
      - Infraordre Lemuriformes Gregory, 1915
        - Superfamília Lemuroidea Gray, 1821
        - Superfamília Cheirogaleoidea Gray, 1872
        - Superfamília Indrioidea Burnett, 1828
        - Superfamília Daubentonioidea Gray, 1863
      - Infraordre Lorisiformes Gregory, 1915
        - Superfamília Lorisoidea Gray, 1821
    - Subordre **Haplorhini** Pocock, 1918
      - Infraordre **Tarsiiformes** Gregory, 1915
        - Superfamília **Omomyoidea**† Trouessart, 1879
        - Superfamília Tarsioidea Gray, 1825
      - Infraordre **Simiiformes** Hoffstetter, 1974 (=**Anthropoidea** Mivart, 1864)
        - Parvordre Platyrrhini Geoffroy Saint-Hilaire, 1812
          - Superfamília Ceboidea Bonaparte, 1831
        - Parvordre **Catarrhini** Geoffroy Saint-Hilaire, 1812
          - Superfamília Propliopithecoidea† Straus, 1961
          - Superfamília **Pliopithecoidea**† Zapfe, 1960
          - Superfamília **Cercopithecoidea** Gray, 1821
          - Superfamília **Hominoidea** Gray, 1825

Taula 1. Classificació sistemàtica de l'odre Primates fins al rang de superfamília. Es ressalten en negreta els grups amb representants en el registre fòssil de la Península Ibèrica, i amb una daga (†) els tàxons extints.

De totes maneres, si tenim en compte també el registre fòssil, la classificació dels primats esdevé més complicada degut a l'existència del grup dels plesiadapiformes. La seva inclusió dins l'ordre dels primats ha estat controvertida, i diferents autors tenen opinions diverses al respecte, tot i que en aquest treball s'ha seguit la visió d'incloure'ls com un grup parafilètic de primats basals.

Si es considera per tant que els tàxons inclosos en el semiordre Plesiadapiformes són primats basals, incloem en aquest cas els primats estrepsirins i haplorins, fòssils i actuals, dins el semiordre Euprimates (euprimats o primats *sensu stricto*), també anomentats primats corona o primats d'aspecte modern, que constitueixen un grup monofilètic (Szalay i Delson, 1979; Kay et al., 1997; Fleagle, 1999; Bloch et al., 2007).

Tradicionalment també s'ha subdividit l'ordre dels primats en els prosimis i els simis. Com que el terme prosimis és un agrupament dels primats que queden fora del clade dels simis o Anthropoidea, i que per tant designa un grup parafilètic (estrepsirins i tarsers), considerem el seu ús només de manera informal (seguint Godinot, 2010), tot i que alguns autors l'han fet servir de manera formal com a subordre Prosimii.

Els euprimats actuals es distingeixen d'altres ordres de mamífers per certes sinapomorfies o característiques anatòmiques derivades compartides (Martin, 1990; Cartmill, 1992; Rasmussen, 2002):

- Mans i peus prènsils, amb polzes i hàl·lux (primer dir del peu) normalment oposables.
- Ungles enlloc d'urpes en la majoria de dits, tot i que hi ha excepcions com els tamarins i els titís.
- Convergència orbital amb visió estereoscòpica: els ulls es situen a la part frontal del crani, de manera que es perd camp de visió però es guanya visió frontal degut a que els camps visuals d'ambdós ulls es solapen i permeten veure-hi de manera tridimensional.
- Bul·la auditiva petrosa: covertura esquelètica que protegeix part de l'oïda interna, formada per os petrós, a diferència d'altres grups de mamífers en els que la bul·la auditiva es forma a partir d'un altre centre d'ossificació.

- Barra postorbital: òrbites oculars envoltades d'os totalment o parcial, que protegeixen l'ull més efectivament. El tancament és més complet en haplorins que en estrepsirins.
- Alt grau d'encefalització: cervell gran en comparació amb la mida corporal.

A banda d'aquestes característiques que trobem comunes a tots els primats, n'hi ha d'altres que fan referència a característiques que no es poden reconèixer en el registre fòssil, com ara el fet de tenir normalment una sola cria per part, un cicle de vida lent, i altres trets referents als teixits tous.

A continuació es detallen certs aspectes sobre l'origen dels primats i els principals grups que apareixen durant els primers estadis de l'evolució del grup (Pleasiadapiformes, Adapoidea i Omomyoidea), que són els estudiats en aquesta tesi doctoral.

1.1. L'origen dels primats

Els primats, que apareixen en el registre fòssil per primera vegada durant el Paleogen, són un ordre modern, si tenim en compte l'existència d'altres grups de mamífers durant el Mesozoic. A finals de l'era mesozoica, que va dels 225 als 65 milions d'anys, es van produir importants canvis climàtics que van causar l'extinció dels dinosaures no avians i tanmateix van suposar unes condicions favorables per als mamífers insectívors, ja que l'absència de grans depredadors va deixar nínxols ecològics buits que ells van poder ocupar i els va permetre diversificar-se. Molts d'aquests grups de mamífers es troben en jaciments mesozoics i van sobreviure fins al Paleocè, la primera època del Cenozoic després del límit Cretaci-Terciari o límit K/T (fa 65 milions d'anys).

Molts d'aquests mamífers primitius són formes arcaiques de les que no es coneixen les seves relacions filogenètiques amb els grups actuals. Aquest és el cas també dels possibles ancestres dels primats.

La major part dels ordres moderns de mamífers es troben representats per primera vegada al registre fòssil d'Àsia, Europa i Nord Amèrica a principis del Paleogen (McKenna, 1983; Gingerich, 1989; Krause i Maas, 1990; Beard, 1998; Hooker, 1998;

Beard i Dawson, 1999). Les restes fòssils de primats *sensu lato*, és a dir, incloent els plesiadapiformes, es troben ja durant el Paleocè (Bloch et al., 2007). La primera aparició dels euprimats (primats *sensu stricto*) pel que fa al registre fòssil és de fa uns 56 milions d'anys durant l'Eocè Inferior (Rasmussen, 2002). Tot i així, diferents estudis amb dades moleculars han estimat que el moment de la seva aparició es podria remuntar al període Cretaci (Hedges et al., 1996; Arnason et al., 1998; Eizirik et al., 2001; Tavaré et al., 2002). Els darrers estudis, que combinen dades genètiques amb el registre fòssil, sugereixen que els euprimats van aparèixer per primer cop prop del límit Cretaci/Terciari, i possiblement durant el Paleocè (Steiper i Seiffert, 2012).

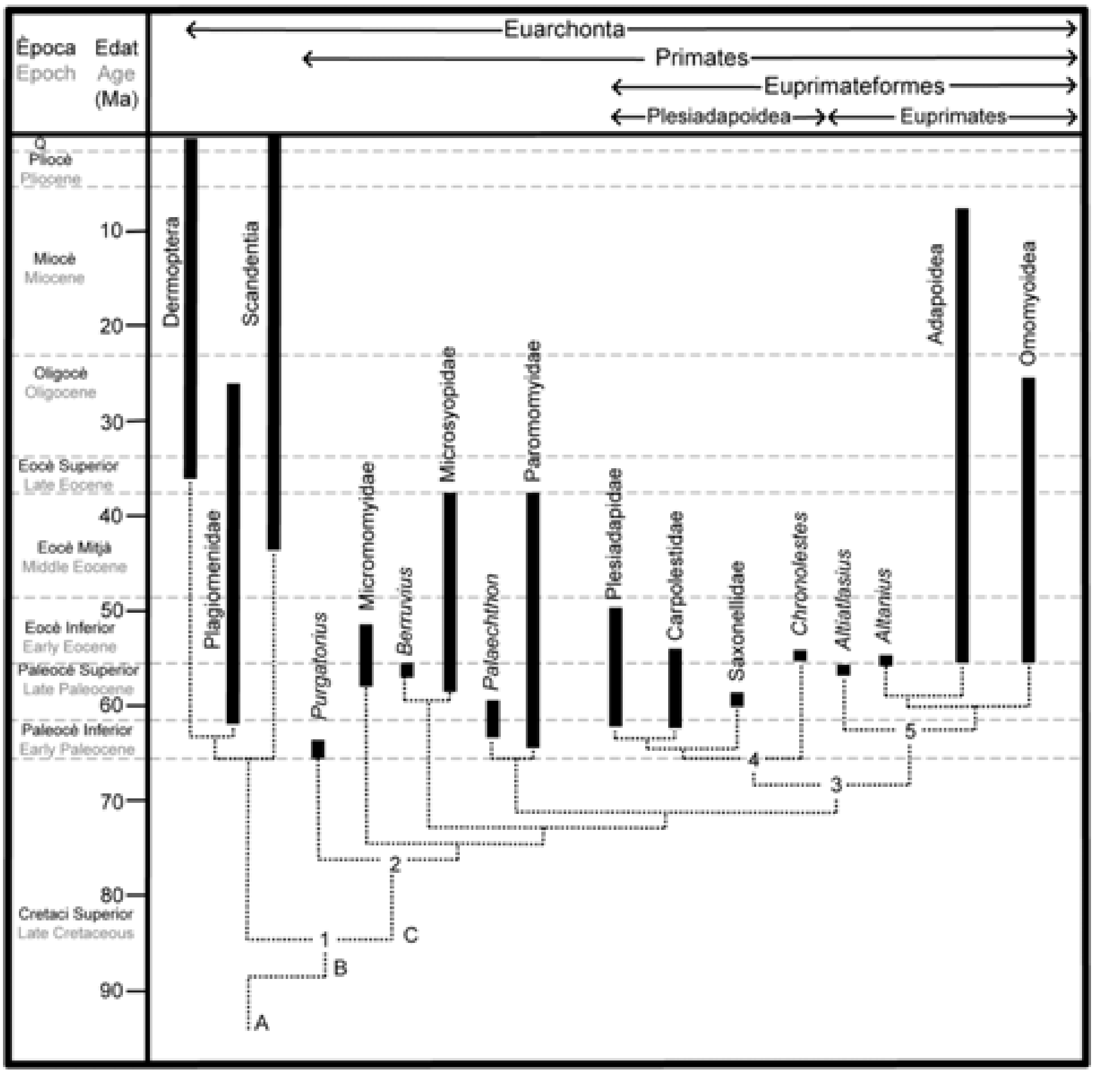
El context geogràfic i filogenètic de l'origen dels primats és una font considerable d'interès i el centre de nombrosos debats. Pel que fa al seu lloc d'origen, la diferència d'opinions entre diferents autors ve originada pel fet que els primats apareixen de forma aproximadament simultània en el registre fòssil tant a Europa Occidental com a Amèrica del Nord, com molts altres grups faunístics del moment (Fleagle, 1999; Gingerich, 2006; Silcox, 2008). Degut a la seva aparició brusca, alguns autors creuen que el seu lloc d'origen podria haver estat un altre on la seva presència no s'hagi detectat degut a un mostreig insuficient, com ara Asia (Beard, 1998; Bowen et al., 2002) o Àfrica (Gingerich, 1990), tot i que altres descarten el continent asiàtic i defensen fermament que Nord Amèrica, Europa i Àfrica tenen més potencial per afegir noves dades sobre l'origen del grup (Silcox, 2008).

Pel que fa al seu origen filogenètic, també és controvertit. D'entre els mamífers actuals, els primats (Primates), les tupaies (Scandentia), els lèmurs voladors (Dermoptera) i els quiròpters (Chiroptera) estan més relacionats entre ells que no pas amb la resta de mamífers (Wible i Covert, 1987; MacPhee, 1993). Aquests ordres s'agrupen, juntament amb el grup dels plesiadapiformes, dins el superordre Archonta o dins els Euarchonta, si s'exclouen els rat-penats (Adkins i Honeycutt, 1991; Waddell et al., 1999; Liu et al., 2001; Murphy et al., 2001a, b; Springer et al., 2003, 2004). Sargis (2002) sugereix que l'ancestre comú dels Euarchonta seria una forma arbòria de mida petita semblant a l'actual membre dels Scandentia *Ptilocercus.* Els Euarchonta han estat recentment agrupats en diferents anàlisis moleculars amb els Glires (rosegadors i lagomorfs; p. ex. Waddell et al., 1999; Murphy et al., 2001a, b; Springer et al., 2003, 2004) en un clade anomenat Euarchontoglires per Murphy et al. (2001b).

Dins els Euarchonta, diferents relacions interordinals han estat proposades. Els primers plesiadapiformes que es van descriure es van incloure dins els primats (Matthew i Granger, 1921; Gidley, 1923), principalment basant-se en similituds de les restes dentàries. Més tard, Martin (1968) i Cartmill (1972) van dubtar que fossin primats, tot i que només van tenir en compte les característiques de membres actuals del grup. Wible i Covert (1987) van argumentar que els Scandentia eren un taxó germà més provable dels euprimats que no pas els plesiadapiformes. D'altra banda, restes cranials i postcranials de plesiadapiformes trobades més tard i anàlisis cladístics del moment es van interpretar com a proves de la relació més estreta que hi havia entre Plesiadapiformes i Dermoptera (Beard, 1990, 1993a, b; Kay et al., 1990, 1992), tot i que aquestes conclusions han estat posades en dubte per un gran nombre d'autors (Krause, 1991; Szalay i Lucas, 1993, 1996; Wible, 1993; Wible i Martin, 1993; Van Valen, 1994; Runestad i Ruff, 1995; Stafford i Thorington, 1998; Hamrick et al., 1999; Stafford i Szalay, 2000; Bloch i Silcox, 2001; Bloch i Boyer, 2002, 2003; Sargis, 2002; Silcox, 2003, 2007; Bloch et al., 2007, entre altres). A banda d'això, estudis moleculars recents sugereixen un clade que inclouria Dermoptera i Scandentia (Liu et al., 2001; Murphy et al., 2001a, b; Springer et al., 2003, 2004).

Diferents anàlisis cladístics de plesiadapiformes i altres Archonta donen suport a la idea de que Euprimates i Plesiadapiformes són grups germans (Silcox, 2001; Bloch i Boyer, 2002, 2003; Bloch et al., 2007), tot i que es considera els plesiadapiformes com un grup parafilètic. Degut a que els anàlisis filogenètics i les troballes fòssils més recents sugereixen un retorn a punts de vista anteriors com els de Szalay i Delson (1979) i Szalay et al. (1987) de que l'ordre Primates s'hauria de redefinir de manera que inclogués els plesiadapiformes, en aquest treball s'ha seguit aquest punt de vista i s'ha considerat les restes de plesiadapiformes estudiades en aquesta tesi com a primats (veure figura 1).

Figura 1 (pàgina 14). Filogènia dels Euarchonta. 1=Euarchonta; 2=Primates, 3=Euprimateformes; 4=Plesiadapoidea; 5=Euprimates; A=Estimació molecular de l'origen dels Euarchontoglires; B=Estimació molecular de l'origen dels Euarchonta; C=Estimació molecular de l'origen dels primats. Q=Quaternari/Quaternary. Modificada de Bloch et al. (2007).



1.2. Els plesiadapiformes

Les restes fòssils pertanyents a aquest grup s'han trobat a Nord Amèrica, Europa, Asia, i possiblement Àfrica (Silcox, 2001; Tabuce et al., 2004; Bloch et al., 2007), en jaciments del Paleocè a l'Eocè. Els plesiadapiformes són un dels grups de mamífers paleògens més diversos i ben coneguts, amb més de 120 espècies classificades en 11 famílies: Purgatoriidae, Micromomyidae, Microsyopidae, Palaechthonidae, Paromomyidae, Plesiadapidae, Carpolestidae, Saxonellidae, Picrodontidae, Picromomyidae i Toliapinidae (Silcox, 2001; Silcox et al., 2005). Tot i que els tàxons fòssils atribuïts a plesiadapiformes es considera que estan estretament relacionats, molts autors els consideren un grup no monofilètic (Gingerich, 1976; Szalay et al., 1987;

Beard, 1993a; Silcox, 2001; Bloch i Boyer, 2002; Bloch et al., 2007; Boyer i Bloch, 2008; Silcox et al., 2009; entre altres).

Tots els plesiadapiformes tenen generalment en comú una sèrie de característiques que inclouen unes incisives centrals superiors i inferiors grosses i procumbents, unes molars de corona baixa amb talònids amples i un hipoconúlid gran a les terceres molars inferiors. Pel que fa a les restes postcranials, els membres d'aquest grup presenten característiques pròpies d'animals amb un mode de vida arbori però no especialitzats en el salt (Szalay et al., 1975, 1987; Szalay i Drawhorn, 1980; Bloch i Boyer, 2002, 2003, 2007). Tradicionalment s'han diferenciat dels euprimats per algunes característiques com ara un musell més allargat i estret, un cervell més petit, l'absència de barra postorbital, òrbites oculars en posició lateral, bul·la auditiva no formada per os petrós, absència d'hàl·lux i polzes oposables, presència d'urpes enlloc d'ungles i incisives grosses seguides d'un diastema (Fleagle, 1999). De totes maneres, segons estudis més recents, alguns membres d'aquest grup no presentarien totes aquestes característiques, de forma que els criteris per diferenciar-los dels euprimats no estarien encara clars del tot (Bloch i Silcox, 2001, 2006; Bloch i Boyer, 2002, 2003; Silcox, 2003). Per opinions contràries, veure Kirk et al. (2003) i Godinot (2007).

El membre més antic recuperat atribuït als plesiadapiformes és *Purgatorius ceratops* (Família Purgatoriidae), trobat a Amèrica del Nord, en jaciments que daten del Cretaci Superior (Van Valen i Sloan, 1965; Van Valen, 1994) o del Paleocè Inferior segons Lofgren (1995) i Clemens (2004).

A Europa, la primera aparició del grup data del Paleocè Inferior, amb el gènere *Berruvius* i altres membres de les famílies Saxonellidae i Plesiadapidae a França i Alemanya (Silcox, 2001; Bloch et al., 2007). En canvi, pel que fa a la Península Ibèrica, el primer registre de plesiadapiformes no apareix fins l'Eocè Inferior, encara que s'ha de tenir en compte que l'absència del registre d'aquest grup durant el Paleocè podria estar relacionada amb l'escassedat de jaciments continentals amb restes de vertebrats d'aquesta època. El registre de plesiadapiformes a la Península queda restringit al gènere *Arcius* (Família Paromomyidae) dels jaciments de Silveirinha (Conca de Mondego, Portugal; Estravís, 2000) i de Masia de l'Hereuet (Conca Sudpirinenca Central, Lleida). El material d'aquest últim jaciment representa un dels treballs ja publicats que s'inclouen en aquesta tesi doctoral (Capítol 5).

1.3. Els adapoïdeus i els omomioïdeus

Durant l'Eocè trobem ja representants de molts ordres moderns de mamífers, incloent membres indubtables de l'ordre Primates. Tot i que els dos grups més abundants d'euprimats (o primats *sensu stricto*) presents a l'Eocè són les dues superfamílies Adapoidea i Omomyoidea, possibles representants de Lorisoidea s'han trobat a l'Eocè d'Àfrica (Seiffert et al., 2003, 2005a; Tabuce et al., 2009), i durant l'Eocè Superior, els antropoïdeus més antics (Parapithecoidea) es troben representats pel gènere *Biretia* també al continent africà (De Bonis et al., 1988; Jaeger et al., 2010; Seiffert et al., 2005b). Altres gèneres de primats trobats a l'Eocè d'Àsia, per exemple *Eosimias*, *Amphipithecus* i *Pondaungia,* han estat considerats antropoïdeus per alguns autors, encara que aquesta atribució és controvertida (Beard et al., 1994, 1996, 2009; Kay i Williams, 1994; Kay et al., 1997; Ross et al., 1998; Gunnell et al., 2002; Takai et al., 2003, 2005; Takai i Shigehara, 2004; Chaimanee et al., 2012).

L'aparició dels adapoïdeus i els omomioïdeus durant l'Eocè ha estat documentada des de principis del segle XX (Stehlin, 1912; Gregory, 1920). Els adapoïdeus són estrepsirins fòssils. En canvi, els omomioïdeus s'inclouen dins els Tarsiiformes, i per tant són considerats primats haplorins. Tot i que els adapoïdeus i els omomioïdeus més primitius tenen fórmules dentàries semblants (2.1.4.3/2.1.4.3) i molars també similars, alguns trets generals els diferencien, com ara que els adapoïdeus solen tenir uns ulls més petits, un musell més llarg, unes incisives més petites i unes canines més grans, així com també unes premolars menys comprimides mesiodistalment (Fleagle, 1999). A més a més, pel fet de pertànyer a dos grups ben diferenciats de primats, estrepsirins i haplorins respectivament, existeixen altres diferències tant esquelètiques com dels teixits tous que els diferencien molt bé i que poden ser observades en espècimens excepcionalment ben conservats (veure Williams et al., 2010; Lebrun et al., 2012). Els omomioïdeus són també generalment més petits, normalment sense superar els 500 g de massa corporal estimada, tot i que hi ha adapoïdeus també molt petits, com el gènere *Anchomomys*, la massa corporal del qual s'estima en 100-150 g (Fleagle, 1999; Moyà-Solà et al., 2011). Les restes postcranials associades a omomioïdeus sugereixen que en general eren quadrúpedes arboris actius amb bones habilitats pel salt com els lèmurs nans (Cheirogaleidae) i gàlags (Galagidae) actuals (Gunnell i Rose, 2002); en canvi els adapoïdeus eren quadrúpedes arboris més lents capaços de trepar però sense estar tan adaptats per al salt (Gebo, 2002).

Tot i que hi ha diverses classificacions depenent de diferents autors, els adapoïdeus es solen separar en 3 famílies (Adapidae, Notharctidae i Sivaladapidae), i els omomioïdeus en una sola família (Omomyidae), dividida en 3 subfamílies (Omomyinae, Anaptomorphinae i Microchoerinae; veure taula 2).

- Infraordre Adapiformes Hoffstetter, 1977
  - Superfamília Adapoidea Trouessart, 1879
    - Família Notharctidae Trouessart, 1879
      - Subfamília Notharctinae Trouessart, 1879
        - *Cantius* Simons, 1962
      - Subfamília Cercamoniinae Gingerich, 1975
        - *Donrussellia* Szalay, 1976
        - *Agerinia* Crusafont Pairó, 1973
        - *Anchomomys* Stehlin, 1916
        - ***Mazateronodon*** Marigó, Minwer-Barakat i Moyà-Solà, 2010
        - ***Nievesia*** Marigó, Minwer-Barakat i Moyà-Solà, en premsa
      - Subfamília Asiadapinae Rose, Rana, Sahni, Kumar, Missiaen, Singh i Smith, 2009
    - Família Adapidae Trouessart, 1879
      - Subfamília Adapinae Trouessart, 1879
        - *Adapis* Cuvier, 1821
        - *Leptadapis* Gervais, 1876
        - *Microadapis* Szalay, 1974
    - Família Sivaladapidae Thomas i Verma, 1979
      - Subfamília Sivaladapinae Thomas i Verma, 1979
      - Subfamília Hoanghoniinae Gingerich, Holroyd i Ciochon, 1994
- Infraordre Tarsiiformes Gregory, 1915
  - Superfamília Omomyoidea Trouessart, 1879
    - Família Omomyidae Trouessart, 1879
      - Subfamília Microchoerinae Lydekker, 1887
        - *Microchoerus* Wood, 1844
        - *Necrolemur* Filhol, 1873
        - *Pseudoloris* Stehlin, 1916
      - Subfamília Anaptomorphinae Cope, 1883
      - Subfamília Omomyinae Trouessart, 1879
  - Superfamília Tarsioidea Gray, 1825
    - Família Tarsiidae Gray, 1825

Taula 2. Classificació sistemàtica dels infraordres Adapiformes i Tarsiiformes fins al rang de subfamília, incloent només els gèneres que es troben en el registre fòssil de la Península Ibèrica. Es ressalten en negreta els nous gèneres descrits en treballs inclosos en aquesta tesi doctoral.

Els representants més antics atribuïts a adapoïdeus són *Cantius*, un gènere recuperat a Europa i Nord Amèrica, i *Donrussellia* trobat només a Europa (Godinot, 1978, 1992; Godinot et al., 1987; Gingerich et al., 1991), i pel que fa als omomioïdeus els gèneres *Teilhardina*, d'Amèrica del Nord, Europa i Àsia, i *Steinius* d'Amèrica del Nord (Simpson, 1940; Bown, 1976; Rose i Bown, 1991; Rose, 1995; Ni et al., 2004).

Pel que fa al registre fòssil dels euprimats més antics al continent africà, aquest és molt més escàs i algunes troballes no queda clar si són adapoïdeus, omomioïdeus, o fins i tot si es considerarien o no primats. El gènere *Altiatlasius* del Paleocè Superior del Marroc, descrit originalment per Sigé et al. (1990) com un omomioïdeu, és possiblement l'euprimat més antic conegut (Godinot, 1994; Seiffert et al., 2010), tot i que la seva posició sistemàtica ha estat el centre de molts debats, ja que es va arribar a sugerir que podia estar relacionat amb els plesiadapiformes (Gingerich, 1990; Hooker et al., 1999).

A la Península Ibèrica, el registre d'euprimats presenta força diversitat durant l'Eocè, amb ambdós grups, adapoïdeus i omomioïdeus, representats. Els adapoïdeus els trobem per primera vegada alhora que els plesiadapiformes, durant el Neustrià (veure figura 2 i annex I), amb el gènere *Donrussellia* a la Conca de Mondego (Portugal). Més endavant, durant el Grauvià, trobem els gèneres *Cantius* i *Agerinia* en diferents jaciments de les conques pirinenques i de l'Ebre. Concretament, el gènere *Agerinia* el trobem representat a la Península fins el Geiseltalià.

Durant el Robiacià trobem la major diversitat d'adapoïdeus a la Peínsula Ibèrica, tant a les conques pirinenques com a la Conca el Duero, on hi trobem abundants restes dels gèneres *Anchomomys, Mazateronodon, Microadapis, Adapis* i *Leptadapis,* els dos darrers també identificats en nivells de l'Headonià. Pel que fa al registre d'omomioïdeus a la Península, el més antic que es troba és el gènere *Pseudoloris* al jaciment de Casa Ramón (Geiseltalià). Aquest gènere també es troba ben representat, juntament amb *Necrolemur,* en nivells del Robiacià i Headonià, mentre que *Microchoerus* es troba també en diferents jaciments de l'Headonià. Dos d'aquests gèneres d'omomioïdeus trobats a la Península Ibèrica, *Pseudoloris* i *Microchoerus,* sobrepassen el límit Eocè-Oligocè, com demostren algunes cites puntuals en nivells de l'Oligocè Inferior. Aquesta abundàcia i diversitat tant d'adapoïdeus com d'omomioïdeus a la Península durant l'Eocè, concorda amb el màxim de diversitat que els euprimats van assolir durant l'Eocè a tot l'hemisferi nord (Fleagle, 1999).

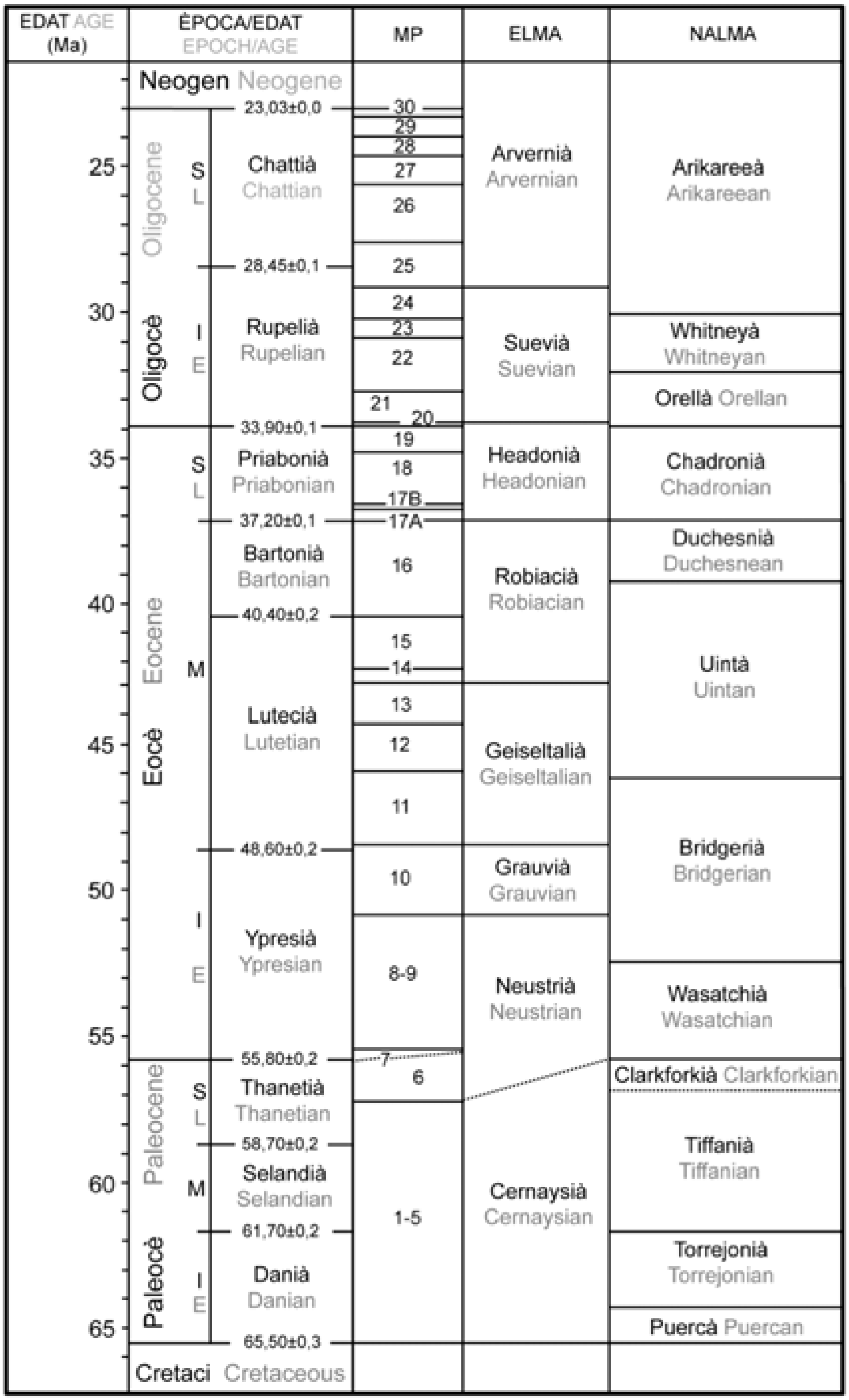


Figura 2. Taula que inclou l'edat en milions d'anys de cada època o edat, i les equivalències amb les subdivisions continentals en MP ("Mammalian Paleogene reference levels", nivells de referència de mamífers del Paleogen), ELMA ("European Land Mammal Ages", edats de mamífers continentals europees) i NALMA ("North American Land Mammal Ages", edats de mamífers continentals nord-americanes). Modificada de Luterbacher et al., 2004.

1.4. Clima i paleobiogeografia durant el Paleogen

El Paleogen (65,5-23 milions d’anys) comprèn tres èpoques ben diferenciades: el Paleocè (65,5-55,8 milions d’anys), l’Eocè (55,8-33,9 milions d’anys) i l’Oligocè (33,9-23 milions d’anys).

Durant el Paleocè, els ecosistemes terrestres eren dominats per petits mamífers de grups avui desapareguts, com els condilartres i els multituberculats, que van experimentar una important diversificació després de l’extinció en massa del límit Cretaci-Terciari. Entre aquests mamífers, trobem ja les primeres restes de primats *sensu lato*, pertanyents al grup dels plesiadapiformes, que apareixen en jaciments d’Europa, Nord Amèrica i Àsia (Beard i Wang, 1995).

L’Eocè és una època molt interessant degut a l’aparició de la majoria dels ordres de mamífers moderns com ara els quiròpters, els artiodàctils i els perissodàctils. És també en esta època quan apareixen les primeres restes atribuïdes de forma indubtable a euprimats. L’Eocè representa l’època més càlida del Terciari. El principi de l’Eocè va venir marcat pel màxim tèrmic del Paleocè-Eocè o “Paleocene/Eocene Thermal Maximum”, seguit d’un període d’escalfament global conegut com l’òptim climàtic de l’Eocè Inferior o “Early Eocene Climatic Optimum” (Zachos et al., 2001).

Les altes temperatures i unes estacions gens marcades van afavorir el desenvolupament de boscos tropicals en latituds de fins a 50º nord (Collison i Hooker, 2003). Aquests canvis ecològics van propiciar la diversificació dels mamífers del moment com ara rosegadors, quiròpters i sobretot primats. Els mamífers arboris més exitosos de l’Eocè van ser els euprimats, representats per dues superfamílies, els adapoïdeus i els omomioïdeus, mentre que els plesiadapiformes van patir un declivi durant aquesta època (Fleagle, 1999; Rose, 2006).

Al principi de l’Eocè, moltes àrees de l’actual Euràsia eren sota el mar, degut a la pujada del nivell d’aquest per les altes temperatures. Europa consistia en diferents illes emergides que formaven una espècie d’arxipèlag (veure figura 3). L’illa central europea estava formada per parts de les actuals Anglaterra, França i Alemanya, tot i que estava localitzada força més al sud, aproximadament a la latitud actual del sud d’Itàlia. Importants jaciments de l’Eocè Inferior com ara Dormaal (Bèlgica), Avenay (França) i Bembridge beds (Anglaterra) es situen en aquesta zona. A l’est, el Mediterrani s’extenia formant un mar ampli, ja que Turquia, Iraq i Iran eren encara terres submergides. A l'est del Urals, l'estret de Turgai encara connectava les aigües calentes del Mar de Tethys amb el Mar Polar (Smith et al., 1994; Scotese, 2001; Beard, 2008), tot i que en alguns moments a partir de l'Eocè Inferior s'han detectat també intercanvis faunístics entre Europa i Àsia a través de l'estret de Turgai (Savage i Russell, 1983; Hooker i Dashzeveg, 2003).

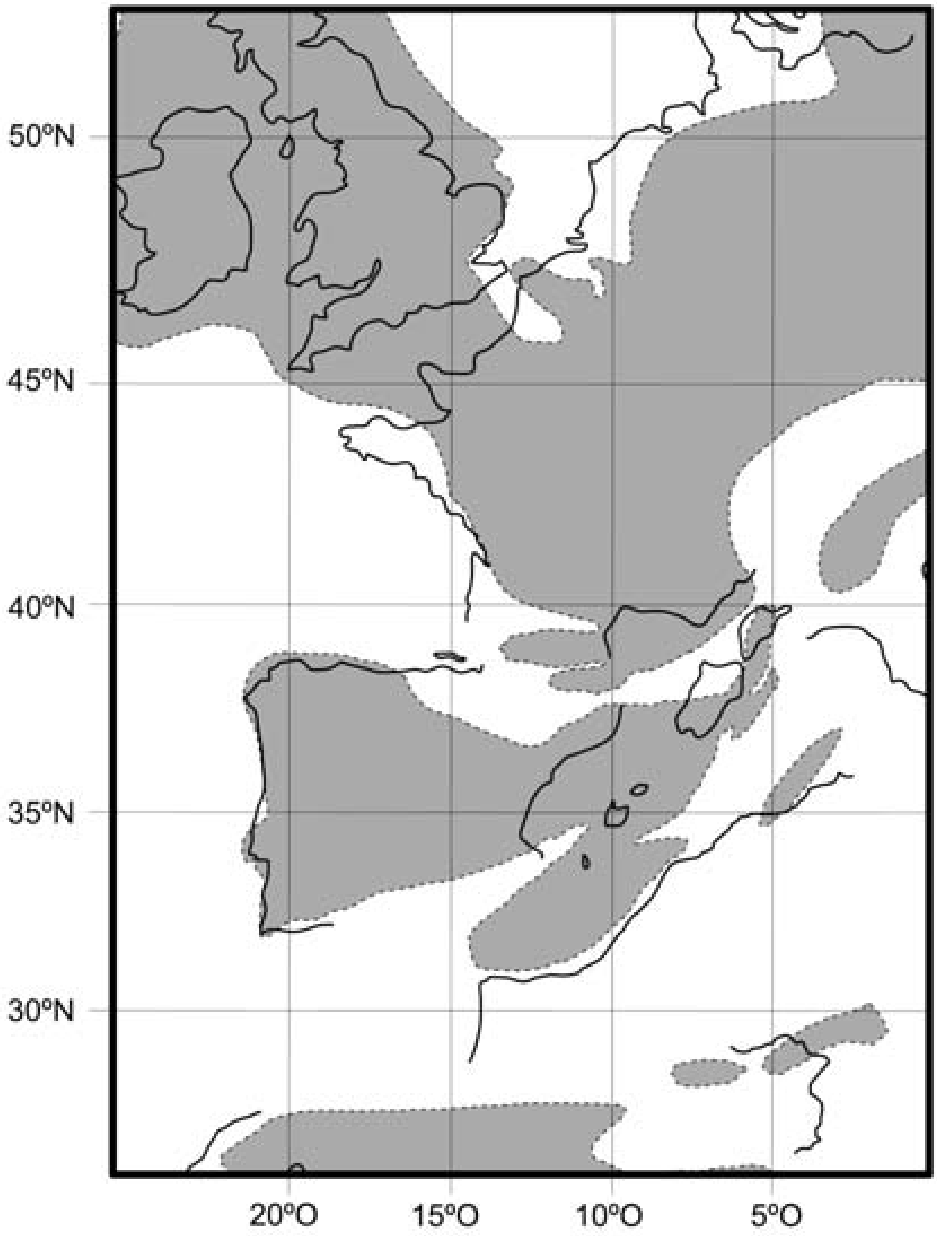


Figura 3. Paleogeografia de l'oest d'Europa durant l'Eocè Inferior. Les zones emergides es marquen en gris, i les zones submergides en blanc. S'indiquen amb línia contínua alguns trams de les línies de costa actuals. Modificada de Marandat et al. (2012).

Igualment, entre Nord Amèrica i Àsia existien connexions de terra a la zona de l’actual mar de Bering, i també Nord Amèrica i el nord d’Europa eren zones intermitentment connectades a través de Groenlàndia i Escòcia durant el Paleocè i l’Eocè Inferior (Beard i Dawson, 1999; Bowen et al., 2002; Beard, 2008), permetent intercanvis faunístics com en el cas del primat omomioïdeu *Teilhardina* (Ni et al., 2005; Smith et al., 2006; Beard, 2008). Pel que fa a l’actual Península Ibérica, una placa que incloía Portugal i Espanya central (Placa Ibèrica) formava una altra gran illa d’aquest arxipèlag, localitzada més al sud que l’illa central europea.

Durant l’Eocè Mitjà i Superior, les faunes de mamífers de les conques ibèriques centrals i occidentals eren clarament diferents de les de les conques pirinenques, sent aquestes últimes semblants a les de la resta d’Europa (França i Suïssa). Aquesta diferenciació faunística, observada principalment en perissodàctils, artiodàctils i rosegadors, va permetre la definició de la Bioprovíncia Occidental Ibèrica (Western Iberian Bioprovince; Cuesta Ruiz-Colmenares, 1991), que incloïa diferents conques de les zones centrals i occidentals de la Península Ibèrica (Conques del Duero, d’Almazán, d’Oviedo i de Miranda-Trebiño) caracteritzades per faunes de mamífers de l’Eocè diferents de les dels Pirineus i la resta d’Europa. Altres estudis d’aquests grups de mamífers han donat suport a aquestes observacions (Casanovas Cladellas, 1975; Casanovas-Cladellas i Santafé-Llopis, 1987, 1989, 1991; Casanovas i Moyà-Solà, 1992; Peláez-Campomanes, 1993; Casanovas Cladellas et al., 1998; Cuesta Ruiz-Colmenares, 1999, 2003; Badiola, 2004; Cuesta Ruiz-Colmenares et al., 2006; Badiola et al., 2009).

El límit Eocè-Oligocè va venir marcat per una renovació faunística que va afectar dramàticament les associacions de vertebrats continentals i que va suposar l’extinció d’un gran número de mamífers eocens. El paleontòleg suís Stehlin (1910) va batejar aquesta renovació en les faunes de mamífers com a “Grande Coupure”. Aquest esdeveniment estava relacionat amb el deteriorament climàtic que va tenir lloc durant la transició Eocè-Oligocè, que va provocar grans pèrdues en la diversitat de les faunes tant marines com continentals (Prothero, 1994; Hooker et al., 2004).

El començament de la glaciació antàrtica i el creixement de capes de gel van provocar una important baixada del nivell del mar. Molts mars soms epicontinentals van esdevenir àrees emergides; van iniciar-se la desaparició de l’arxipèlag europeu i la continentalització d’Europa prop del límit Eocè-Oligocè (Rögl, 1999).

La “Grande Coupure” també va afectar els primats i el número d’espècies tant d’adapoïdeus com d’omomioïdeus, grups que havien estat molt exitosos durant l’Eocè, va disminuir dràsticament durant l’Oligocè Inferior. Els adapoïdeus van sobreviure fins el Miocè, tot i que el seu registre és escàs i geogràficament restringit al sud-est asiàtic (Gebo, 2002), mentre que a Europa no s’hi han trobat restes després del límit Eocè-Oligocè. Pel que fa als omomioïdeus, trobem algunes restes a l’Oligocè i al Miocè Inferior de Nord Amèrica (Macdonald, 1963; Albright, 2005) i d’Egipte (Simons et al., 1986). A Europa, però, després de la “Grande Coupure”, el registre d’omomioïdeus queda restringit a dues troballes a l’Oligocè Inferior de la Península Ibèrica. El gènere *Pseudoloris* va sobreviure les extincions del límit Eocè-Oligocè, com demostren les restes de *Pseudoloris godinoti* de les localitats del Suevià de Fonollosa i Santpedor a la Conca de l’Ebre (Köhler i Moyà-Solà, 1999). Igualment, una única molar inferior de l’Oligocè Inferior d’Aguatón evidencia la persistència del gènere *Microchoerus* a la Conca de Calatayud-Teruel (Peláez-Campomanes, 2000). Per tant, almenys dos dels tres gèneres de microchoerins que habitaven la Península Ibèrica durant l’Eocè (*Pseudoloris* i *Microchoerus*) van persistir fins l’Oligocè Inferior, representant l’únic registre d’aquest grup a Europa. Això podria estar relacionat amb la posició més meridional que ocupa la Península Ibèrica respecte altres àrees europees, i que hauria afavorit el manteniment de temperatures més altes que haurien permès la persistència d’àrees de boscos tropicals i subtropicals i la supervivència d’aquests primats fins l’Oligocè Inferior.

En aquest context, per tant, la recuperació i l’estudi de noves restes fòssils d’aquests primats eocens és fonamental per comprendre l’origen i l’evolució del grup, especialment durant les seves primeres etapes, i la seva distribució paleobiogeogràfica.

2

ESTRUCTURA DE LA TESI, ANTECEDENTS I OBJECTIUS

2.1. Estructura de la tesi

En aquesta tesi s'aborda l'estudi de noves restes de primats (plesiadapiformes, adapoïdeus i omomioïdeus) de diferents jaciments de la Península Ibèrica: Masia de l'Hereuet (Eocè Inferior), Sant Jaume de Frontanyà i Mazaterón (Eocè Mitjà), i Sossís (Eocè Superior).

La tesi s'estructura com a compendi de publicacions, de manera que, a part dels capítols introductoris (Capítols 1-4), dels resultats i discussió generals (Capítol 11) i de les conclusions finals (Capítol 12), cadascun dels altres capítols que formen part de la tesi representa un treball publicat o acceptat per publicació en una revista internacional inclosa dins el Science Citation Index (SCI), amb descripcions de nou material dentari, comparacions, i en alguns casos ereccions de nous gèneres i/o noves espècies i anàlisis filogenètics.

Els articles inclosos com a capítols en aquest tesi doctoral són els següents:

- Marigó, J., Minwer-Barakat, R., Moyà-Solà, S., López-Torres, S., 2012. First record of Plesiadapiformes (Primates, Mammalia) from Spain. Journal of Human Evolution 62, 429-433 (Capítol 5).
- Marigó, J., Minwer-Barakat, R., Moyà-Solà, S., 2011. New *Anchomomys* (Adapoidea, Primates) from the Robiacian (Middle Eocene) of northeastern Spain. Taxonomic and evolutionary implications. Journal of Human Evolution 60, 665-672 (Capítol 6).
- Minwer-Barakat, R., Marigó, J., Moyà-Solà, S., 2010. A new species of *Pseudoloris* (Omomyidae, Primates) from the Middle Eocene of Sant Jaume de Frontanyà (Eastern Pyrenees, Spain). American Journal of Physical Anthropology 143, 92-99 (Capítol 7).
- Marigó, J., Minwer-Barakat, R., Moyà-Solà, S., 2010. New Anchomomyini (Adapoidea, Primates) from the Mazaterón Middle Eocene locality (Almazán Basin, Soria, Spain). Journal of Human Evolution 58, 353-361 (Capítol 8).

- Minwer-Barakat, R., Marigó, J., Moyà-Solà, S., 2012. *Pseudoloris cuestai*, a new microchoerine (Primates, Omomyidae) from the Middle Eocene of the Iberian Peninsula. Journal of Vertebrate Paleontology 32 (2), 407-418 (Capítol 9).
- Marigó, J., Minwer-Barakat, R., Moyà-Solà, S., en premsa. *Nievesia sossissensis*, a new anchomomyin (Adapiformes, Primates) from the early Late Eocene of the Southern Pyrenees (Catalonia, Spain). Journal of Human Evolution (Capítol 10).

La tesi compta també amb un annex que representa un article que encara es troba en procés de revisió en una revista inclosa al Science Citation Index:

- Marigó, J., Susanna, I., Minwer-Barakat, R., Madurell-Malapeira, J., Moyà-Solà, S., Casanovas-Vilar, I., Robles, J.M., Alba, D.M., en revisió. The primate fossil record in the Iberian Peninsula. Journal of Iberian Geology (Annex I).

2.2. Antecedents

L'estudi dels primats de l'Eocè de la Península Ibèrica ha rebut una especial atenció durant les darreres dècades, principalment degut a l'excepcional representació de sèries continentals d'aquesta època especialment ben exposades i contínues, amb abundants restes de vertebrats. Els primers treballs sobre primats de l'Eocè de la Península van ser desenvolupats per l'Institut de Paleontologia de Sabadell (actual Institut Català de Paleontologia Miquel Crusafont, ICP) durant la dècada de 1960. Els doctors Crusafont i Rosell van fer la primera caracterització dels nivells continentals de l'àrea d'Àger (Crusafont Pairó i Rosell Sanuy, 1966), on s'havia realitzat la primera troballa de prosimis fòssils a Catalunya al jaciment de Sossís (Crusafont Pairó, 1965). També es van descobrir diferents jaciments que proporcionaren altres restes de prosimis com ara Sant Cugat de Gavadons (Conca de l'Ebre) i Les Saleres (Conca Sudpirinenca Central) (Crusafont Pairó, 1965, Crusafont-Pairó, 1967; Crusafont Pairó i Golpe Posse, 1968; Crusafont-Pairó i Golpe-Posse, 1974). Aquests primers estudis (Crusafont-Pairó, 1967) inclogueren la definició de diferents gèneres i espècies com ara *Agerina roselli, Arisella capellae, Pivetonia isabenae* i *Pseudoloris reguanti*, tot i que algunes es van transferir posteriorment a altres gèneres. A la tesi doctoral de Casanovas Cladellas (1975) també s'hi descriuen restes de primats atribuïdes a *Adapis magnus* i *Necrolemur antiquus* del jaciment de Roc de Santa (Conca Sudpirinenca Central).

Més endavant, durant la dècada de 1990, més estudis duts a terme per investigadors d'aquesta mateixa institució van permetre el descobriment d'altres jaciments eocens que contenien restes de primats, com ara Sant Jaume de Frontanyà (Conca Sudpirinenca Oriental), on tres primats diferents hi van ser identificats i descrits de forma preliminar per Moyà-Solà i Köhler (1993). L'erecció de l'espècie *Pseudoloris godinoti* del jaciment de Fonollosa (Conca de l'Ebre) representa una de les poques espècies de microchoerins que van sobreviure la crisi climàtica del límit Eocè-Oligocè (Köhler i Moyà-Solà, 1999), a part de *Microchoerus* sp. del jaciment d'Aguatón (Teruel; Peláez-Campomanes, 2000). Durant aquesta dècada, més restes de primats de l'Eocè van ser documentades de la Conca del Duero, en jaciments com Santa Clara, Caenes, Mazaterón i Miñana (Moyà-Solà i Köhler, 1992), en col·laboració amb un equip de la Universitat de Salamanca; tot i així, el material d'aquestes localitats era molt escàs.

També en aquesta mateixa dècada es va publicar l'últim treball que sintetitzava les troballes de mamífers de l'Eocè de la Península Ibèrica (Antunes et al., 1997). A l'article, emmarcat en el Congrés BiochroM'97 que va tenir lloc a Montpellier, es donaven els noms de les localitats amb restes de mamífers trobades fins el moment, amb la seva edat i els llistats faunístics corresponents.

D'altra banda, pel que fa a primats en jaciments portuguesos, només se n'ha documentat la cita de l'adapoïdeu *Donrussellia lusitanica* i el plesiadapiforme *Arcius zbyszewskii* al jaciment de l'Eocè Inferior de Silveirinha (Conca de Mondego, Portugal). Aquest jaciment va ser descobert el 1977 pel Professor Rui Pena dos Reis de la Universitat de Coimbra, i la seva fauna va ser estudiada en detall per Estravís (2000).

Finalment, a partir de l'any 2008, una tercera fase en l'estudi de prosimis de l'Eocè de la Península va començar, quan un equip d'investigadors de l'Institut Català de Paleontologia Miquel Crusafont va tornar a recuperar aquesta línia d'investigació, estudiant en detall el material ja dipositat a les col·leccions de l'Institut, recuperat en dècades anteriors, així com també començant a prospectar noves àrees de Catalunya on hi afloren dipòsits paleògens. Aquesta darrera fase d'estudi, representada en bona part pel contingut de la tesi doctoral que aquí es presenta, ha lliurat resultats molt interessants.

A part del material estudiat de la Península que es presenta en aquesta tesi doctoral, hi ha més restes de primats de l'Eocè en fase d'estudi dels jaciments de Sossís (Conca

Sudpirinenca Central), Caenes (Conca del Duero) i Zambrana (Conca de Miranda-Trebiño) dels que s’han publicat ja resultats preliminars (Marigó et al., 2011a, b, 2012a, b; Minwer-Barakat et al., 2011, 2012a, b).

A continuació s’enumeren de forma més detallada alguns treballs dedicats a l’estudi de diferents grups de vertebrats en els quatre jaciments estudiats en aquesta tesi: Masia de l’Hereuet, Sant Jaume de Frontanyà, Mazaterón i Sossís.

2.2.1. Masia de l’Hereuet

Durant les prospeccions realitzades a principis de la dècada de 1990 a la zona d’Àger (La Noguera) es van identificar diferents localitats de l’Eocè Inferior. Concretament, al jaciment de Masia de l’Hereuet (Conca Sudpirinenca Central), s’hi van trobar restes dentàries atribuibles a *Diacodexis* sp. (Casanovas i Moyà-Solà, 1992), *Propachynolophus* sp. i *Lophiodon* sp., a més a més de restes de micromamífers (Checa Soler, 1994). Un llistat faunístic complet dels mamífers d’aquest jaciment, així com l’estudi de les restes fòssils de plesiadapiforme (*Arcius* sp.) recuperades allí es pot trobar al capítol 5 d’aquesta tesi doctoral.

Aquest jaciment té una importància rellevant degut a que conté una de les faunes de vertebrats continentals més antiga de l’Eocè de Catalunya (Badiola et al., 2006, 2009). L’edat del jaciment va ser primerament assignada al Grauvià (MP10) per Antunes et al. (1997), tot i que Badiola et al. (2009) va determinar que era encara més antiga (Neustrià, MP8+9), després de la revisió de la fauna d’artiodàctils, perissodàctils i rosegadors que s’hi havia trobat.

2.2.2. Sant Jaume de Frontanyà

El jaciment de Sant Jaume de Frontanyà (Conca Sudpirinenca Central), a la comarca del Berguedà, va ser mostrejat durant la dècada de 1990 pels doctors Moyà-Solà i Köhler en el marc d’un projecte d’estudi dels 1500 m de potència de la Formació Bellmunt als Pirineus Orientals. En aquesta sèrie de dipòsits continentals s’hi van trobar grans quantitats de restes fòssils de petits mamífers com ara marsupials, insectívors, quiròpters i rosegadors, i també primats (Moyà-Solà i Köhler, 1993).

L'edat dels nivells fossilífers de Sant Jaume de Frontanyà va ser establerta mitjançant l'ús de dues escales bioestratigràfiques diferents, basades en caròfits i mamífers, que en aquest cas presenten un elevat grau de coincidència (Busquets et al., 1992). En concret, la presència en els nivells denominats SJF-3C i 3D d'una forma primitiva del gènere d'artiodàctil *Robiacina*, així com d'una forma del rosegador *Elfomys*, més evolucionada que la descrita al jaciment de Laprade (Sudre et al., 1990) permeten situar aquests nivells entre les unitats MP14 i MP15 (Moyà-Solà i Köhler, 1993).

Les restes de vertebrats trobades en aquesta localitat van ser citades per primera vegada per Moyà-Solà et al. (1991), i posteriorment es van fer diferents estudis més detallats d'alguns tàxons com ara la descripció de perissodàctils (Checa Soler, 1993, 1994) i la definició d'un nou gènere de rosegador (Quer i Agustí, 2010).

Pel que fa als primats, Busquets et al. (1992) citen la presència de *Necrolemur* sp. i *Anchomomys* sp. al nivell SJF-1, *Necrolemur* sp. a SJF-2, i tres formes diferents de primats als nivells més rics, SJF-3C i 3D, identificades en aquell moment com *Adapis* sp., *Pivetonia* o *Pseudoloris* sp. i *Anchomomys* sp. (aquesta última estudiada de forma preliminar per Moyà-Solà i Köhler, 1993). L'estudi detallat de dos d'aquests primats, recentment definits com *Anchomomys frontanyensis* i *Pseudoloris pyrenaicus,* es troba en els capítols 6 i 7 d'aquesta tesi doctoral. Al capítol 7 també s'hi inclou el llistat faunístic actualitzat dels mamífers trobats al nivell 3C.

2.2.3. Mazaterón

El jaciment de Mazaterón (Conca del Duero), a la província de Sòria, era desconegut per la comunitat científica fins que J. Bond (University of Cambridge), mentre feia el treball de camp de la seva tesi doctoral, en va comunicar la troballa a la Universidad Complutense de Madrid. D'altra banda, I. Armenteros i R. Guisado també van informar de la troballa a E. Jiménez de la Universidad de Salamanca. L'equip de Madrid es va limitar a agafar mostres de micromamífers, mentre que l'equip de Salamanca va dedicar-se a extreure les restes de macrovertebrats (Cuesta Ruiz-Colmenares i Jiménez Fuentes, 1994).

S'hi van fer mostrejos durant els anys 1987 i 1988, i més tard durant els anys 1989 i 1990, s'hi va excavar amb el patrocini de la Junta de Castilla y León, i es van començar a publicar els primers resultats (Cuesta Ruiz-Colmenares, 1988; Jiménez Fuentes et al., 1989; Peláez-Campomanes et al., 1989).

Els primers llistats faunístics de vertebrats fòssils els van recopilar Cuesta Ruiz-Colmenares (1991) i Gil Tudanca (1992). Cuesta Ruiz-Colmenares (1991) també indicava la presència al jaciment d'abundants gastròpodes d'aigua dolça, així com també pol·len i espores. D'entre els vertebrats, la major part de restes trobades al jaciment eren de perissodàctils (Cuesta Ruiz-Colmenares, 1988). D'altra banda, al jaciment també s'hi van trobar peixos, tortugues, cocodrils i llangardaixos (Jiménez Fuentes et al., 1989; Cuesta Ruiz-Colmenares i Jiménez Fuentes, 1994). La presència de diferents formes de primats va ser indicada per Moyà-Solà i Köhler (1992), encara que les restes no es van estudiar de forma exhaustiva fins l'inici d'aquesta tesi doctoral.

L'edat del jaciment va ser establerta com Eocè Mitjà (MP16-17; Cuesta Ruiz-Colmenares, 1991) en base als perissodàctils, tot i que més endavant Peláez-Campomanes (1993) va proposar una edat més antiga en base als rosegadors (MP15). Finalment, en base també als perissodàctils, es va poder precisar una edat corresponent a la MP15-16 (Cuesta Ruíz-Colmenares, 1996).

La contribució de la fauna de mamífers de Mazaterón ha estat fonamental en treballs biogeogràfics. L'estudi del caràcter endèmic dels perissodàctils de Mazaterón, juntament amb altres jaciments de la Conca del Duero, va permetre establir l'existència d'una provincia faunística (la Bioprovincia Occidental Ibèrica) individualitzada de la regió sudpirinenca i de la resta d'Europa (Cuesta Ruiz-Colmenares 1991, 1993). Més endavant, el mateix es va observar en les faunes d'artiodàctils i rosegadors (Peláez-Campomanes et al., 1989; Peláez-Campomanes, 1992, 1993; Cuesta Ruiz-Colmenares et al., 2006; Badiola et al., 2009). Estudis recents inclosos en aquesta tesi doctoral han permès comprovar que també els primats d'aquesta localitat mostren un caràcter endèmic: als capítols 8 i 9 es descriuren dos dels primats trobats en aquest jaciment, *Mazateronodon endemicus* i *Pseudoloris cuestai*, i es discuteix més extensament l'existència de la Bioprovincia Occidental Ibèrica. També al capítol 9 s'hi inclou un llistat faunístic actualitzat de les restes trobades en aquesta localitat.

2.2.4. Sossís

D’entre les localitats clàssiques de l’Eocè de la Península Ibèrica, Sossís (Conca Sudpirinenca Central), a la comarca del Pallars Jussà, és una de les més importants degut a la riquesa del conjunt de restes fòssils que s’hi han trobat (Casanovas Cladellas, 1998). A part de la indubtable informació paleontològica que ha aportat, també ha permès la correlació amb altres localitats del Paleogen europeu (López Martínez, 1998).

A l’àrea de la Pobla de Segur, a part del jaciment de Sossís, hi trobem dos jaciments més anomenats Claverol i Roc de Santa, de la mateixa edat (López Martínez, 1998). La correlació entre aquests tres jaciments va ser establerta independentement en base a la litoestratigrafia (Casanovas Cladellas, 1975) i a la biocronologia (van Dam, 1998). D’altra banda, en mostrejos fets per alguns autors (López Martínez, 1998) es distingeixen diferents nivells dins de cadascun d’aquests jaciments. El material estudiat en aquesta tesi doctoral només prové del jaciment de Sossís. Durant la recol·lecció del material dipositat a l’Institut Català de Paleontologia Miquel Crusafont no es va fer cap distinció entre els diferents nivells descrits per López Martínez (1998), de forma que en aquesta tesi el jaciment es considera com una única unitat.

El jaciment es coneix des que l’any 1942, quan el Dr. J.R. Bataller va ser avisat de la troballa d’un crani durant l’explotació de les mines de lignits. Al principi, els jaciments de lignit de Sossís eren considerats cretacis, i més endavant es va creure que eren oligocens. Tot i això, la troballa de restes de mamífers va fer suposar, tant a Bataller com a geòlegs de la Université de Toulouse, que en realitat el jaciment era Eocè Superior (Casanovas Cladellas, 1998).

Fins que intervé a la zona l’Institut de Paleontologia de Sabadell, només s’havien trobat restes de mamífers als lignits explotats a les mines de Sossís, i principalment aquestes troballes havien estat fetes pels mateixos miners, que en molts casos havien destruït el patrimoni inconscientment. A partir doncs de la dècada de 1960 es comencen a buscar restes a les margues grises intercalades entre els lignits, i és quan es comencen a recuperar restes de micromamífers (Casanovas Cladellas, 1998), moltes d’elles encara inèdites.

En aquest jaciment, diferents gèneres de marsupials, insectívors, rosegadors, carnívors, perissodàctils, artiodàctils i primats hi han estat identificats. Tot i que alguns d’ells han estat estudiats en diferents treballs (Villalta i Crusafont, 1944; Crusafont

Pairó i Truyols Santoja, 1964; Thaler, 1966; Golpe Posse, 1971; Crochet, 1978; Hartenberger, 1973; Sigé, 1976; Sudre, 1977; Checa Soler i Casanovas Cladellas, 1989-1990; Checa Soler, 1994; Cuesta Ruiz-Colmenares et al., 2006), hi ha encara a dia d'avui molt de material inèdit o poc estudiat. Per exemple, el material de llangardaixos i amfisbènids d'aquest jaciment encara es troba en una fase preliminar d'estudi (veure Bolet i Evans, 2012, en premsa). A part de les restes de vertebrats trobades a Sossís, també s'hi han recuperat ostràcodes, gastròpodes i pol·len (Civis et al., 1998).

Pel que fa als primats, una premolar i una molar superiors atribuïdes a *Adapis* cf. *parisiensis* i dos microchoerins, *Pseudoloris parvulus* i *Microchoerus erinaceus*, ja han estat citats en aquesta localitat (Crusafont Pairó, 1965; Crusafont-Pairó, 1967; Crusafont-Pairó i Golpe-Posse, 1974; Antunes et al., 1997). Tot i així, en campanyes posteriors, s'hi va recuperar una gran quantitat de material de primats que encara no s'ha descrit en detall. A més a més de noves restes de *Pseudoloris parvulus* i del microchoerí prèviament identificat com *Microchoerus erinaceus* (estudiat de forma preliminar per Minwer-Barakat et al., 2012a, b), s'hi han trobat diverses peces dentàries d'un nou gènere i espècie d'adapoïdeu, *Nievesia sossissensis*, la descripció del qual es troba en el capítol 10 d'aquesta tesi doctoral. En aquest mateix capítol s'hi inclou un llistat faunístic actualitzat dels mamífers d'aquesta localitat.

2.3. Objectius

Tot i que la Península Ibèrica compta amb un dels registres fòssils més complets de vertebrats paleògens d'Europa, degut a l'existència de seqüències estratigràfiques molt completes i ben exposades en diferents conques, els primats de l'Eocè que s'hi han trobat han estat escassament estudiats. Tenint en compte la gran quantitat de restes recuperades en diferents campanyes en varis jaciments durant dècades, queden encara moltes restes per identificar i estudiar en detall.

D'aquesta forma, el principal objectiu d'aquesta tesi doctoral és la descripció, comparació i determinació taxonòmica (incloent, en el seu cas, la definició de nous tàxons) de les restes dentàries de diferents primats (plesiadapiformes, adapoïdeus i omomioïdeus) de varis jaciments emmagatzemades a les col·leccions del museu de l'Institut Català de Paleontologia Miquel Crusafont.

Aquest objectiu general es pot dividir en els següents objectius concrets:

1. Revisió bibliogràfica detallada de tot el registre de primats de la Península Ibèrica (Annex I).
2. Estudi de les restes fòssils dentàries d'un plesiadapiforme del jaciment de Masia de l'Hereuet, Eocè Inferior, Lleida (Capítol 5).
3. Estudi de les restes fòssils dentàries d'*Anchomomys*, un petit adapoïdeu del jaciment de Sant Jaume de Frontanyà, Eocè Mitjà, Barcelona (Capítol 6).
4. Estudi de les restes fòssils dentàries d'un petit omomioïdeu del jaciment de Sant Jaume de Frontanyà (Capítol 7).
5. Estudi de les restes fòssils dentàries d'un adapoïdeu del jaciment de Mazaterón, Eocè Mitjà, Sòria (Capítol 8).
6. Estudi de les restes fòssils dentàries d'omomioïdeu del jaciment de Mazaterón (Capítol 9).
7. Estudi de les restes fòssils dentàries d'un adapoïdeu de mida petita del jaciment de Sossís, Eocè Superior, Lleida (Capítol 10).
8. Anàlisi filogenètic i interpretació de les relacions entre diferents membres d'adapoïdeus de la tribu Anchomomyini i amb la resta de primats estrepsirins (Capítols 6 i 10).

3

LOCALITZACIÓ GEOGRÀFICA, CONTEXT GEOLÒGIC I DESCRIPCIÓ DELS JACIMENTS ESTUDIATS

En aquest apartat es descriu la localització geogràfica i geològica d'aquells jaciments dels que s'han estudiat restes de primats fòssils en aquesta testi doctoral (Capítols 5-10).

Aquests jaciments (figura 4) es troben en dues grans conques ibèriques: a la Conca Sudpirinenca s'hi toben els jaciments de Masia de l'Hereuet i Sossís (concretament a la zona denominada Conca Sudpirinenca Central o Conca de Tremp-Graus), i el de Sant Jaume de Frontanyà 3 (a l'anomenada Conca Sudpirinenca Oriental), i a la Conca del Duero hi trobem el jaciment de Mazaterón (concretament al sector oriental o Conca d'Almazán).

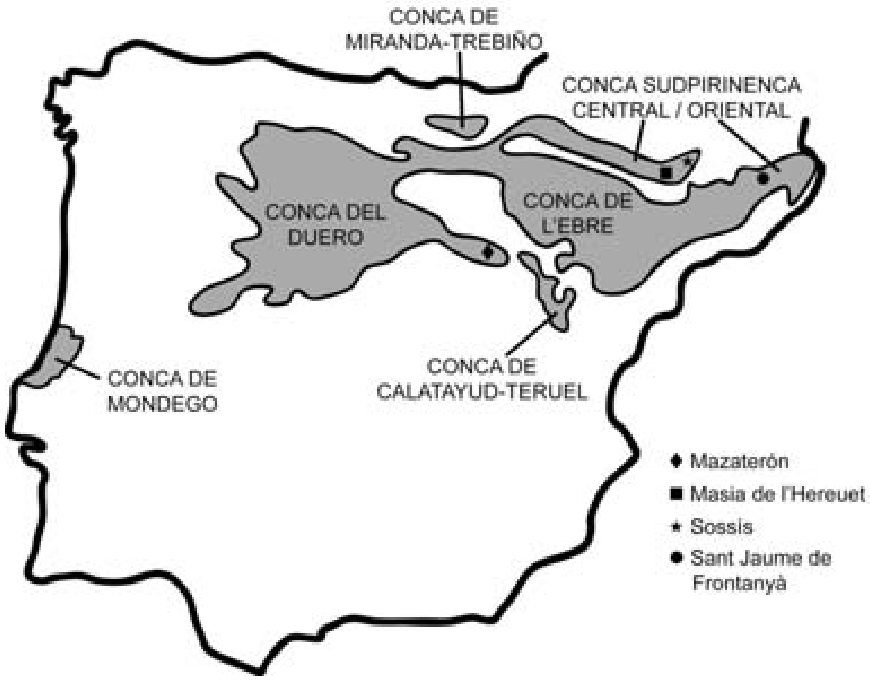


Figura 4. Mapa de la Península Ibèrica amb les principals conques paleògenes i la localització dels jaciments on s'han trobat restes de primats que s'estudien en aquesta tesi doctoral (modificat d'Antunes et al., 1997 i Badiola et al., 2009).

Des d'un punt de vista geogràfic, el jaciment de Masia de l'Hereuet es troba a la comarca de la Noguera (provincia de Lleida), al municipi d'Àger, prop de la masia que duu el mateix nom, en un camí que surt del sender de gran recorregut GR-1 que va d'Agulló a Corçà. El jaciment de Sossís es troba també a la comarca de la Noguera, a la zona de la Pobla de Segur, dins el municipi de Conca de Dalt, al qual pertany el poble de Sossís, del que la localitat fossilífera prèn el nom. D'altra banda, el jaciment de Sant

Jaume de Frontanyà 3 es troba a la comarca del Berguedà (provincia de Barcelona), a la carretera que uneix els pobles de Borredà i Sant Jaume de Frontanyà (BV-4656). Finalment, el jaciment de Mazaterón es troba a 2,5 km a l'ENE del poble del mateix nom, a la provincia de Sòria, al topònim "La Solana", 200 m al sud del camí que uneix Mazaterón amb Peñalcázar, al marge dret del barranc Renavares (Cuesta Ruiz-Colmenares i Jiménez Fuentes, 1994).

A continuació es descriuen els principals trets geològics d'aquestes dues conques, i de forma detallada cadascuna de les seccions on es troben els jaciments estudiats.

3.1. Conca Sudpirinenca

La Serralada Pirinenca inclou la totalitat de l'alineació muntanyosa que voreja el nord d'Espanya, des del Cap de Creus, a Catalunya, fins a Galicia, tot i que alguns autors consideren la Serralada Cantàbrica una unitat geològica independent, reservant el nom de Pirineus per a la porció de la serralada que s'extén entre el Golf de Lleó, al Mediterrani, i el Golf de Biscaia, a l'oceà Atlàntic, separada de la Serralada Cantàbrica per la falla de Pamplona (Barnolas i Pujalte, 2004). La seva evolució geològica és el resultat de canvis sedimentaris, tectònics, paleogeogràfics i paleoclimàtics ocorreguts al marge septentrional de la Placa Ibèrica des de finals del Paleozoic fins l'actualitat, induïts principalment per la seva deriva latitudinal i la seva interacció amb la Placa Europea. En resum, l'àrea pirinenca va ser sotmesa durant el Mesozoic a condicions distensives intermitents, reflexades en extensió i aprimament cortical, vulcanisme, desenvolupament de conques sedimentàries fortament subsidents i, eventualment, separació entre Ibèria i Europa. Posteriorment, del Cretaci final fins el Miocè, la convergència i col·lisió obliqua de les dues plaques va causar la deformació de les conques sedimentàries mesozoiques, procés que es va denominar Orogènia Alpina o Pirinenca; en aquesta fase es va deformar altra vegada el substrat varisc infrajacent (Muñoz, 1992; Beaumont et al., 2000; Barnolas i Pujalte, 2004).

A la Serralada Pirinenca s'hi delimiten tres zones principals, de nord a sud. La Zona Nordpirinenca es caracteritza per una sèrie d'afloraments del basament varisc, que corresponen a blocs aïllats, coneguts com Massissos Nordpirinencs. La Zona Axial, separada de l'anterior per l'anomenada Falla Nordpirinenca, és un extens aflorament de basament varisc en el que es troben alguns dels pics més elevats dels Pirineus.

Finalment, la Zona Sudpirinenca inclou el material post-varisc que cobreix la Zona Axial (Barnolas i Pujalte, 2004). En aquest capítol ens centrarem en les característiques d'aquesta última zona, que és on es troben tres dels jaciments estudiats en aquesta tesi doctoral.

A la Zona Sudpirinenca, el Maastrichtià superior, el Paleocè i l'Ilerdià inferior estan representats per una successió sedimentària de potència variable en diferents sectors, representativa d'una àmplia gamma d'ambients, des de continentals a marins profunds. Durant l'Ilerdià mitjà, Cuisià (subdivisions locals de l'Ypresià), Lutecià i Bartonià (Eocè Inferior-Mitjà), la Conca Sudpirinenca es va compartimentar en subconques amb característiques estructurals i sedimentàries pròpies (Conca Sudpirinenca Oriental, Central i Occidental; Barnolas et al., 2004). En aquest capítol només s'hi detallaran les característiques de les dues primeres, ja que cap dels jaciments estudiats es troba a la Conca Sudpirinenca Occidental.

3.1.1. Conca Sudpirinenca Oriental

El coneixement estratigràfic bàsic de la Conca Sudpirinenca Oriental queda reflectit en els treballs de Reguant (1967), Kromm (1968), Gich (1969, 1972), Pallí (1972), Ferrer (1971), Serra-Kiel (1984) i Burbank et al. (1992), entre altres. La Conca Sudpirinenca Oriental, on es troba el jaciment de Sant Jaume de Frontanyà, correspon a la zona compresa entre el Mar Mediterrani i l'alineació estructural del Segre. A l'est del Segre, la Conca Sudpirinenca s'estreny considerablement. Tot i haver-hi nombroses subdivisions de la zona basades en criteirs paleogeogràfics i tectònics, en línies generals, sobre el basament varisc, hi apareix un Mesozoic potent, especialment pel que fa al Cretaci, sobre el que es disposa el Paleocè i, en algunes ocasions, directament l'Eocè (Barnolas i Pujalte, 2004). A la Conca Sudpirinenca Oriental, s'hi van desenvolupar plataformes carbonatades al marge d'avantpaís (Ebre) i sistemes deposicionals siliciclàstics en el marge orogènic (Pirineus), amb falques clàstiques que culminen amb sediments continentals (Barnolas i Pujalte, 2004).

Concretament, el jaciment de Sant Jaume de Frontanyà es troba a la Unitat del Cadí (Muñoz et al., 1986), formada per un basament varisc sobre el que es troben directament el Garumnià (materials del trànsit Mesozoic-Cenozoic, de color principalment vermell, constituïts per lutites, gresos i conglomerats d'origen essencialment al·luvial, a vegades amb intercal·lacions lacustres de fàcies i potències molt variables) i l'Eocè Inferior i Mitjà del Sinclinori de Ripoll (Barnolas i Pujalte, 2004). Es tracta d'una unitat tectònica que, mitjançant la falla de Vallfogona, cabalga cap al sud sobre els materials autòctons d'avantpaís que constitueixen la Depressió Central Catalana (Muñoz et al., 1986), formant el límit meridional dels Pirineus a la zona compresa entre els rius Ter-Freser i Llobregat (Busquets et al., 1992). La Unitat del Cadí està estructurada internament mitjançant un conjunt de plecs que permeten l'aforament de materials sinorogènics de més de 3000 m de potència, constituïts per un tram inferior marí de caràcter turbidític (Formació Vallfogona), un tram intermedi transicional (Formacions Beuda i Cal Bernat) i un tram superior continental (Formació Bellmunt) (Busquets et al., 1992).

La Formació Bellmunt s'extén àmpliament per la zona meridional del Pirineu Oriental i forma el nucli del Sinclinori de Ripoll. Consisteix en uns 1500 m de sediments de caràcter continental, que corresponen a un sistema al·luvial que prograda sobre les fàcies litorals marines de la formació Cal Bernat, atribuïda al Lutecià en base a nummulits i nanoplàncton calcari (Ramos-Guerrero et al., 1992). La Formació Bellmunt inclou dues megaseqüències en les que, de base a sostre, s'hi produeix un increment dels dipòsits gresosos i conglomeràtics sobre els sediments lutítics més distals. En aquests sediments lutítics, que corresponen a dipòsits de plana d'inundació, s'hi intercalen dipòsits lacustres i palustres, donant trams de potència variable d'entre 4 i 17 m. En aquests trams lacustres-palustres, a part d'alguns nivells de margocalcàries i calcàries, la litologia dominant està constituïda per margues grises amb un alt contingut de matèria orgànica, amb fines intercalacions de carbó amb restes abundants de plantes i vertebrats fòssils (Ramos-Guerrero et al., 1992; Moyà-Solà i Köhler, 1993). Aquestes margues s'interpreten com sediments originats en un medi palustre desenvolupat a favor de les zones topogràficament més deprimides de la plana d'inundació fluvial, on es degueren produir basses, i on ocasionalment hi deuria haver condicions reductores (Busquets et al., 1992; Ramos-Guerrero et al., 1992).

Les successions lacustres-palustres es troben desconnectades entre sí. En una d'elles, que aflora entre els punts kilomètrics 4 i 9 de la carretera que uneix els pobles de Borredà i Sant Jaume de Frontanyà, en el flanc meridional del Sinclinori de Ripoll (Busquets et al., 1992), s'hi han localitzat quatre nivells de margues amb restes de vertebrats, anomenats Sant Jaume de Frontanyà 1, 2, 3C i 3D, d'edat Robiacià (Eocè Mitjà; veure figura 5). En aquesta tesi s'hi estudien les restes de dues espècies de primats procedents dels dos nivells més antics d'aquesta secció, Sant Jaume de Frontanyà 3C i 3D, corresponents a les unitats MP14-15.

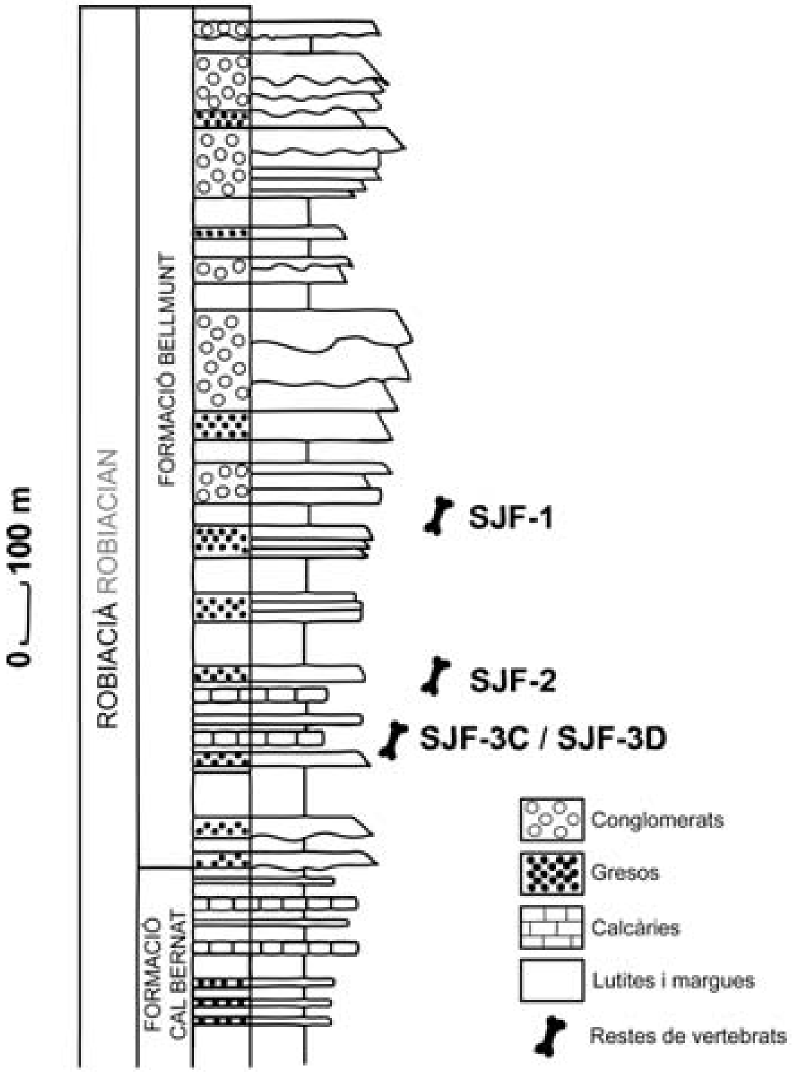


Figura 5. Columna estratigràfica del jaciment de Sant Jaume de Frontanyà on es detalla la posició dels nivells SJF-1, 2, 3C i 3D, on s'han trobat restes fòssils de vertebrats. Les restes de primats estudiades en aquesta tesi doctoral provenen dels nivells 3C i 3D, que corresponen a la mateixa edat. Modificada de Moyà-Solà i Köhler (1993).

A més a més dels vertebrats, en aquests nivells s'hi han trobat restes de gastròpodes i vegetals, que inclouen restes macroscòpiques, pol·len, espores i oogonis de caròfits. L'associació paleobotànica sugereix unes condicions tropicals o subtropicals humides.

L'associació de vertebrats, entre els que dominen els primats i els artiodàctils de mida petita, indica l'existència d'un paisatge de bosc dens amb un abundant estrat herbaci, sent també freqüents els mamífers d'hàbitats humits o entollats. Tot això, juntament amb les litofàcies del jaciment, indica un conjunt de subambients constituït per diferents àrees palustres i lacustres, desconnectades entre sí, que es desenvoluparen a favor de petites depressions en zones d'intercanals de plana d'inundació i en algun cas per l'abandonament de canals (Busquets et al., 1992).

3.1.2. Conca Sudpirinenca Central

El coneixement estratigràfic bàsic de la Conca Sudpirinenca Central queda reflectit en els treballs de Van Eden (1970), Luterbacher (1973), Garrido-Megías (1973), Nijman i Nio (1975), Schaub (1981), Fonnesu (1984), Mutti et al. (1985, 1988), Crumeyrolle (1987), Einchenseer (1988), Cuevas-Gozalo (1989), Barnolas et al. (1991), Serra-Kiel et al. (1994) i Nijman (1998), entre altres. La Conca Sudpirinenca Central (denominada per alguns autors Conca de Tremp-Graus i en la que es localitzen els jaciments de Masia de l'Hereuet i Sossís) correspon al sector comprès entre l'estructura del Segre i els afloraments mesozoics i cenozoics que constitueixen el límit occidental de la Unitat Sudpirinenca Central, a la vall del Cinca (Barnolas i Pujalte, 2004).

La seva estratigrafia consisteix, en l'àrea on es troben els jaciments estudiats, en un Triàsic que constitueix la unitat sobre la que llisca la làmina encabalgant, formada per un Juràssic reduït parcialment erosionat sota el Cretaci Inferior, un Cretaci Superior-Paleocè en fàcies del Garumnià, un Eocè Inferior i Mitjà especialment ben representat a la zona de Tremp-Graus, i finalment uns conglomerats de l'Eocè Superior-Oligocè (Barnolas i Pujalte, 2004).

A la Conca Sudpirinenca Central s'hi troben, fins a principis del Cuisià inferior, fàcies de plataforma carbonatada al marge meriodional que passen cap al nord a fàcies de rampa distal i talús amb aportacions siliciclàstiques procedents de l'orogen. A partir del Cuisià inferior, la sedimentació de la conca passà a ser gairebé exclusivament siliciclàstica, amb medis sedimentaris terrígens continentals i marins poc profunds. Concretament, en aquesta àrea s'hi va desenvolupar un sistema fluvio-deltàic a l'eix de la conca, interdigitat amb ventalls al·luvials procedents del marge pirinenc. Ja durant el Bartonià, existeix a la Conca de Tremp-Graus un important desenvolupament de ventalls al·luvials vorejant la Zona Axial dels Pirineus, que persistiran fins l'Oligocè Inferior (Barnolas et al., 2004).

S'inclouen a la Conca de Tremp-Graus els sediments paleògens del sinclinal d'Àger, freqüentment referits en alguns treballs com Conca d'Àger. A l'Eocè continental de la Vall d'Àger hi afloren uns nivells de margues i lutites grogues o verdes i gresos grisos o marrons, de gra groller i localment conglomeràtic. En ambdós tipus de fàcies s'hi han trobat restes d'òssos i dents de mamífers. Aquests gresos corresponen a canals complexes de rius trenats, mentre que les margues i lutites corresponen a àrees d'inundació cobertes temporalment per aigua (Rosell Sanuy i Llompart Díaz, 1988; Checa Soler, 1994). Aquests materials afloren en diferents sectors de la zona d'Àger, i apareixen especialment ben exposats al camí que va d'Agulló a Corçà. En aquesta zona hi trobem el jaciment de Masia de l'Hereuet (veure figura 6), d'edat Eocè Inferior, que es troba en contacte directe amb el Cuisià marí, raó per la qual es considera aquest jaciment el més baix de la sèrie sedimentària que aflora en aquest sector (Checa Soler, 1994). Les restes de vertebrats procedeixen d'un nivell de gresos de color vermellós que representen reompliments de canal.

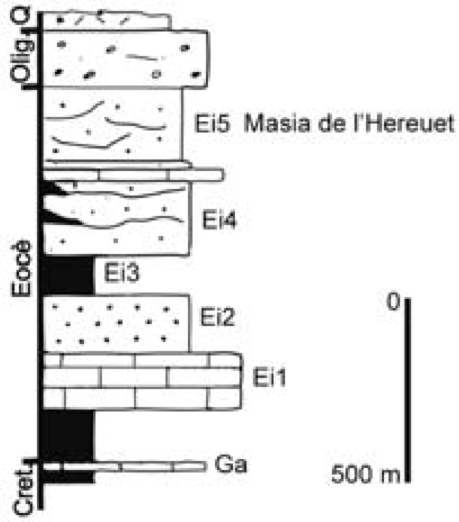


Figura 6. Columna estratigràfica sintètica de la zona de la Vall d'Àger on es troba el jaciment de Masia de l'Hereuet. Ga=Garumnià; Ei=Eocè Inferior; 1=calcàries amb alveolines; 2=gresos; 3=lutites; 4=gresos i calcàries; 5=conglomerats, gresos i lutites; Q=Quaternari. Modificada de Rosell Sanuy i Llompart Díaz (1988).

D'altra banda, al nord i a l'est de la Pobla de Segur hi afloren els materials continentals de l'Eocè de la Formació Collegats, que en aquesta zona no tenen correlació directa amb dipòsits marins. L'edat d'aquesta formació va ser establerta com Eocè Superior en base als mamífers del jaciment de Sossís (Crusafont et al., 1954, 1956), i confirmada més tard per Casanovas Cladellas (1975) amb els de Roc de Santa. Altres autors consideren que l'edat d'aquesta formació arriba fins l'Oligocè degut a les seves relacions estratigràfiques i tectòniques amb altres àrees (López Martínez, 1998). La seva successió litològica, amb una potència total de fins a 1000 m, és fonamentalment conglomeràtica amb intercalacions lutítiques (López Martínez, 1998). Dins d'aquesta formació, s'hi han trobat jaciments clàssics com ara Sossís, Claverol i Roc de Santa (Crusafont-Pairó, 1967; Crusafont Pairó i Golpe Posse, 1968), formant part del denominat al·logrup Ermita (Mellere i Marzo, 1992).

L'al·logrup Ermita aflora especialment en el curs del riu Noguera Pallaresa, on arriba a tenir una potència d'uns 250 m, i representa un sistema de ventalls deltàics interdigitats amb un sistema lacustre, amb dipòsits de carbonats, margues i lignits en els que es troben els nivells fossilífers (Mellere i Marzo, 1992). Robles (1984) i Robles i Ardévol (1984) distingeixen fins a sis intercalacions lacustres de gruix i extensió decreixent. La més baixa és la més important, denominada Membre Sossís per Rosell i Riba (1966), amb una potència que supera els 100 m. En ella es situen els jaciments de Sossís, Claverol i Roc de Santa (López Martínez, 1998; veure figura 7).

El jaciment de Sossís es troba en margues i llims grisos i negres intercalats en un tram de margues blanques, uns 15 m per sobre dels lignits explotats a les antigues mines de galeria, aflorant a l'escombrera situada al nord del poble de Sossís (López Martínez, 1998). Segons les seves característiques sedimentològiques, es desprèn que en aquesta zona hi havia grans extensions d'aigua a mode de petits llacs, relativament poc profunds, amb càrregues estacionals suaus d'aigua i sediments, en un clima subtropical o temperat, amb fases àrides alternant amb èpoques més plujoses. Això permetria mantenir una vegetació desenvolupada a causa de la humitat regnant (Casanovas Cladellas, 1975).

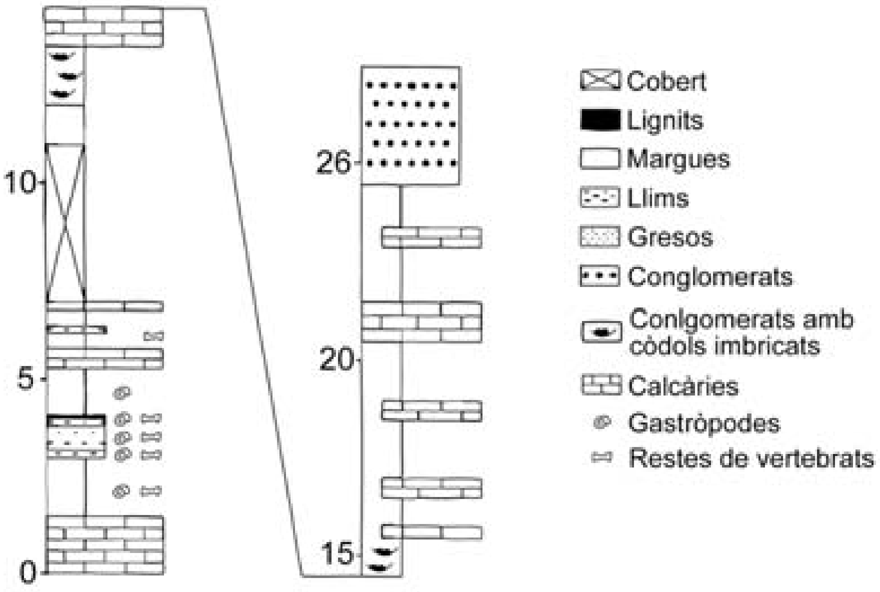


Figura 7. Columna estratigràfica amb la localització dels diferents nivells del jaciment de Sossís on s'han trobat restes fòssils. Modificada de Peláez-Campomanes (1998). Durant la recol·lecció del material estudiat en aquesta tesi doctoral, no es va fer cap distinció entre els diferents nivells descrits per López Martínez (1998), de forma que en aquesta tesi el jaciment es considera com una única unitat.

3.2. Conca del Duero

El coneixement estratigràfic bàsic de la Conca del Duero queda reflectit en els treballs de Portero et al. (1982, 1983), Corrochano i Armenteros (1989), Armenteros i Corrochano (1994), Armenteros et al. (2002), Alonso-Gavilán et al. (2004), entre altres.

La Conca continental cenozoica del Duero es troba al nord-oest de la Península Ibèrica, i és la més gran en extensió (al voltant dels 50000 km^2). És una conca intraplaca d'evolució complexa que començà a definir-se a finals del Cretaci. La resposta a la convergència de les plaques Europea i Ibèrica, la col·lisió de les plaques Ibèrica i Africana i el canvi de règim extensional mesozoic a compressional terciari van donar lloc a l'estructuració i l'evolució dels fronts muntanyosos que van constituir els marges de la conca i a la seva evolució dinàmica i sedimentària (Alonso-Gavilán et al., 2004). A la Conca del Duero s'hi distingeixen diferents sectors amb característiques tectosedimentàries pròpies, relacionades amb les Serralades Cantàbrica i Ibèrica i amb el Sistema Central. El sector oriental, en el que es troba el jaciment de Mazaterón, es va comportar, almenys a partir de l'Eocè, com una conca d'avantpaís relacionada amb l'evolució alpina de la Serralada Ibèrica (Casas-Sainz et al., 2000).

El registre sedimentari de la conca reflexa canvis climàtics al llarg de la seva història, relacionats amb el canvi de latitud de la Península Ibèrica dels 30ºN durant el Cretaci als 40ºN durant el Neogen, i amb la creació de barreres muntanyoses al seu voltant, sent més efectives les corresponents als marges nord, sud i est (Alonso-Gavilán et al., 2004).

Concretament, durant el Paleogen, les condicions foren subtropicals amb marcats períodes secs reflexats per la presència de crostes de carbonat, sílice i guix, juntament amb les indicacions del registre fòssil (Jiménez Fuentes, 1974; Fernández García et al., 1989; Alonso-Gavilán et al., 1986; Armenteros i Bustillo, 1996).

El reompliment de la conca es va dur a terme en tres contextes geodinàmics que van donar lloc a tres seqüències estratigràfiques separades per discontinuïtats a escala de conca: en primer lloc es diposita l'anomenada seqüència finicretàcica-paleocena, sobre ella hi trobem la seqüència eocena-oligocena (desenvolupada en un règim compressiu, que és la de major interès en aquesta tesi) i, finalment, la seqüència neògena (Alonso-Gavilán et al., 2004).

El jaciment de Mazaterón es troba al sector anomenat Conca d'Almazán, que correspon a la part oriental de la Conca del Duero, al nord-oest de la Serralada Ibèrica. Limita al nord amb el Massís de Cameros, al nord-est amb la branca aragonesa de la Serralada Ibèrica, i al sud amb la branca castellana de la Serralada Ibèrica (Alonso-Gavilán et al., 2004).

La sedimentació a la Conca d'Almazán va començar durant l'Eocè Mitjà, coincidint amb l'aixecament de la Serralada Ibèrica en el context de la compressió alpina. Els sectors nord i nord-est de la Conca d'Almazán estan principalment ocupats per materials paleògens, representant ventalls al·luvials, sistemes fluvials, sistemes lacustres/palustres i planes lutítiques/evaporítiques (Huerta i Armenteros, 2006). Als sectors sud i oest, les roques paleògenes estan cobertes per dipòsits neògens. La potència màxima de la successió terciària s'estima en 3500-4000 m (Huerta et al., 2006). El reompliment de la conca està dividit en quatre seqüències deposicionals, l'edat de les quals no es pot establir de forma precisa degut a la falta de dades paleontològiques (Huerta i Armenteros, 2006). El jaciment de Mazaterón, situat a la més antiga d'aquestes seqüències, uns 350 m sobre la base de la successió terciària, data de l'Eocè Mitjà (Robiacià, MP15-16) i és el nivell fossilífer més antic identificat en aquesta conca (Cuesta Ruiz-Colmenares, 2003; Huerta et al., 2006). A part de Mazaterón, les úniques localitats fòssils reconegudes de la conca són Deza (Eocè Superior; Cuesta Ruiz-Colmenares i Jiménez Fuentes, 1994; Cuesta Ruiz-Colmenares, 2003), i les localitats del Miocè Inferior de Cetina (Álvarez-Sierra, 1986) i Ariza (Cuenca, 1991).

El jaciment de Mazaterón pertany a la Formació Mazaterón, composta per calcàries, dolomies i margues amb intercalacions lutítiques (veure columna estratigràfica del jaciment als capítols 8 i 9 d'aquesta tesi doctoral), i representa un sistema de llac amb àrees centrals permanentment inundades. Les oscil·lacions estacionals del nivell del llac van permetre el dipòsit d'una orla palustre, en connexió amb una altra orla externa de calcretes que separava el sistema lacustre dels dipòsits al·luvials (Huerta et al., 2006). Les margues grises que contenen les restes de vertebrats corresponen a sediments lacustres dipositats en el fons anòxic central, i canvien lateralment i vertical a dipòsits palustres formats en àrees estacionalment exposades (Cuesta i Badiola, 2009). El jaciment té una extensió lateral considerable (uns 400 m) i una potència màxima de 5 a 8 m (Jiménez Fuentes et al., 1989).

4

MATERIAL I MÈTODES

El material estudiat per dur a terme aquesta tesi doctoral fou recuperat durant la dècada de 1990 pels doctors Salvador Moyà Solà i Meike Köhler juntament amb col·laboradors. Totes les peces dentàries incloses en aquest estudi es troben dipositades al museu de l'Institut Català de Paleontologia Miquel Crusafont (Sabadell, Barcelona).

Les tècniques utilitzades per a l'extracció de restes de micromamífers són diferents de les emprades en l'estudi d'altres grups de fòssils, degut a la seva petita mida. En el cas dels micromamífers, no són aplicables les tècniques d'excavació i recol·lecció superficial emprades per a l'obtenció de fòssils de mamífers de mida gran, sinó que s'utilitzen principalment les de rentat-tamisat pròpies de la Micropaleontologia. Tot i així, a diferència del cas de microfòssils d'invertebrats marins, per tal d'aconseguir una quantitat significativa de restes és necessari processar grans volums de sediment. Per això, per a l'estudi de micromamífers fòssils s'utilitzen unes tècniques i un instrumental específics que permeten, d'una banda, el processat ràpid de mostres molt voluminoses i, d'altra banda, la reducció de la major part dels residus obtinguts després d'un primer rentat, amb la finalitat de facilitar al màxim l'extracció de les restes.

Les tècniques aplicades en aquest estudi per a l'extracció de les restes fòssils poden dividir-se en tres grups: 1) tècniques de camp, 2) de laboratori i 3) de gabinet. Al final d'aquesta secció s'especifiquen també les tècniques emprades per a la medició de les peces dentàries, per a la realització dels anàlisis filogenètics, i per a l'obtenció d'imatges i il·lustracions.

4.1. Tècniques de camp

4.1.1. Prospecció

La prospecció consisteix en l'exploració sistemàtica de la zona objecte d'estudi per buscar jaciments de micromamífers. Generalment, les restes de micromamífers no poden observar-se en un aflorament, degut a la seva petita mida i a la seva baixa concentració en els jaciments. Tot i que algunes vegades es pot observar la presència de fragments d'os a simple vista, es tracta de casos excepcionals. Per tant, s'han de fer servir indicis indirectes per tal d'escollir els nivells que poden contenir restes. S'escullen capes de sediment de tamany de gra fi (argiles o margues), generalment de colors foscos, que indiquen un alt contingut de matèria orgànica.

Un cop escollits els nivells, es procedeix a la recollida de mostres de prova. Per això es neteja el lloc de l'aflorament, eliminant la part més superficial amb una aixada, amb la finalitat d'observar bé els contactes entre les capes, i s'extreu el sediment fent servir un pic i una pala. Aquestes mostres es recullen en sacs degudament marcats amb les sigles assignades al jaciment i es processen posteriorment aplicant les tècniques que es descriuran en els següents apartats. El mostreig de prova pretén evidenciar l'existència de restes fòssils de micromamífers en els nivells seleccionats, així com estimar-ne la seva abundància.

Durant aquesta fase es realitza també la documentació de tots els jaciments mostrejats, que inclou una breu descripció cartogràfica, estratigràfica i sedimentològica, la realització de dibuixos del tall i la presa de fotografies de conjunt i de detall i, en suma, el registre de qualsevol aspecte que permeti la localització dels nivells per a una possible explotació posterior.

4.1.2. Recollida de mostres d'estudi

Un cop processades les mostres de prova i analitzats els resultats obtinguts, es procedeix al mostreig intensiu de determinats jaciments mitjançant l'extracció del que denominem mostres d'estudi. La decisió sobre quins nivells han de ser sotmesos a un mostreig intensiu no només depèn de la quantitat de peces dentàries per unitat de pes de sediment trobades durant el mostreig de prova, sinó també de la importància de l'obtenció de dades en un determinat punt de l'àrea d'estudi. Tot i així, quan es tenen diferents nivells molt pròxims entre ells en els que es detecta la presència de dents de micromamífers durant el mostreig de prova, a vegades només s'exploten els més rics.

La mida de la mostra definitiva depèn de l'abundància de fòssils observada durant el mostreig de prova, però també d'altres factors com ara les condicions de l'aflorament, el gruix del nivell mostrejat, l'accessibilitat del jaciment, el comportament de la mostra de prova durant el processat i la proporció de residu resultant. De totes maneres, un bon resultat durant el mostreig de prova no sempre garantitza la presència d'una quantitat significativa de fòssils en una mostra més gran.

4.2. Tècniques de laboratori

4.2.1. Rentat

La tècnica d'extracció de fòssils de micromamífers, que consisteix en passar els sediments que els contenen per un tamís sota l'aigua, va ser introduïda per Lartet durant el segle XIX i ha estat emprada posteriorment per molts paleontòlegs. Però la seva aplicació a gran escala no es va aconseguir fins la segona meitat del segle XX, quan va ser perfeccionada per investigadors holandesos (Freudenthal et al., 1976; Daams i Freudenthal, 1988).

El procés de rentat es pot fer també al camp, prop d'un riu o pantà, sempre tenint en compte que necessitarem grans quantitats d'aigua. Perquè les mostres es disgreguin fàcilment amb l'aigua és necessari que estiguin totalment seques. Per això s'exposen al sol o es posen dins un forn a una temperatura de 40-60ºC. Un cop estan totalment seques, es posen en cubetes i s'omplen d'aigua fins que el sediment queda totalment cobert. El temps necessari per aconseguir la disgregació completa de les mostres és diferent segons el tipus de sediment, i pot variar des d'uns minuts a algunes hores.

Posteriorment, el material es passa per l'anomenada "taula Freudenthal", que consta de tres tamisos d'alumini superposats, d'uns 100 x 50 cm, amb ulls de malla decreixents, de 2,5, 0,7 i 0,5 mm (figura 8). D'aquesta forma s'aconsegueix eliminar la fracció més fina, de mida de gra menor de 0,5 mm, que no conté peces útils de micromamífers. Aquest equip, de grans dimensions, es manté fix, de manera que el rentat es fa amb l'ajuda de mangueres mòbils.

El residu obtingut s'asseca novament al sol i després s'emmagatzema en bosses. El concentrat provinent de cada tamís es recull per separat. Aquesta separació en tres fraccions facilita el tractament posterior.

En algunes ocasions la quantitat de residu resultant del rentat és molt gran. Això passa normalment quan les mostres de sediment no s'han assecat bé abans del procés de rentat, i per tant no es disgreguen completament al submergir-les en aigua. En aquests casos és convenient deixar assecar el residu una altra vegada i tornar-lo a rentar.

Figura 8. Procés de rentat on es pot observar la taula Freudenthal amb els tamisos d’alumini amb diferents ulls de malla superposats.

4.2.2. Fraccionament

Aquesta tècnica consisteix en separar els concentrats, un cop secs, en diferents fraccions, amb la finalitat d’homogeneïtzar la mida de gra i facilitar el procés de triat. Si el residu no es fracciona, la presència durant el triat de partícules de mides molt diferents podria fer que les restes fòssils més petites passessin desaparcebudes. Per aconseguir el fraccionament, es passa el concentrat per una sèrie de tamisos d’un diàmetre d’entre 30 i 50 cm, de diferents ulls de malla, d’entre 2 i 0,5 mm.

4.3. Tècniques de gabinet

4.3.1. Triat

El triat consisteix en la separació de les restes fòssils de la fracció mineral que constitueix la major part del residu final. El triat de les fraccions més grolleres (amb tamany de partícula de 2 mm o superior) es realitza a simple vista, extenent el concentrar sobre una superfície plana i extraient les restes fòssils amb l’ajuda d’unes pinces. Per triar les fraccions de mida més petita, és necessari l’ús de la lupa binocular. Es dipositen petites porcions de concentrat en una safata que a la base hi té dibuixada una graella, i s’examinen sota la lupa, seleccionant els fòssils. Durant el triat no només s’extreuen les dents, sinó també petits ossos, sencers o fragmentats, així com caròfits o altres restes fòssils que hi pugui haver.

4.3.2. Ordenació de les mostres

Totes les peces dentàries completes trobades i aquells fragments dels que es pot mesurar almenys un paràmetre, o dels que es pot observar algun tret morfològic característic es munten sobre peces de Lego® amb l’ajuda de BluTack®. Les peces que presenten concrecions són netejades amb l’ajuda d’agulles i/o aigua. Les dents que tenen esquerdes es consoliden amb Paraloid® B-72 (dissolt en acetona al 2%, 5% o 10%).

Posteriorment, a la part restant del Lego®, al costat de la peça fòssil, s’hi escriu el número de registre que correspon a cada peça (figura 9). Aquest número de registre, juntament amb la identificació de cada peça s’inclou en el llibre de registre del museu de l’Institut Català de Paleontologia Miquel Crusafont de Sabadell, per tal de tenir tot el material identificat i ubicat dins les col·leccions.

Figura 9. Fotografia de les col·leccions de material de primats de l’Eocè de l’Institut Català de Paleontologia Miquel Crusafont on es poden veure les peces de Lego® amb BluTack® on es munten els fòssils i el número de registre corresponent a cada peça (A), i els armaris on s’emmagatzemen les capses que contenen les peces fòssils (B).

4.4. Descripció del material dentari

La descripció del material dentari s’ha fet seguint la nomenclatura de diferents autors, depenent del grup d’estudi (veure figura 10).

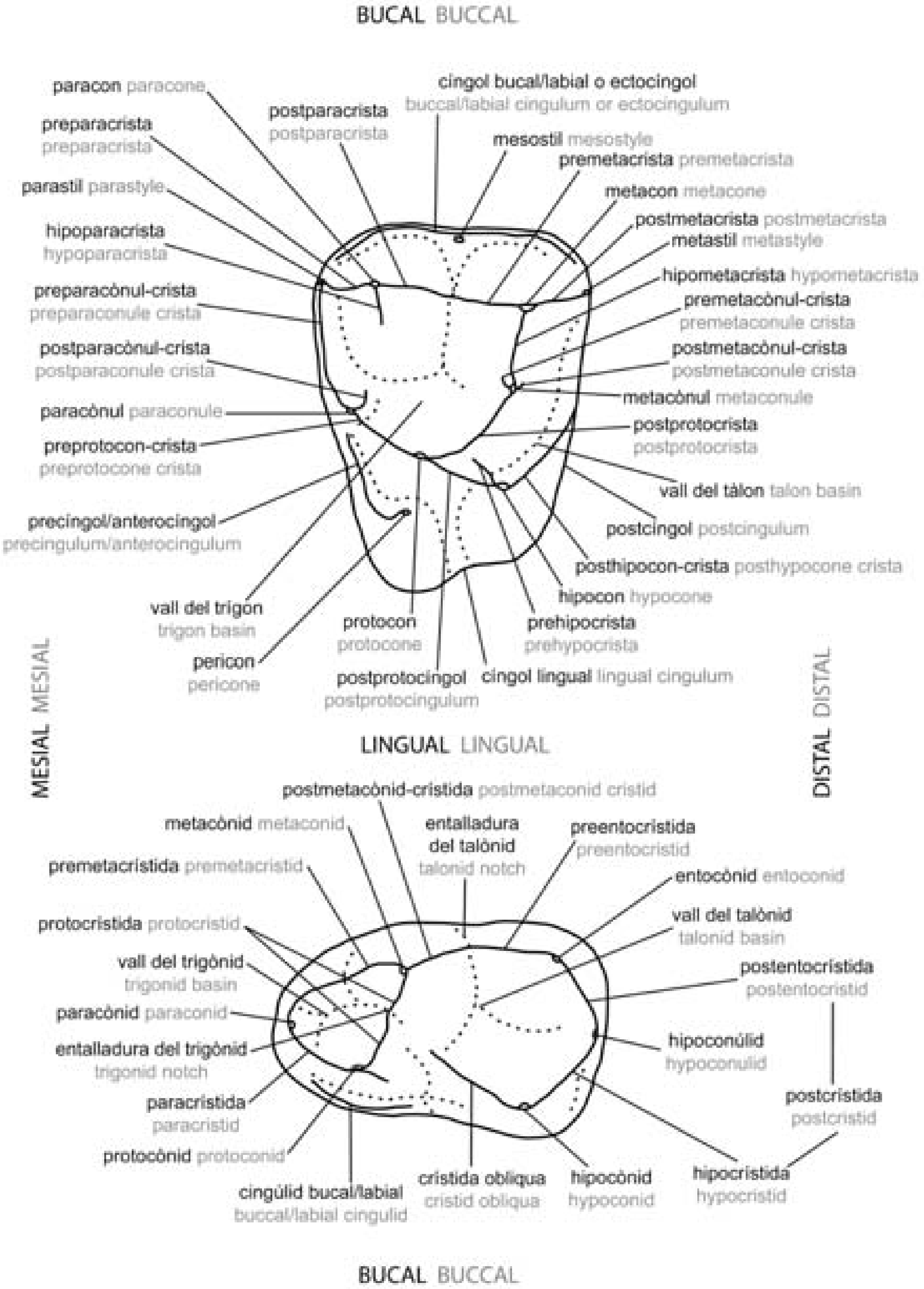


Figura 10. Morfologia dental general en vista oclusal de les molars superiors (a dalt) i inferiors (a baix) dels primats estudiats en aquesta tesi doctoral i nomenclatura usada per a la descripció de les peces dentàries, basada en Hooker (1986) i Szalay i Delson (1979).

Pel que fa al plesiadapiforme *Arcius* sp. de Masia de l'Hereuet (Capítol 5) i als omomioïdeus (*Pseudoloris pyrenaicus* i *P. cuestai*) de Sant Jaume de Frontanyà i Mazaterón respectivament (Capítols 7 i 9), s'ha seguit la nomenclatura de Hooker (1986). Per les descripcions dels adapoïdeus *Anchomomys frontanyens, Mazateronodon endemicus* i *Nievesia sossissensis* de Sant Jaume de Frontanyà, Mazaterón i Sossís respectivament (Capítols 6, 8 i 10) la nomenclatura dentària utilitzada és la de Szalay i Delson (1979).

A les descripcions s'ha fet servir la terminologia clàssica mesial/distal i bucal (o labial)/lingual, tot i que en les descripcions de les incisives de *P. cuestai* (Capítol 9) s'han utilitzat els termes "anterior" i "posterior" específicament. S'ha seguit aquesta terminologia perquè tot i que els termes posterior i distal signifiquen el mateix, degut al posicionament de les incisives, els termes anterior i mesial no signifiquen el mateix en aquest cas (seguint Hooker i Harrison, 2008).

Cada dent en qüestió s'indica de la següent manera: I (incisiva), C (canina), d (dent decídua), P (premolar) i M (molar). La posició de cada dent es fa saber amb el número en subíndex, si és inferior, o amb superíndex, si és superior. Al capítol 9, seguint les normes de la revista on s'ha publicat l'article, en comptes de fer servir subíndexs i superíndexs, s'indica si la dent és inferior o superior posant les lletres en minúscula (per les inferiors) o en majúscules (en el cas de les superiors). D'aquesta manera, per exemple, al capítol 9, quan es parla d'una segona molar inferior, s'escriu m2 enlloc d'M_2 com a la resta de capítols.

4.5. Mesures del material dentari

Pel que fa a les mesures del material dentari atribuït a *Arcius* sp., aquestes han estat fetes seguint el sistema de Bloch i Gingerich (1998). Els criteris de mesura utilitzats en l'estudi dels adapoïdeus *Mazateronodon endemicus, Anchomomys frontanyensis* i *Nievesia sossissensis*, són els descrits al capítol 8 d'aquesta tesi doctoral. En el cas dels omomioïdeus *P. cuestai* i *P. pyrenaicus,* les mesures es van fer seguint les indicacions de Godinot (2003) per a totes les dents exceptuant les canines superiors, de les que només es van mesurar la llargada i l'amplada màximes, agafades en angle recte.

En tots els casos, les mesures han estat preses a l’Institut Català de Paleontologia Miquel Crusafont, amb una lupa binocular “Nikon Measuroscope 10” connectada a un monitor “Nikon SC112”. Per mesurar les dents, es disposen amb la superfície oclusal perpendicular al pla visual.

4.6. Anàlisis filogenètics

Els anàlisis filogenètics que es presenten en diferents capítols de la tesi s’han fet utilitzant el programa PAUP* 4.0b10 (Swofford, 1998), amb la matriu proporcionada per Seiffert et al. (2010). En cada capítol es donen més detalls sobre cadascun dels anàlisis, així com de les modificacions fetes a la matriu original en cada cas.

4.7. Imatges del material estudiat

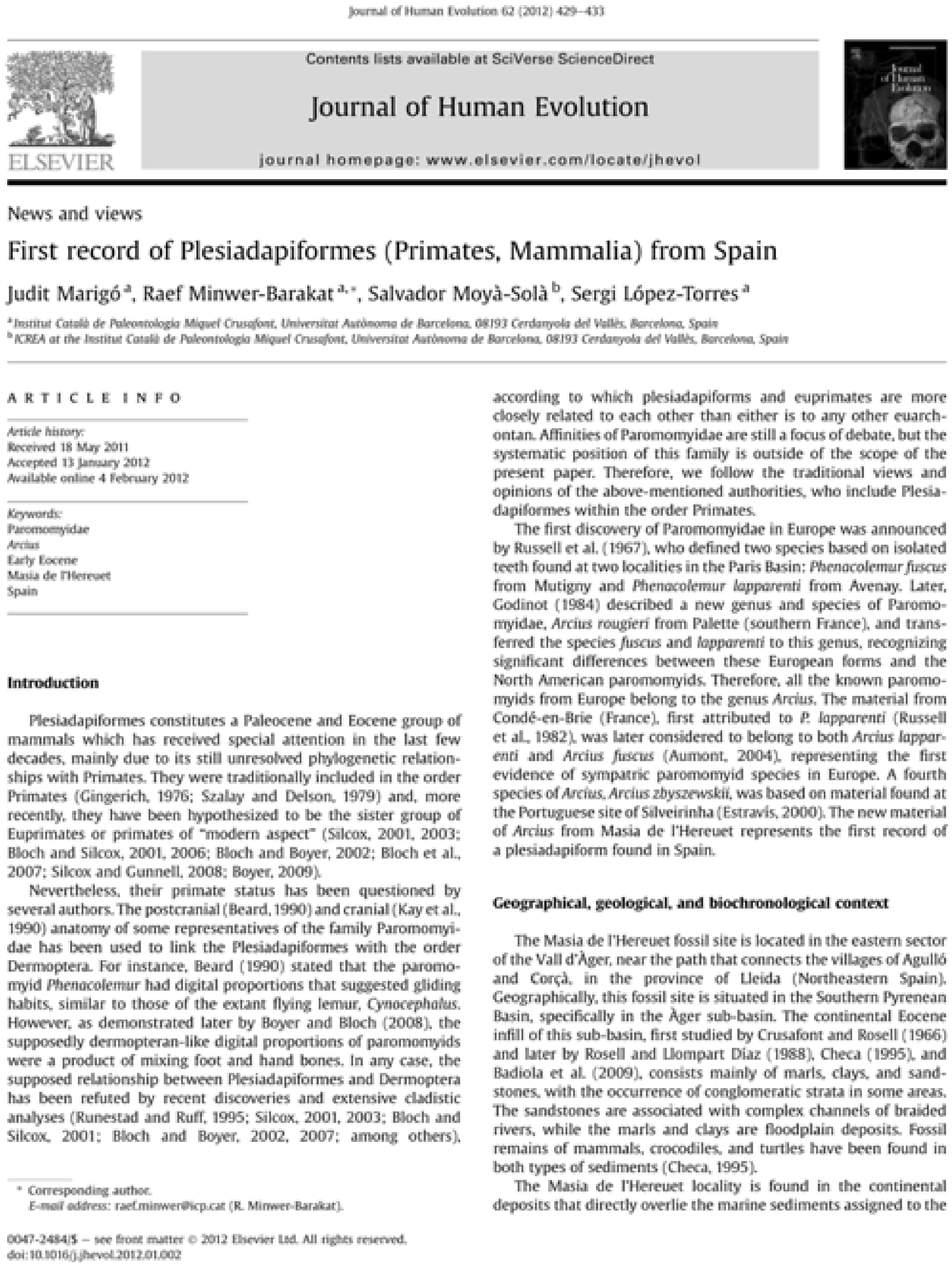
Les imatges de microscopi electrònic ambiental (ESEM) de les dents d’*Arcius* sp., *Anchomomys frontanyensis, Pseudoloris cuestai* i *Nievesia sossissensis* es van obtenir amb el microscopi Quanta 200 del Servei de Microscopia Electrònica de la Universitat de Barcelona (UB). En el cas de *Mazateronodon endemicus* i *Pseudoloris pyrenaicus*, es van realitzar amb el microscopi electrònic de rastreig (SEM) “Hitachi S-570” del Servei de Microscopia Electrònica de la Universitat Autònoma de Barcelona (UAB).

Les fotografies del material dentari s’han realitzat amb un estereomicroscopi “Leica MZ 16 A” connectat a un ordinador.

Els dibuixos del material dentari s’han fet amb una lupa binocular “Leica MZ 6” amb càmara clara.

5

FIRST RECORD OF PLESIADAPIFORMES (PRIMATES, MAMMALIA) FROM SPAIN



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News and views

First record of Plesiadapiformes (Primates, Mammalia) from Spain

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Introduction

Plesiadapiformes constitutes a Paleocene and Eocene group of mammals which has received special attention in the last few decades, mainly due to its still unresolved phylogenetic relationships with Primates. They were traditionally included in the order Primates (Gingerich, 1976; Szalay and Delson, 1979) and, more recently, they have been hypothesized to be the sister group of Euprimates or primates of "modern aspect" (Silcox, 2001, 2003; Bloch and Silcox, 2001, 2006; Bloch and Boyer, 2002; Bloch et al., 2007; Silcox and Gunnell, 2008; Boyer, 2009).

Nevertheless, their primate status has been questioned by several authors. The postcranial (Beard, 1990) and cranial (Kay et al., 1990) anatomy of some representatives of the family Paromomyidae has been used to link the Plesiadapiformes with the order Dermoptera. For instance, Beard (1990) stated that the paromomyid *Phenacolemur* had digital proportions that suggested gliding habits, similar to those of the extant flying lemur, *Cynocephalus*. However, as demonstrated later by Boyer and Bloch (2008), the supposedly dermopteran-like digital proportions of paromomyids were a product of mixing foot and hand bones. In any case, the supposed relationship between Plesiadapiformes and Dermoptera has been refuted by recent discoveries and extensive cladistic analyses (Runestad and Ruff, 1995; Silcox, 2001, 2003; Bloch and Silcox, 2001; Bloch and Boyer, 2002, 2007; among others), according to which plesiadapiforms and euprimates are more closely related to each other than either is to any other euarchontan. Affinities of Paromomyidae are still a focus of debate, but the systematic position of this family is outside of the scope of the present paper. Therefore, we follow the traditional views and opinions of the above-mentioned authorities, who include Plesiadapiformes within the order Primates.

The first discovery of Paromomyidae in Europe was announced by Russell et al. (1967), who defined two species based on isolated teeth found at two localities in the Paris Basin: *Phenacolemur fuscus* from Mutigny and *Phenacolemur lapparenti* from Avenay. Later, Godinot (1984) described a new genus and species of Paromomyidae, *Arcius rougieri* from Palette (southern France), and transferred the species *fuscus* and *lapparenti* to this genus, recognizing significant differences between these European forms and the North American paromomyids. Therefore, all the known paromomyids from Europe belong to the genus *Arcius*. The material from Condé-en-Brie (France), first attributed to *P. lapparenti* (Russell et al., 1982), was later considered to belong to both *Arcius lapparenti* and *Arcius fuscus* (Aumont, 2004), representing the first evidence of sympatric paromomyid species in Europe. A fourth species of *Arcius*, *Arcius zbyszewskii*, was based on material found at the Portuguese site of Silveirinha (Estravís, 2000). The new material of *Arcius* from Masia de l'Hereuet represents the first record of a plesiadapiform found in Spain.

Geographical, geological, and biochronological context

The Masia de l'Hereuet fossil site is located in the eastern sector of the Vall d'Àger, near the path that connects the villages of Agulló and Corçà, in the province of Lleida (Northeastern Spain). Geographically, this fossil site is situated in the Southern Pyrenean Basin, specifically in the Àger sub-basin. The continental Eocene infill of this sub-basin, first studied by Crusafont and Rosell (1966) and later by Rosell and Llompart Díaz (1988), Checa (1995), and Badiola et al. (2009), consists mainly of marls, clays, and sandstones, with the occurrence of conglomeratic strata in some areas. The sandstones are associated with complex channels of braided rivers, while the marls and clays are floodplain deposits. Fossil remains of mammals, crocodiles, and turtles have been found in both types of sediments (Checa, 1995).

The Masia de l'Hereuet locality is found in the continental deposits that directly overlie the marine sediments assigned to the

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Early Eocene. The site was assigned to the Grauvian (MP10) by Antunes et al. (1997) on the basis of its mammalian fauna. However, after revision of the artiodactyl, perissodactyl, and rodent assemblage, Badiola et al. (2009) concluded that this level is older than previously considered, corresponding to the Neustrian (MP8+9, 51–56 Ma), and represents the oldest continental locality of the Àger sub-basin. The updated faunal list of the Masia de l'Hereuet locality is shown in Table 1.

Material and methods

The sample studied consists of four isolated molars, identified as two left upper molars, corresponding to either M^1 or M^2, from now on referred to as M^{1-2} (IPS57508 and IPS57509), a right lower molar, corresponding to either M_1 or M_2, from now on referred to as M_{1-2} (IPS57510) and a right M_3 (IPS57511). One of the upper molars (IPS57509) has not been measured because of the poor preservation of its enamel. The material is curated at the Institut Català de Paleontologia Miquel Crusafont (Barcelona, Spain). The abbreviation "IPS" corresponds to "Institut de Paleontologia de Sabadell", the previous name of the Institut Català de Paleontologia Miquel Crusafont.

The nomenclature used in the descriptions of the teeth is that of Hooker (1986). Measurements have been taken as defined by Bloch and Gingerich (1998) using an optic caliper "Nikon measuroscope 10" connected to a monitor "Nikon SC112". Micrographs were taken using the Environmental Scanning Electron Microscope (ESEM) at the Universitat de Barcelona (UB).

Systematic paleontology

Order Primates Linnaeus, 1758.
Suborder Plesiadapiformes Simons, 1972.
Family Paromomyidae Simpson, 1940.
Genus *Arcius* Godinot, 1984.
Arcius sp.
Fig. 1

Description

M^{1-2} (IPS57508 and IPS57509): The two described specimens may correspond to either M^1 or M^2. The paracone is slightly higher than the metacone, and similar in height to the protocone. The postparacrista and the premetacrista are strong. The trigon and posterolingual basins are deep and well separated by the postprotocrista. The tooth is narrower posteriorly than anteriorly. The posterior margin of the tooth is almost straight. The preprotocrista connects the protocone to a small paraconule; in the better-preserved specimen (IPS57508) this crest appears interrupted because of breakage. From the paraconule, a postparaconule crista and a preparaconule crista run labially, reaching the paracone and the parastyle, respectively, and delimiting a small basin. The postprotocrista connects the protocone with a minuscule metaconule, which is linked to the metacone by a hypometacrista. The postprotocingulum starts at the protocone and surrounds the posterolingual end of the tooth, continuing in a postcingulum and closing the posterolingual basin. There is no hypocone. The labial cingulum is wide, especially at the anterolabial end of the tooth, where it thickens forming a distinct parastyle. There is a small protuberance on the labial border, constituting an incipient mesostyle. A metastyle is absent; there is, however, a strong postmetacrista, which joins the labial cingulum. The precingulum is short and well marked, occupying the anterolingual border of the tooth and delimiting a small basin on the anterior base of the protocone. There is another, very weak, cingulum on the labial portion of the anterior border, extending from the base of the paraconule to the parastyle. A poorly marked lingual cingulum can be also observed.

Table 1
Mammalian faunal list for Masia de l'Hereuet (after Antunes et al., 1997 and Badiola et al., 2009).

- PERISSODACTYLA
  - *Propachynolophus* sp.
  - *Lophiodon* sp.
- ARTIODACTYLA
  - *Diacodexis* sp.
- RODENTIA
  - *Eogliravus* n. sp.
  - *Pantrogna* n. sp.
  - Ischyromyidae indet. 1
  - Ischyromyidae indet. 2
  - Ischyromyidae indet. 3
- PRIMATES
  - *Arcius* sp.
- MARSUPIALIA
  - Marsupialia indet.
- LIPOTYPHLA
  - Lipotyphla indet.

M_{1-2} (IPS57510): the trigonid and the talonid are similar in width. The anterior border is slightly concave. The metaconid is somewhat higher than the protoconid and bears a short and poorly differentiated premetacristid. The paracristid is strong; it descends from the protoconid, thickens forming a small bulge that protrudes on the anterolabial corner of the tooth, and continues occupying the entire anterior border. The paracristid rises at its lingual end, but there is not a distinct paraconid. The cristid obliqua ends relatively low on the trigonid wall and in a labial position, at the posterolingual base of the protoconid. The hypoconid and entoconid are hardly distinguishable and notably lower than the protoconid. The hypoconulid, poorly differentiated, appears located in a very labial position, near the hypoconid.

M_3 (IPS57511): The trigonid is notably higher than the talonid. The metaconid is higher than the protoconid and situated in a slightly more posterior position. There is a marked premetacristid. A sharp paracristid occupies the anterior border of the tooth, but a paraconid is absent. The cristid obliqua is located more labially than on the M_{1-2}. The entoconid and the hypoconid, better individualized than in the M_{1-2}, are approximately the same size. The hypoconulid lobe is very broad.

Measurements

See Table 2

Comparisons and discussion

The molars from Masia de l'Hereuet are notably larger than those of the type species of the genus, *A. rougieri* (Table 2). Morphologically, the main difference is the presence in the lower molars of *A. rougieri* of a clearly distinct paraconid (Godinot, 1984), while this cusp is absent in the teeth from Masia de l'Hereuet. Moreover, the hypoconid and entoconid are more clearly differentiated in the M_1 and M_2 of *A. rougieri* than in the specimen from Masia de l'Hereuet. The poorly differentiated hypoconulid is placed in a more labial position on the tooth from Masia de l'Hereuet than on the molars from Palette. Regarding the upper molars, the M^{1-2} from Masia de l'Hereuet differ from those of *A. rougieri* in the stronger labial cingulum and the presence of a well differentiated parastyle.

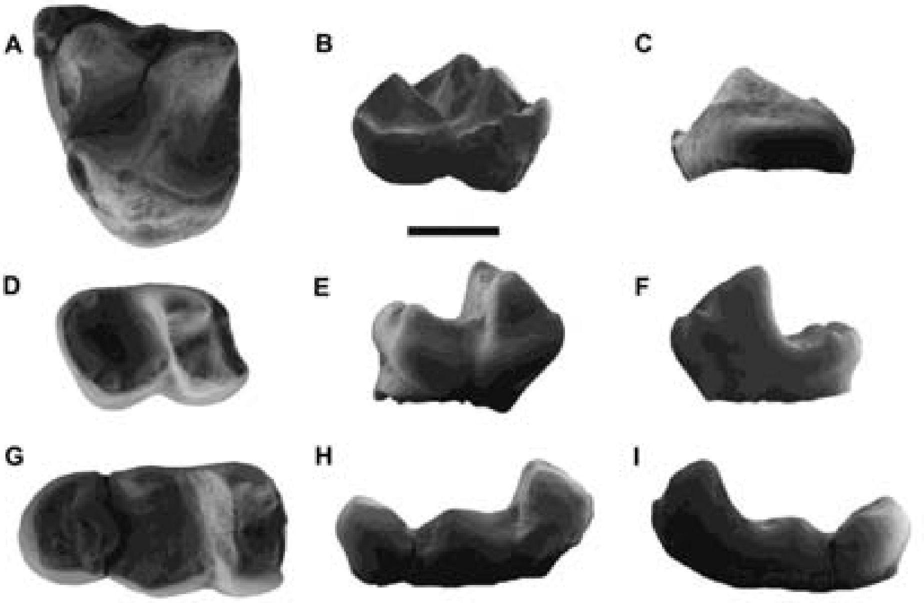

Figure 1. ESEM images of the teeth of *Arcius* sp. from Masia de l'Hereuet. (A–C) Left M^{1-2} (IPS57508) in occlusal (A), labial (B) and lingual (C) views; (D–F) Right M_{1-2} (IPS57510) in occlusal (D), labial (E) and lingual (F) views; (G–I) Right M_3 (IPS57511) in occlusal (G), labial (H) and lingual (I) views. Scale represents 1 mm.

The M_{1-2} of *Arcius* sp. from Masia de l'Hereuet falls within the size range of *A. fuscus* from its type locality, Mutigny (Russell et al., 1967); the M^{1-2} is longer but similar in width to those of *A. fuscus*, and the M_3 is clearly larger. The size of the lower molars from Masia de l'Hereuet clearly exceeds that of the rare specimens of *A. fuscus* from Condé-en-Brie (Aumont, 2004); data on the upper molars from this locality are not available. With regard to their morphology, the M_1's and M_2's of *A. fuscus* from Mutigny differ from the specimen from Masia de l'Hereuet in the presence of labial and posterior cingulids and in the existence of a distinct paraconid (this cusp is absent in only one out of eight specimens from Mutigny). However, some of the M_1's and M_2's of *A. fuscus* from Condé-en-Brie also lack the paraconid (Aumont, 2004), as is the case in the specimen from Masia de l'Hereuet. The metaconid is more posterior with respect to the protoconid in the molar from Masia de l'Hereuet than in those of *A. fuscus* from Mutigny. The M_3 from Mutigny is very similar in morphology to the tooth from Masia de l'Hereuet; in contrast, the single figured M_3 of *A. fuscus* from Condé-en-Brie (Aumont, 2004) has a narrower and better differentiated hypoconulid lobe. The upper molars of *A. fuscus* have a nearly rectangular outline, with approximately the same width along the anterior and posterior borders; in contrast, specimens from Masia de l'Hereuet are clearly broader anteriorly, and bear a distinct parastyle. The M^1's and M^2's of *A. fuscus* from Condé-en-Brie lack the precingulum that is present in the specimens from Mutigny and Masia de l'Hereuet.

The dimensions of the teeth from Masia de l'Hereuet resemble the minimum values of the rare specimens of *A. lapparenti* from its type locality, Avenay (Russell et al., 1967), with the widths of the M_{1-2} and M^{1-2} from Masia de l'Hereuet being smaller. The M_3 is similar in size to the specimens of *A. lapparenti* from Condé-en-Brie (Aumont, 2004), but the M_{1-2} from Masia de l'Hereuet is smaller than similar teeth from Condé-en-Brie. As is the case in *A. fuscus* from the same locality, comparison of the sizes of the upper molars is not possible due to the absence of data. Morphologically, the M_{1-2} of *Arcius* sp. differs from those of *A. lapparenti* in the absence of a distinct paraconid and in the less accentuated difference in width between the trigonid and the talonid. Moreover, the entoconid of the M_3 is less prominent lingually in the specimen from Masia de l'Hereuet than in those from Avenay and Condé-en-Brie;

Table 2
Measurements (in mm) of the molars of *Arcius* sp. from Masia de l'Hereuet and all the known species of the genus *Arcius*. Data for *A. rougieri* from Palette from Godinot (1984); data for *A. fuscus* from Mutigny and *A. lapparenti* from Avenay from Russell et al. (1967); data for *A. zbyszewskii* from Silveirinha from Estravis (2000).

		Arcius sp. Masia de l'Hereuet		*Arcius rougieri*		*Arcius fuscus*		*Arcius lapparenti*		*Arcius zbyszewskii*	
		N	Range	N	Range	N	Range	N	Range	N	Range
M^1 and M^2	Length	1	2.44	2	1.7–1.9	13	1.7–2.3	5	2.2–2.5	1	1.62
	Width	1	2.67	2	2.3	13	2.4–2.9	5	2.8–3.3	1	1.17
M_1 and M_2	Length	1	2.16	2	1.9–2.0	8	1.9–2.4	3	2.0–2.7	3	1.67
	Width	1	1.56	2	1.4–1.5	8	1.5–1.8	3	1.6–2.3	3	1.29–1.42
M_3	Length	1	2.99			2	2.5–2.7	3	2.7–3.6	1	2.33
	Width	1	1.58			2	1.3–1.5	3	1.4–1.8	1	1.25

the figured M_3 from this latter site also has a narrower hypoconulid lobe. Upper molars from Avenay differ from the specimens from Masia de l'Hereuet in the weaker or even absent labial cingulum. One of the upper molars from Avenay lacks the crests connecting the paracone and metacone to the protocone but, as stated by Russell et al. (1967), this tooth is probably an aberrant specimen or a representative of a different form.

Finally, *A. zbyszewskii*, the smallest species of the genus, from the Portuguese locality of Silveirinha (Estravís, 2000), is markedly smaller than *Arcius* sp. from Masia de l'Hereuet. In addition to the notable difference in size, the lower molars of *A. zbyszewskii* differ from those of *Arcius* sp. in the presence of a short but distinct labial cingulid, restricted to the base of the protoconid, and in the existence of a paraconid, which is very small on the M_{1-2} and well developed on the M_3. The hypoconulid lobe of M_3 is narrower in *A. zbyszewskii* than in the specimen from Masia de l'Hereuet. The two M^{1-2} of *A. zbyszewskii* differ from those of *Arcius* sp. in the absence of a metaconule. In addition, the incomplete specimen of *A. zbyszewskii* has a strong cingulum along the lingual border that is absent on the upper molars from Masia de l'Hereuet. The complete tooth from Silveirinha can be distinguished from those of *Arcius* sp. by the less prominent anterolabial corner, without a distinct parastyle, by the presence of a poorly defined crest that descends lingually from the protocone, and by the concavity on the lingual side of the protocone.

In summary, the new material resembles in overall morphology the teeth of the different described species of the genus *Arcius*, allowing a clear assignment to this genus. The size is notably larger than that of *A. rougieri* and *A. zbyszewskii*, somewhat larger or similar to the maximum values of *A. fuscus*, and slightly smaller or similar to the minimum values of *A. lapparenti*. Morphologically, the main differences from *A. lapparenti* are the better developed labial cingulum on the M^{1-2} and the absence of a paraconid on the M_{1-2} of *Arcius* sp. from Masia de l'Hereuet. With respect to *A. fuscus*, the M^1's and M^2's of this species differ from the specimen from Masia de l'Hereuet in their rectangular occlusal outline and in the absence of a distinct parastyle, and the M_1's and M_2's of *A. fuscus* can be distinguished by the presence of cingulids and, in some specimens, of a distinct paraconid.

Therefore, because of the scarcity of material, it is preferable not to make a specific reference within the genus *Arcius* at this time. Further studies leading to the recovery of more abundant collections will help to clarify the position of the paromomyid from Masia de l'Hereuet.

Conclusions

The described material from Masia de l'Hereuet, assigned to the genus *Arcius*, represents the first record of a plesiadapiform from Spain. *Arcius* sp. clearly differs from the species *A. rougieri* and *A. zbyszewskii* in size and morphology. The dimensions of the new molars are intermediate between those of *A. fuscus* and *A. lapparenti*, found at several French localities of MP8+9 age (Mutigny, Avenay, Condé-en-Brie); however, the specimens from Masia de l'Hereuet show several differences from the teeth of these species.

The paucity of the material of all the known species of *Arcius* prevents assessment of intraspecific variability in size and morphology. For this reason, the material recovered from Masia de l'Hereuet, which consists of very few teeth and does not include diagnostic dental elements such as the P_4 or the upper incisors, cannot be assigned to a species at this time. Regardless, this discovery and more extensive sampling of this fossil site, will undoubtedly help us to understand the geographic and temporal distribution, and the phylogeny, of this group of mammals that are particularly uncommon in the European record.

Acknowledgements

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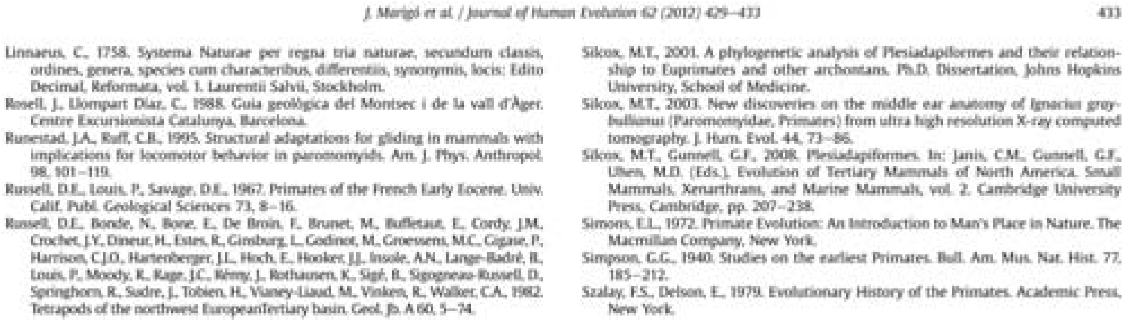

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6

NEW *ANCHOMOMYS* (ADAPOIDEA, PRIMATES) FROM THE ROBIACIAN (MIDDLE EOCENE) OF NORTHEASTERN SPAIN. TAXONOMIC AND EVOLUTIONARY IMPLICATIONS

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News and views

New *Anchomomys* (Adapoidea, Primates) from the Robiacian (Middle Eocene) of northeastern Spain. Taxonomic and evolutionary implications

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Introduction

The genus *Anchomomys* was defined by Stehlin (1916) to describe the type species *Anchomomys gaillardi* from Lissieu (France). Subsequently, Eocene fossil sites have produced many species found at several French and Swiss sites (Table 1). Historically, the ascription of several species to the genus *Anchomomys* has been controversial (Schwartz and Tattersall, 1983; Godinot, 1998, 2006). Here, we present the largest collection of *Anchomomys* ever recovered (more than 200 items), and conduct a preliminary phylogenetic analysis of these materials. These new materials permit description, for the first time, of nearly all the dental elements of this taxon. The new species represented by the materials derives from the Eastern Pyrenean Middle Eocene locality of Sant Jaume de Frontanyà (Moyà-Solà and Köhler, 1993).

The locality of Sant Jaume de Frontanyà (SJF) is included in the Bellmunt Formation (Eastern Pyrenees, Spain), and consists of about 1500 m of middle Eocene continental sediments. These deposits are mainly grey marls with high organic material content, and thin intercalations of coal layers with abundant remains of fossil plants and vertebrates, typical of palustrine environments (Moyà-Solà and Köhler, 1993). Samples from this locality were taken from two different levels called SJF-3C (the richest one) and SJF-3D (approximately 50 cm above SJF-3C). Sant Jaume de Frontanyà-3 has been attributed to the Robiacian (MP14-15) based on the presence of *Elfomys* nov. sp. (also from Laprade [Sudre et al., 1990; Quer and Agustí, 2010]) and the similarity of *Anchomomys* nov. sp. to *Anchomomys pygmaeus* from Egerkingen (Moyà-Solà and Köhler, 1993). Paleobotanical materials reveal a tropical or subtropical paleoenvironment (Busquets et al., 1992).

Morphological similarities between the studied faunas of the two levels C and D, suggest roughly contemporaneous deposits (Minwer-Barakat et al., 2010). The primate fauna of these two levels includes three different taxa: *Adapis* sp. (Moyà-Solà and Köhler, 1993), *Pseudoloris pyrenaicus*, recently defined by Minwer-Barakat et al. (2010), and *Anchomomys frontanyensis* nov. sp., which is the most abundant (Moyà-Solà and Köhler, 1993).

Systematic paleontology

Order Primates Linnaeus, 1758
Suborder Euprimates Linnaeus, 1758
Infraorder Strepsirrhini Geoffroy Saint-Hilaire, 1812
Superfamily Adapoidea Trouessart, 1879
Family Notharctidae Trouessart, 1879
Subfamily Cercamoniinae Gingerich, 1975
Tribe Anchomomyini Szalay and Delson, 1979 (*sensu* Godinot, 1988a)
Genus *Anchomomys* Stehlin, 1916
A. frontanyensis nov. sp.; Figs. 1–3.

Holotype

Specimen IPS8429 (isolated M^{1-2}), from Sant Jaume de Frontanyà-3C, stored at the Institut Català de Paleontologia, Barcelona.

Hypodigm

A total of 132 teeth from SJF-3C and 103 from SJF-3D (for catalog numbers see SOM).

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Table 1
Available *Anchomomys* material from different European fossil sites (data from Rütimeyer, 1890; Stehlin, 1916; Szalay, 1974; Crochet et al., 1981; Godinot, 1983, 1988a,b). The exact age for the fossil sites of Aumelas and St-Martin-de-Londres has not yet been fully established (Godinot, 1988a; Biochrom, 1997).

Level	MP	Fossil site	Available material	Species
Fons 4	17a	Aubrelong 2	?	*A. quercyi*
		La Bouffie	M_1	
		Fons 1	M_{1-2}	
		Quercy (level indet)	Maxilla fragment with P^4-M^2 and alveolus for C-P^3 and M^3	
Robiac	16	Le Bretou	Mandible fragment with P_3-M_2, mandible fragment with M_1-M_2 and M^{1-2}	*A.* cf. *quercyi*
Egerkingen α + β	14-15	Sant Jaume de Frontanyà-3	See Systematic paleontology section	*Anchomomys* sp. nov.
	14	Lissieu	Mandible fragment with M_1-M_3 and maxillar fragment with M^1-M^3	*A. gaillardi*
Geiseltal-Obere Mittelkohle (oMK)	13	Aumelas	M^{1-2}	*A.* cf. *gaillardi*
		Bouxwiller	M_{1-2}	
		Egerkingen γ	1 mandible fragment with P_4-M_3, 1 mandible fragment with M_1-M_2 and 1 isolated M_3	*A.* cf. *pygmaeus*
		Egerkingen Huppersand	$2M^{1-2}$	*A. pygmaeus*
		St-Martin-de-Londres	$2M^{1-2}$, DP_4, M_1 and one mandible fragment with P_3, DP_3, DP_4	*A. crocheti*

Locality and horizon

Sant Jaume de Frontanyà (Catalonia, northeastern Spain). Bellmunt Formation, Robiacian (MP14-15), including the levels SJF-3C and SJF-3D.

Specific diagnosis

Medium-sized *Anchomomys*, larger than *A. gaillardi* and smaller than *A. pygmaeus*, closer to the latter in overall morphology. However, it can be distinguished from other *Anchomomys* species due to its small hypocone, the reduced paraconule and anterocingulum in the upper molars, the M_3 smaller than the M_2, the very high and pointed metaconid in the lower molars, and in the additional talonid cuspules in many M_3 specimens.

Etymology

From the Sant Jaume de Frontanyà fossil site.

Descriptions of maxillary teeth

Only two upper canine specimens were recovered, and show moderate wear. They have buccolingually compressed crowns and single roots. The crown outline is oval, elongated, and curved distally and lingually to the very pointed apex. The buccal cingulum is well developed and closer to the apex on the mesial side than on the distal side. There is no lingual cingulum present.

The P^1 is the smallest of all teeth. It has a circular outline and a sharp paracone occupying most of the tooth. Both buccal and lingual cingula thicken on the mesial and distal parts of the tooth forming two enamel bulges (the lingual cingulum is the more prominent). The tooth is single rooted and the root is mesiodistally compressed.

The P^2 has a subtriangular outline, and the paracone occupies most of the tooth. The apex points distally, and buccal and lingual cingula surround the whole tooth, thickening mesially, and especially, distally. The two roots are sometimes fused, and the distal one is the largest.

The subtriangular P^3 presents a sharp paracone occupying most of the tooth. The preparacrista and the postparacrista are both short. Buccal and lingual cingula surround the tooth, thickening at the bases of the preparacrista and the postparacrista. This tooth has mesiobuccal, distobuccal and lingual roots.

The P^4 has a prominent paracone that is centered on the buccal side, while the anterocingulum runs mesially, thickening to form a small parastyle on the buccal side. The postcingulum runs all over the distal part of the tooth, with an incipient metastyle on the buccal side. The tooth lacks a paraconule, metaconule, and hypocone. The protocone is moderately large, centered in the narrow and elongated protocone lobe. The preprotocrista is not accompanied by postprotocrista. These teeth present three roots, two on the buccal side, where one sits more mesially and another sits distally, and another one on the lingual side, under the protocone lobe.

Of the molars, M^{1-2} is tribosphenic, and has a paracone that exceeds the metacone in size and height. The protocone is the broadest of the three main cusps, and is the second highest of the cusps. Both metastyle and parastyle are weak, and there is no mesostyle. A small paraconule is present (an incipient metaconule sometimes occurs). The trigon basin is broad. The anterocingulum runs from the base of the protocone to reach the preparaconule crista. There is no pericone, and the hypocone is small. The postcingulum is more prominent than the anterocingulum, from the hypocone base to the base of the metastyle. Some specimens present a broader, more quadrate, lingual side and a more developed anterocingulum. All upper molars have three roots.

The subtriangular M^3 has a paracone that is the most prominent cusp of the trigon, and then followed by the protocone in size. The metacone is small, and the tooth lacks a metaconule, but an incipient paraconule may be present. The anterocingulum connects the lingual base of the protocone with the buccal base of the incipient paraconule, and is smaller than the postcingulum, which is well developed and extends from the lingual base of the protocone to the base of the metacone. The trigon basin is broad, and a postparaconule crista is variably present. Sometimes an incipient parastyle occurs, although no metastyle and no hypocone are present.

Descriptions of mandibular teeth

Lower canine specimens present a circular outline, somewhat buccolingually compressed. The extremes of the root and the crown curve distally. The crown is high, with both buccal and lingual cingulids, the former being higher, and the latter reaching its lowest at the distolingual part of the tooth. In some specimens, a wear facet occupies the distolingual side of the tooth (see arrow in Fig. 2A), and may reflect honing with the upper canine (see Rosenberger et al., 1985).

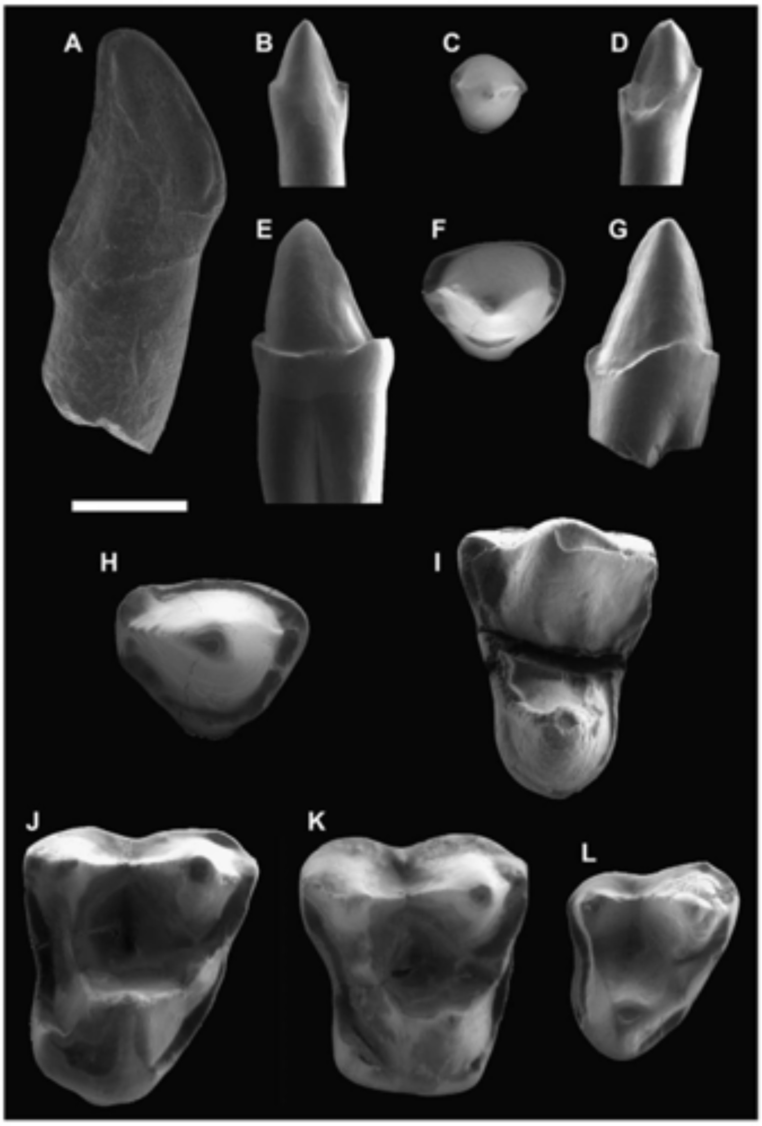

Figure 1. Micrographs of the upper dentition of *Anchomomys frontanyensis*. (A) Right upper canine in lingual view (IPS47951); (B) right P^1 in buccal view (IPS8614); (C) left P^1 in occlusal view (IPS8445); (D) right P_1 in lingual view (IPS47950); (E) right P^2 in buccal view (IPS8443); (F) right P^2 in occlusal view (IPS8441); (G) right P^2 in lingual view (IPS8624); (H) right P^3 in occlusal view (IPS8438); (I) left P^4 in occlusal view (IPS8439); (J) right M^{1-2} in occlusal view (IPS8429); (K) left M^{1-2} in occlusal view (IPS8433), reversed for comparison; (L) right M^3 in occlusal view (IPS8423). Scale bar represents 1 mm.

Specimens of P_1 show buccolingual compression, with a sharp protoconid, single root, and both buccal and lingual cingulids, the latter being higher and more prominent. At the mesiolingual part of the tooth, the cingulid thickens forming an incipient paraconid, and another enamel bulge at the distobuccal part suggests an incipient hypoconid. The tiny talonid basin opens lingually.

The P_2 is shaped similarly to the P_1, although larger. P_2 differs from P_1 in having no enamel bulge at the distobuccal part of the tooth and in having a broader talonid basin. The two roots are fused in some specimens.

Like P_1, P_3 is buccolingually compressed, with a large protoconid occupying the center of the tooth, with a pointy apex. A short paracristid occurs on the mesial part of the tooth, but no paraconid. Distally, the tooth has a cristid obliqua. A small talonid basin, although broader than that of the P_2, opens lingually. Lingual and buccal cingulids are present (the lingual is higher). This tooth is located obliquely in the mandible (see Fig. 3), and presents two roots.

The P_4 is very similar to the P_3 in buccolingual compression and overall shape, although larger. Mesially it shows a small paraconid

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Figure 2. Micrographs of the lower dentition of *Anchomomys frontanyensis*. (A) Left lower canine in distolingual view (IPS8526), arrow indicates contact facet; (B) left lower canine in distal view (IPS8518); (C) left P_1 in lingual view (IPS47945); (D) left P_2 in buccal view (IPS8515); (E) right P_3 in lingual view (IPS8499); (F) left P_1 in occlusal view (IPS8619); (G) left P_2 in occlusal view (IPS47949); (H) left P_3 in occlusal view (IPS8490); (I) left M_1 in lingual view (IPS8613); (J) right P_4 in lingual view (IPS8524); (K) right P_4 in occlusal view (IPS8523); (L) left M_1 in occlusal view (IPS8543); (M) left M_2 in occlusal view (IPS8487); (N) left M_3 in occlusal view (IPS8452); (O) right M_3 in occlusal view (IPS8447); (P) left M_1 in buccal view (IPS8463); (Q) right M_2 in buccal view (IPS8617); (R) tight M_3 in buccal view (IPS8506); (S) right M_3 in buccal view (IPS8449). Images D, F, O, Q, R and S have been reversed for comparison. Scale bar represents 1 mm.

Figure 3. *Fragment of the left mandible of Anchomomys frontanyensis from SJF-3C with incomplete P_3-P_4 and alveoli of M_1-M_2 (IPS8489). Scale bar represents 5 mm.*

and a short paracristid. The protoconid, at the center of the tooth, is large and pointed. The tooth lacks a metaconid. Distally, it has a short cristid obliqua and a small hypoconid. The talonid basin opens lingually and is broader than on the P_3. Buccal and lingual cingulids occur, the latter being highest. The tooth has two roots.

Among molars, M_1 is more buccolingually compressed than the M_2, with a better-developed paracristid and a small paraconid. High protoconid and metaconid present, with the metaconid located distally with respect to the protoconid. Premetacristid and protocristid are also present, as well as a well-developed buccal cingulid and a broad talonid basin. The cristid obliqua extends to the lingual portion of the base of the protoconid in some specimens, and in some others it extends to the buccal portion of the base of the metaconid. The entoconid and the hypoconid are similarly developed, although the entoconid is more distally placed. A very small hypoconulid is directed buccally, closer to the hypoconid than to the entoconid. All lower molars are double-rooted.

Compared to the M_1, the M_2 specimens are less buccolingually compressed, lacking a paraconid. A paracristid extends anteriorly from the protoconid to the metaconid. The hypoconulid is less buccally placed and the talonid basin is broader than in the M_1. Moreover, the metaconid is located more mesially with respect to the protoconid, and the cristid obliqua reaches the lowest point between the protoconid and the metaconid.

Finally, the M_3 is the smallest of the lower molars in both length and width, but both the cristid obliqua and trigonid resemble those of the M_2. However, the metaconid is less distally placed from the protoconid, and both are sometimes aligned buccolingually. This alignment of the two trigonid cuspids is also accompanied by a mesiodistal compression of the whole tooth. This tooth shows high intraspecific variability with half of the specimens showing a mesiodistally elongated hypoconulid lobe placed on the mesiodistal axis of the tooth, while in the other specimens the lobe is protruding less distally. The talonid basin is more buccolingually compressed than that of the M_2. Some specimens present some extra talonid cuspules or protuberances (see Fig. 2N, O, R). The two roots are very close to each other, almost in contact, although not fused.

Measurements

See Table 2.

Comparisons

Regarding size of the upper molars, the M^{1-2} of *A. frontanyensis* is very close to *Anchomomys quercyi* and *Anchomomys cf. gaillardi* from Aumelas (see SOM). It is larger than *A. gaillardi* and *A.* cf. *quercyi* from Le Bretou, and smaller than *A. pygmaeus* and *A. crocheti*. The M^3 is only known for *A. frontanyensis* and *A. gaillardi*, and no upper dentition is known for *A.* cf. *pygmaeus* from Egerkingen γ. Considering the lower molars, the M_1 of *A. frontanyensis* is close in size to *A.* cf. *pygmaeus* and the M_2 of *A. frontanyensis* is close to *A.* cf. *quercyi*. Lower molars of *A. frontanyensis* are larger than those attributed to *A. gaillardi*. M_1 of *A. frontanyensis* are usually shorter (only one specimen almost equal to *A. quercyi* from La Bouffie). However, the only *A. quercyi* M_{1-2} from Fons 1 is much larger than those of *A. frontanyensis*. M_3 are only known for *A. frontanyensis* and *A. gaillardi*, and no lower dentition is known for *A. pygmaeus*.

Table 2
Measurements (in mm) of *Anchomomys frontanyensis* nov. sp. from Sant Jaume de Frontanyà-3C and 3D. Only those specimens perfectly preserved have been measured. Criteria used for tooth measurements are those described in Marigó et al. (2010).

Tooth	Locality	Length				Width			
		N	Min.	Mean	Max.	*N*	Min.	Mean	Max.
C	SJF-3C	1		1.61		1		1.34	
P_1	SJF-3D	3	0.79	0.87	0.94	3	0.67	0.68	0.70
	SJF-3C	1		1.03		1		0.77	
P_2	SJF-3D	4	1.23	1.37	1.48	4	0.85	0.90	0.98
	SJF-3C	4	1.25	1.30	1.35	4	0.84	0.87	0.91
P_3	SJF-3D	5	1.81	1.97	2.06	5	1.15	1.19	1.23
	SJF-3C	2	1.86	1.95	2.04	4	1.07	1.17	1.23
P_4	SJF-3D	11	1.89	2.14	2.24	9	1.19	1.27	1.32
	SJF-3C	9	1.99	2.16	2.29	12	1.11	1.30	1.44
M_1	SJF-3D	4	2.14	2.27	2.40	4	1.30	1.33	1.34
	SJF-3C	10	2.08	2.26	2.40	9	1.23	1.32	1.38
M_2	SJF-3D	7	1.98	2.15	2.30	7	1.35	1.44	1.55
	SJF-3C	7	1.78	2.09	2.19	6	1.21	1.40	1.52
M_3	SJF-3D	5	1.94	1.99	2.07	4	1.19	1.24	1.31
	SJF-3C	4	1.63	1.81	2.07	5	1.17	1.26	1.34
P^1	SJF-3D	1		0.70		1		0.65	
	SJF-3C	2	0.68	0.69	0.69	2	0.66	0.66	0.66
P^2	SJF-3D	2	1.19	1.22	1.25	2	0.92	0.94	0.97
	SJF-3C	6	1.15	1.23	1.30	6	0.91	0.94	1.00
P^3	SJF-3D	2	1.82	1.84	1.86	2	1.38	1.53	1.67
	SJF-3C	3	1.72	1.80	1.92	1		1.32	
P^4	SJF-3D	3	1.87	1.91	1.96				
	SJF-3C	1		1.91					
M^{1-2}	SJF-3D	7	1.98	2.06	2.13	2	2.50	2.55	2.60
	SJF-3C	5	1.95	2.04	2.15	3	2.33	2.41	2.48
M^3	SJF-3D	1		1.84					
	SJF-3C	2	1.50	1.64	1.77	3	1.87	1.94	2.07

In overall morphology of the upper dentition, *A. frontanyensis* resembles more *A. pygmaeus* (Ef372) from Egerkingen Huppersand, although the former has a much reduced hypocone and paraconule, its upper molars have a larger lingually protruding paracone, and they do hot show the development of the anterocingulum of the latter.

When compared to *A.* cf. *pygmaeus* from Egerkingen γ, its P_4 is very similar to that of *A. frontanyensis*, even though lower molars of the latter are larger. Moreover, some P_4 of *A. frontanyensis* present a higher paraconid and hypoconid relative to protoconid height. M_{1-2} of *A. frontanyensis* are higher-crowned than those of *A.* cf. *pygmaeus*, with higher trigonid and paracristid for similar talonid height. *A. frontanyensis* has a larger buccal cingulid and a more buccally placed cristid obliqua. M_1 of *A. frontanyensis* have a more developed paraconid and a less distal metaconid with respect to the protoconid when compared to *A.* cf. *pygmaeus*, and M_2 of *A. frontanyensis* present a broader trigonid. The M_3 of *A. frontanyensis* differ from those of *A.* cf. *pygmaeus* because they present a shorter hypoconulid lobe that projects less distally, a more buccolingually aligned protoconid and metaconid, a more buccal cristid obliqua, and characteristic accessory talonid cuspules.

When compared to *A. gaillardi*, *A. frontanyensis* has a larger hypocone, narrower upper molars and shorter M^3, which is proportionally larger in *A. gaillardi* when compared to M^1 and M^2 of the same species. In addition, M^3 of *A. gaillardi* have a more developed paracone, protruding more mesially. Regarding the lower dentition, *A. frontanyensis* differs from *A. gaillardi* in having a distinct hypoconulid more lingually placed in M_1 and M_2, in the mesiodistally

reduced M_3 with a shorter talonid basin, and in the much more buccal cristid obliqua in the lower molars. Moreover, the M_3 of *A. frontanyensis* differ from those of *A. gaillardi* in the more mesiodistally compressed shape (some specimens even lacking the hypoconulid lobe), in the higher talonids, and in the presence of accessory cuspules in the talonid of some specimens.

The upper molars of *A.* cf. *gaillardi* from Aumelas show similar trigon proportions to *A. frontanyensis*, although they present a slightly larger hypocone, a less developed lingual cingulum and anterocingulum, and a paraconule located further buccally.

A comparison with *A. quercyi* shows that the single P^4 attributed to this species is longer than those of *A. frontanyensis*. Moreover, M_1 of *A. frontanyensis* are usually shorter (one specimen is equal to *A. quercyi* from La Bouffie). However, the only *A. quercyi* lower molar from Fons 1 is much larger than those of *A. frontanyensis*. Moreover, the entoconid of *A. quercyi* projects less distally than that of *A. frontanyensis*, and its paracristid is longer. In addition, the M_1 trigonid of *A. frontanyensis* is shorter and narrower than the La Bouffie *A. quercyi* specimen, and *A. frontanyensis* lower molars present a longer and much more developed buccal cingulid, extending from the buccal part of the paraconid to almost reaching the hypoconid, and in many specimens reappearing again at the distobuccal end of the tooth.

Relative to *A.* cf. *quercyi* from Le Bretou, a P_1 is confirmed for *A. frontanyensis* whereas no alveolus for this tooth is present in the mandible fragment of the former species. The P_2 of *A. frontanyensis* presents two roots, always fused, whereas *A.* cf. *quercyi* presents a single alveolus for this tooth. The P_3 of *A. frontanyensis* has two roots, variably fused, while the P_3 of *A.* cf. *quercyi* presents two individual roots. Moreover, the P_3 of *A.* cf. *quercyi* is longer and narrower with a larger distal part. The P_4 of *A.* cf. *quercyi* is very similar to that of *A. frontanyensis*, although lower molars of the latter are larger. Moreover, some P_4 of *A. frontanyensis* present a higher paraconid and hypoconid relative to protoconid height. Regarding the lower molars, M_1 of *A.* cf. *quercyi* are larger than the M_2, whereas in *A. frontanyensis* the M_1 is usually longer than the M_2. Moreover, the M_1 of *A. frontanyensis* has a more developed paraconid and the M_2 has a more lingual cristid obliqua than *A.* cf. *quercyi*. The M_1 and M_2 of *A. frontanyensis* also have a larger paracristid and buccal cingulid than *A.* cf. *quercyi*.

When compared to *A. crocheti*, *A. frontanyensis* has a much more reduced hypocone and paraconule, apart from not showing any trace of anterocingulum enlargement under the protocone. Moreover, the paracone of *A. crocheti* protrudes much more buccally than that of *A. frontanyensis*. The P_3 of *A. frontanyensis* is very similar in occlusal shape, although that of *A. crocheti* is a little shorter and relatively narrower. The M_1 of *A. crocheti* is wider than those of *A. frontanyensis*, presenting a broader talonid basin, and a buccal cingulid extending more distally. Moreover, the hypoconulid is more buccally placed in the M_1 of *A. frontanyensis*, and the cristid obliqua is a bit more lingual.

Among all the Anchomomyini, the genus *Anchomomys* resembles the recently described *Mazateronodon* (Marigó et al., 2010) more than any other member of the tribe. *A. frontanyensis* is much smaller and has sharper molar cusps than *Mazateronodon endemicus*, suggesting a more insectivorous diet. Moreover, *A. frontanyensis* presents a small but distinct paraconid in the M_1, a more mesial cristid obliqua in M_1 and M_2, a hypoconulid more mesially placed and a narrower talonid basin in the lower molars. The M^{1-2} of *A. frontanyensis* has a more developed paraconule and a less developed paracone. In addition, some specimens present an incipient metaconule.

M. endemicus lacks a P_1, and probably lacked P^1. P_2 of *M. endemicus* have not been preserved, although a mandibular alveolus in a mandible fragment indicates one root. In contrast, P_2 of *A. frontanyensis* always present two roots that are fused in some specimens. Crowns of lower canines of *M. endemicus* are subtriangular at the base and present buccolingually compressed roots, whereas those of *A. frontanyensis* are more oval and have buccolingually compressed crowns and roots. The upper canines present buccolingually compressed crowns with lingually curved tips in both species. However, the root of the upper canine is circular in *A. frontanyensis* but buccally compressed in *M. endemicus*. The only upper canine of *A. frontanyensis*, although worn, seems to lack the buccal cingulum and the cusp at the base of the mesiolingual groove that are present in *M. endemicus*.

Phylogenetic analyses

The rich assemblage of dental specimens from SJF-3, as well as the recently described Iberian Anchomomyin taxa (Marigó et al., 2010) allows preliminary tests of the phylogenetic relationships of the genus *Anchomomys* with the members of the Anchomomyini clade and other primates. On the basis of the matrix provided by Seiffert et al. (2010), two different phylogenetic hypotheses emerge based on analyses in *PAUP** 4.0b10 (Swofford, 1998). We utilize additional taxa such as *A. frontanyensis*, *M. endemicus*, *Periconodon huerzeleri* and *Buxella prisca* (for more information see SOM). In Hypothesis 1 Anchomomyini are more closely related to extant lemurs and lorises (Fig. 4A). In Hypothesis 2, Anchomomyini they are considered the sister-clade of *Asiadapis* and *Marcgodinotius* (Fig. 4B). Nevertheless, all the Anchomomyini are closely related in all the analyses, even though the relationships among the genera included in this tribe are different. We urge caution in interpreting these results, pending further analysis.

Discussion

The evolution of the genus *Anchomomys* in Europe was considered to correspond to a single lineage from *A. crocheti* to *A. quercyi*, with a first phase of reduction of the hypocone and the overall size between *A. crocheti* and *A. gaillardi*, and a second one, between *A. gaillardi* and *A. quercyi*, defined by a slight increase in upper molar size and a tendency towards more bunodont cusps (Godinot, 1988a). Godinot (1988a) also noticed the phyletic reduction of the transverse breadth of the upper molars through the whole lineage, while the lower dentition remained similar for the different species.

However, the fact that the Sant Jaume de Frontanyà-3 level in the Eastern Pyrenees (Catalonia, Spain) where *A. frontanyensis* was recovered has a similar age than the French locality of Lissieu (MP14), where the type species *A. gaillardi* was found, implies the existence of an independent lineage in the Iberian Peninsula and a more complex phylogenetic scenario than previously supposed (Godinot, 1988a).

The scarcity of fossil material probably accounts for the disagreements concerning the content and the phylogenetic relationships of the Anchomomyini. This tribe Anchomomyini included the genera *Anchomomys*, *Periconodon* and *Buxella* according to Godinot (1988a). However, a recent phylogenetic analysis places *Periconodon* as sister-taxon of *Pronycticebus* and does not support an Anchomomyini clade including the former taxon (Tabuce et al., 2009), although *Buxella* was not included in this analysis. Moreover, a recent analysis suggests that *Anchomomys* is the sister-taxon of the Adapidae (Rose et al., 2009), whereas other analyses suggest that *Anchomomys*, represented by its type species *A. gaillardi*, could be the sister-taxon of the Afro-arabian strepsirrhines (Seiffert et al., 2009; Tabuce et al., 2009).

Turning to phylogenetic analyses, our analyses suggest that Hypothesis 1 (Fig. 4A) is consistent with anchomomyins being closely related to extant Lemuroidea and Lorisoidea. However, the fact that

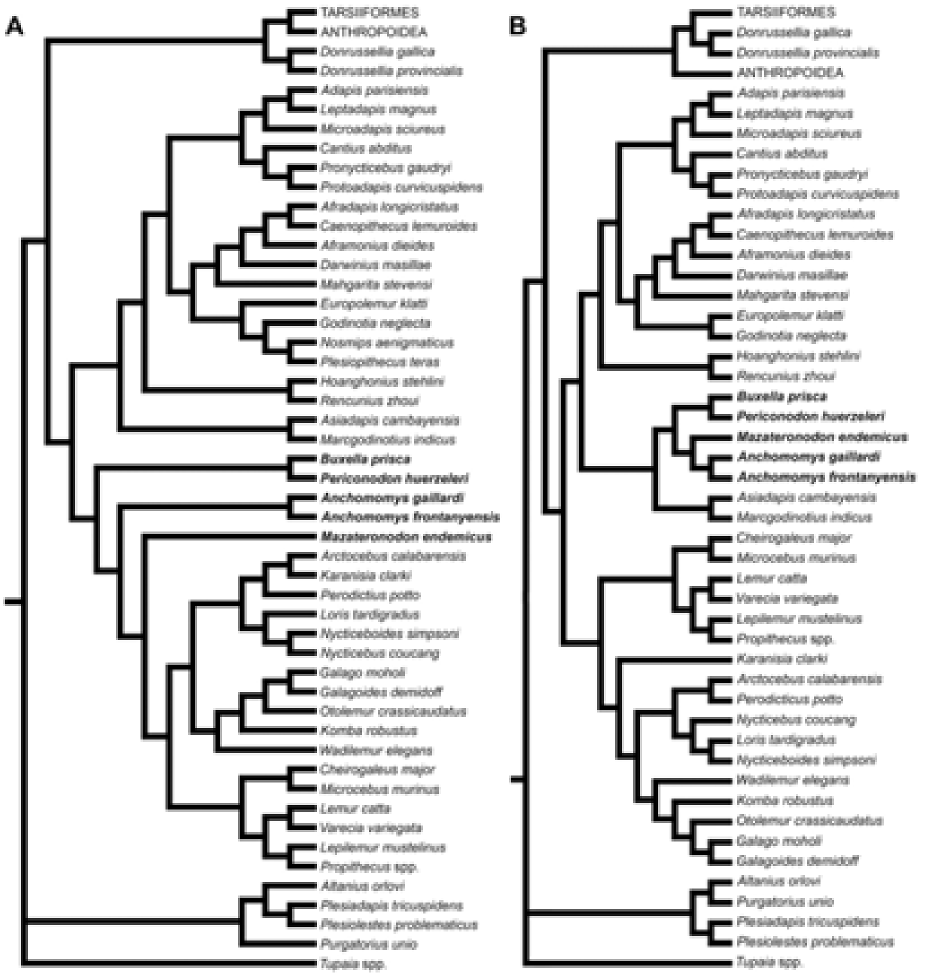

Figure 4. Phylogenetic analyses results. (A) Hypothesis 1: Simplified tree drawn from strict consensus following hypothesis 1 (premolar reacquisition not allowed), tree length: 2210.285, consistency index: 0.197, retention index: 0.577. (B) Hypothesis 2: Simplified tree drawn from strict consensus following hypothesis 2 (premolar reacquisition allowed), tree length: 2193.410, consistency index: 0.201, retention index: 0.563.

anchomomyin-like molar features appear much later in European taxa than in African taxa has made some authors argue in favor of convergence instead of the possibility of an Eocene faunal trans-Tethyan migration from Europe to Africa that may have allowed European anchomomyins to give rise to the Afro-Arabian strepsirrhine clade (Seiffert et al., 2005; Godinot, 2006). Hypothesis 2 (Fig. 4B) suggests that anchomomyins as more closely related to the Subfamily Asiadapinae (*Asiadapis* and *Marcgodinotius*). Terrestrial migrations and faunal exchanges from Asia to Europe would have been easier, even though in order for Hypothesis 2 to be plausible reacquisition of previously lost premolars needs to be allowed while performing the analysis. However, we must take into account that the reacquisition of premolars following an earlier loss is very unlikely to happen in primates (Seiffert et al., 2009). We must also take into account that some species included in the analyses are known only from isolated teeth, with few dental elements represented. The possibility of anchomomyins being more closely related to asiadapines, although it seems to be more plausible due to paleogeographical reasons, it is less probable because of reacquisition of previously lost premolars is not known in primates. On the other hand, the relationship between anchomomyins and extant lemurs and lorises seems the best option, even though no evidence of Eocene trans-Tethyan faunal interchanges have been found. Further research may provide more abundant samples that will reveal more information about the phylogeny of this group.

Conclusions

We present a new species of *Anchomomys* from the middle Eocene site of Sant Jaume de Frontanyà (SJF), representing the largest collection of *Anchomomys* ever described. The assemblage allows an initial full description of the dental morphology of this

genus. *A. frontanyensis* from SJF is similar to *A. pygmaeus* from Egerkingen γ (Ef 372) although it has a more reduced hypocone and paraconule, its hypocone is less projected lingually, and its upper molars have a less developed anterocingulum extending further lingually. *A. frontanyensis*, despite sharing different features with other taxa traditionally included in the tribe Anchomomyini (*Anchomomys*, *Periconodon*, *Buxella* and *Mazateronodon*), presents characters similar to those of extinct asiadapines and extant lemur and lorises. Our descriptions and analyses help clarify the *Anchomomys* phylogeny, revealing a new lineage in the Iberian Peninsula, and narrowing the possibilities regarding the relationships between the Anchomomyini and asiadapines or, alternatively, crown strepsirrhines. Phylogenetic analyses reveal at least two possibilities regarding anchomomyin relationships within primates, and neither can be discarded according to the scarce information available.

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Appendix. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jhevol.2010.12.006.

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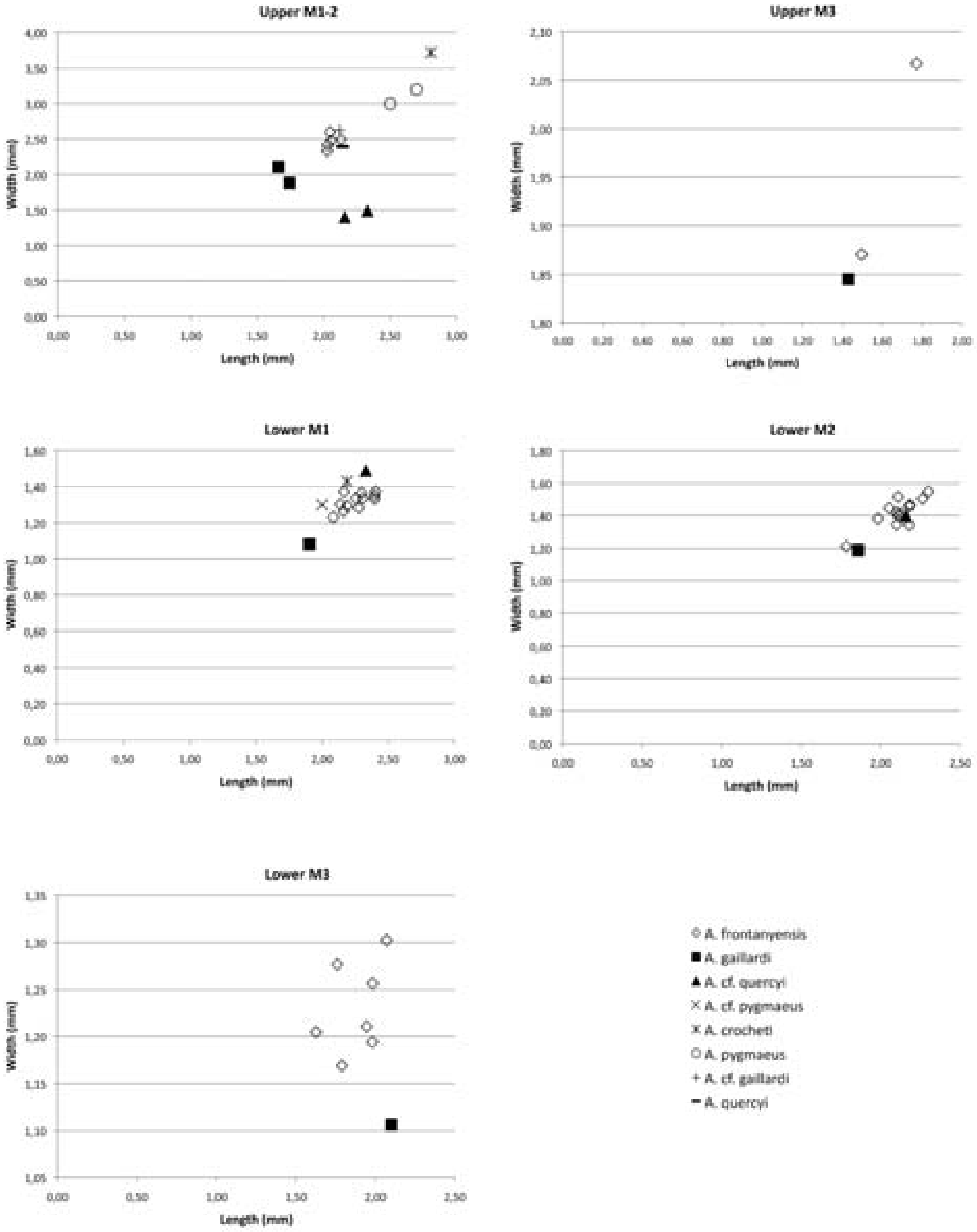
Supplementary online material (SOM) – Part I:



Supplementary figure. Boxplots of length and width for all upper and lower molars of all *Anchomomys* species. Measurements are in mm.

Supplementary online material (SOM) – Part II:

Hypodigm and catalog numbers

Material from SJF-3C:

Two incomplete lower canines (IPS8434, IPS55146), one complete P_1 (IPS8619), five complete P_2 (IPS8437, IPS8459, IPS8482, IPS8483, IPS8486), two complete P_3 (IPS8484, IPS8485), three incomplete P_3 (IPS8455, IPS55134, IPS55135), ten complete P_4 (IPS8469, IPS8470, IPS8473-IPS8475, IPS8477-IPS8481), three incomplete P_4 (IPS8471, IPS8476, IPS55133), two incomplete DP_4 (IPS8492, IPS8567), ten complete M_1 (IPS8431, IPS8454, IPS8458, IPS8463-IPS8466, IPS8613, IPS8616, IPS8623), one incomplete M_1 (IPS8468), two complete $M_{1\text{-}2}$ (IPS8440, IPS8622), ten incomplete $M_{1\text{-}2}$ (IPS8440, IPS8453, IPS8491, IPS8622, IPS47941, IPS47943, IPS55136, IPS55140, IPS55143, IPS55145), five complete M_2 (IPS8460-IPS8462, IPS8570, IPS8617), six incomplete M_2 (IPS8456, IPS8565, IPS8566, IPS8568, IPS8569, IPS55139), five complete M_3 (IPS8447, IPS8449, IPS8450, IPS8452, IPS47942), two incomplete M_3 (IPS8446, IPS8451), one series from M_1 to M_2 (IPS8487), one series from P_4 to M_1 (IPS8488), one series from P_3 to M_2 lacking M_1 (IPS8490), one mandible fragment with incomplete P_3-P_4 and alveoli for M_1-M_2 (IPS8489), one complete upper canine (IPS55142), two complete P^1 (IPS8445, IPS8614), six complete P^2 (IPS8436, IPS8441-IPS8444, IPS8624), two complete P^3 (IPS8438, IPS8626), two incomplete P^3 (IPS8548, IPS8618), one complete P^4 (IPS8439), three incomplete P^4 (IPS8435, IPS47944, IPS55141), one complete M^1 (IPS8428), two complete M^2 (IPS8433, IPS8494), thirty incomplete $M^{1\text{-}2}$ (IPS8426, IPS8430, IPS8432, IPS8472, IPS8545-IPS8547, IPS8549-IPS8552, IPS8554, IPS8557, IPS8558, IPS8560-IPS8564, IPS8615, IPS8621, IPS8627, IPS8633-IPS8637, IPS55137, IPS55138, IPS55144), three complete M^3 (IPS8423-IPS8425), two incomplete M^3 (IPS8427, IPS8620).

Material from SJF-3D:

Three incomplete lower canines (IPS8518, IPS8526, IPS8582), three complete P_1 (IPS8530, IPS47945, IPS47946), five complete P_2 (IPS8514-IPS8516, IPS8538, IPS47949), five complete P_3 (IPS8497, IPS8499, IPS8534, IPS8535, IPS8610), two incomplete P_3 (IPS8537, IPS8500), ten complete P_4 (IPS8495, IPS8496, IPS8498, IPS8522-IPS8525, IPS8604, IPS8609, IPS47955), three incomplete P_4 (IPS8583, IPS47868, IPS47872), three complete M_1 (IPS8543, IPS8601, IPS8611), six incomplete M_1 (IPS8501, IPS8502, IPS8588, IPS8591, IPS8592, IPS47874), five complete M_2 (IPS8504, IPS8505, IPS8513, IPS8521, IPS8532), eight incomplete M_2 (IPS8503, IPS8527, IPS8540, IPS8590, IPS8594, IPS8595, IPS8605, IPS47877), three incomplete $M_{1\text{-}2}$ (IPS8589, IPS8593, IPS8596), five complete M_3 (IPS8506, IPS8507, IPS8531, IPS8599, IPS8600), three incomplete M_3 (IPS8529, IPS8539, IPS47875), one complete upper canine (IPS47951), one complete P^1 (IPS47950), two complete P^2 (IPS8533, IPS8598), two complete P^3 (IPS8511, IPS8602), two incomplete P^3 (IPS8519, IPS8581), one incomplete $P^{3\text{-}4}$ (IPS8606), eight incomplete P^4 (IPS8528, IPS8541, IPS8577, IPS8584, IPS8585, IPS8587, IPS8607, IPS47869), one complete M^1 (IPS8520), one complete M^2 (IPS8508), seventeen incomplete $M^{1\text{-}2}$ (IPS8509, IPS8510, IPS8512, IPS8571-IPS8576, IPS8578, IPS8579, IPS8586, IPS8608, IPS47870, IPS47871, IPS47873, IPS47876), three incomplete M^3 (IPS8542, IPS8580, IPS47947).

Phylogenetic analyses

The character-taxon matrix in this study is a modified version of the matrix provided and published by Seiffert et al. (2010). We modified some of the character coding of *Anchomomys gaillardi* and added the taxa *Anchomomys frontanyensis*, *Mazateronodon endemicus*, *Periconodon huerzeleri* and *Buxella prisca*. The resulting matrix (361 morphological characters scored for each species, inclunding 100 living and extinct taxa) was analyzed under maximum parsimony using the heuristic search option in *PAUP** 4.0b10 (Swofford, 1998) with random addition sequence and the tree bisection and reconnection branch swapping algorithm across 5000 replicates, following two different hypotheses. For hypothesis 1, no premolar reacquisition was allowed, and some multistate characters were ordered and scaled so that any single change within a character could only contribute a maximum of one step to the tree length (Figure 5A). For hypothesis 2, some multistate characters were also ordered and scaled, but premolar reacquisition was allowed following an earlier loss (Figure 5B). Polymorphisms were scored as an intermediate character state in all cases. In both analyses, the monophyly of Malagasy lemurs and an *Arctocebus-Perodictius* clade was enforced, as supported by abundant DNA sequence and SINE data, following Seiffert et al. (2010), and specimen

NMMP20 was not assigned to *Poundaungia cotteri*. All tree lengths were recalculated after networks were re-rooted with *Tupaia* spp.

The character-coding for the modified and added taxa is as follows:

A. gaillardi	??????????	??????????	????????-2	0?????????	
	??????????	????????60	0-002246-4	24220-2032	
	24-600020-	1400021000	0?????????	??????????	
	??????????	??????????	?????02022	000-000000	
	0202040200	02022040??	?10???????	??????????	
	??????????	??????????	??????????	??????????	
	??????????	??????????	??????????	??????????	
	??????????	??????????	??????????	??????????	
	??????????	??????????	??????????	??????????	?
A. frontanyensis	??0???????	?????00???	01004400-2	0225810--2	
	000002?320	?00022A760	2000204634	24220-2022	
	243500060-	1400021000	0?????????	????4??0?0	
	1010000002	0101010000	0202?0?012	000-000000	
	02010?0200	12022010??	?0????????	??????????	
	??????????	??????????	??????????	??????????	
	??????????	??????????	??????????	??????????	
	??????????	??????????	??????????	??????????	
	??????????	??????????	??????????	??????????	?
B. prisca	??????????	??????????	?????400-2	022???????	
	??????????	????????64	23002?3244	24220-2012	
	233500020-	2200021000	0?????????	??????????	
	??????????	??????????	?????2?022	0100000000	
	02000?2101	02022330??	??????????	??????????	
	??????????	??????????	??????????	??????????	

	??????????	??????????	??????????	??????????	
	??????????	??????????	??????????	??????????	
	??????????	??????????	??????????	??????????	?
M. endemicus	??0???????	?????10???	22???400-2	1226810--2	
	000002?420	200022A???	0-022?2234	24220-2022	
	243400060-	1120121000	0?????????	????4??0?1	
	221??0?000	0200010000	0202?0?212	000-000000	
	02000?0200	02021010??	?1????????	??????????	
	??????????	??????????	??????????	??????????	
	??????????	??????????	??????????	??????????	
	??????????	??????????	??????????	??????????	
	??????????	??????????	??????????	??????????	?
P. huerzeleri	??????????	??????????	??????????	?????10--2	
	0001122420	???020A054	?3002?3234	24220-2022	
	244400020-	2410121000	0?????????	??????????	
	??????????	??????????	?????3?220	0101000000	
	02040?2002	110???????	?0????????	??????????	
	??????????	??????????	??????????	??????????	
	??????????	??????????	??????????	??????????	
	??????????	??????????	??????????	??????????	
	??????????	??????????	??????????	??????????	?

7

A NEW SPECIES OF *PSEUDOLORIS* (OMOMYIDAE, PRIMATES) FROM THE MIDDLE EOCENE OF SANT JAUME DE FRONTANYÀ (EASTERN PYRENEES, SPAIN)

AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 143:92–99 (2010)

A New Species of *Pseudoloris* (Omomyidae, Primates) from the Middle Eocene of Sant Jaume de Frontanyà (Eastern Pyrenees, Spain)

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KEY WORDS Microchoerinae; Robiacian; Iberian Peninsula

ABSTRACT In this article we describe a new species of *Pseudoloris* (Omomyidae, Primates) from the Robiacian (middle Eocene) locality of Sant Jaume de Frontanyà (Eastern Pyrenees, Spain). *Pseudoloris pyrenaicus* is characterized by its medium size, thickened paracristid, absence of a distinct paraconid, and well-developed buccal cingulid in the lower molars, large hypoconulid in the M_3, paraconule and hypocone reduced in the M^1 and M^2 and absent in the M^3. The material from Sant Jaume de Frontanyà constitutes the most abundant sample of the genus *Pseudoloris* found until now in the Iberian Peninsula. Almost all the dental elements have been recovered, including those teeth hardly known for other species of the genus, such as lower and upper incisors. The new species shows intermediate features between *Pseudoloris isabenae* from Capella and *Pseudoloris parvulus*, present in different Spanish and French sites. Therefore, we consider that *Pseudoloris pyrenaicus* is an intermediate form between these two species. Am J Phys Anthropol 143:92–99, 2010. ©2010 Wiley-Liss, Inc.

The family Omomyidae groups several species of small-bodied Primates, which were very abundant and diverse in the Northern Hemisphere during the Eocene, with only few exceptions surviving into the Oligocene (Köhler and Moyà-Solà, 1999). Contrary to the Omomyinae and Anaptomorphinae, which are found mainly in North America, the subfamily Microchoerinae is exclusively European. Representatives of this subfamily are scarce in the fossil record. However, very recent findings have contributed to increase the knowledge about Microchoerinae (Hooker, 2007; Hooker and Harrison, 2008).

Pseudoloris is a very small microchoerine, in some aspects morphologically similar to the living *Tarsius*, sharing strong dental convergences (Szalay and Delson, 1979). Besides France and Germany, this genus is known from several Spanish localities (Crusafont, 1967; Moyà-Solà and Köhler, 1992; Peláez-Campomanes, 1995; Köhler and Moyà-Solà, 1999), where its remains are very scarce.

In the 1990s, several levels containing fossil Primates were identified in the Middle Eocene series of the Bellmunt Formation (Eastern Pyrenees), an alluvial unit mainly formed by lutites, sandstones and conglomerates, which also includes lacustrine and palustrine levels (Busquets et al., 1992). The fossiliferous beds correspond to dark marls with a high content of organic matter, presenting abundant remains of plants and vertebrates. The richest of these levels is Sant Jaume de Frontanyà-3C (SJF-3C), which has yielded abundant mammal remains, including dental and postcranial primate elements. In addition to *Pseudoloris pyrenaicus* (depicted in this article), two other primates have been identified from this level: *Anchomomys* nov. sp. and *Adapis* sp. (Moyà-Solà and Köhler, 1993). The level called Sant Jaume de Frontanyà-3D (SJF-3D), ~50 cm above SJF-3C, contains a very similar fauna, including also *Anchomomys* nov. sp. and *Pseudoloris pyrenaicus*.

The mammal assemblage from SJF-3C is shown in Table 1. The presence of *Elfomys* nov. sp., also found in the locality of Laprade (Sudre et al., 1990), and the similarity of *Anchomomys* nov. sp. to *A. pygmaeus* from Egerkingen (Stehlin, 1916) allows to assign the site to the Robiacian (MP14-15) (Moyà-Solà and Köhler, 1993). Thus, this locality is properly correlated with the Mammal Paleogene reference levels (Schmidt-Kittler, 1987, updated by Aguilar et al., 1997), the most widely employed biochronological scale for the Paleogene continental deposits of Europe.

The primates from Sant Jaume de Frontanyà remain mostly unpublished. In this article we describe *Pseudoloris pyrenaicus*, which represents the most abundant sample of this genus described up to now from the Iberian Peninsula. In addition, we depict the anterior dentition (incisors and canines) of *Pseudoloris*, previously

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TABLE 1. Mammal faunal list of the level of Sant Jaume de Frontanyà-3C, after Moyà-Solà and Köhler (1993)

- Creodonta indet.
- Perissodactyla indet.
- Artiodactyla
  - *Robiacina* nov. sp.
  - *Leptothiridium* sp.
  - Haplobunodontinae indet.
  - Dichobunodontinae indet.
- Rodentia
  - *Stellomys* sp.
  - *Elfomys* nov. sp.
  - cf. *Ectropomys* sp.
  - Rodentia indet.
- Lipotyphla
  - *Saturninia* sp.
  - Palaeoryctidae indet.
- Primates
  - *Anchomomys* nov. sp.
  - *Adapis* sp.
  - *Pseudoloris pyrenaicus* nov. sp.

only figured for *P. parvulus* from Perrière (Godinot, 1983). Thus, this new finding contributes to the knowledge of the complete dental morphology of *Pseudoloris* and also allows the understanding of the relationships between the oldest and the youngest representatives of the genus.

Dental terminology and measurement methods

The nomenclature used in the descriptions of the teeth is that of Hooker (1986). Measurements have been taken as defined by Godinot (2003) for all the teeth except for the C^1, in which only the maximal length and the width, taken at right angles to the length, have been measured.

Systematic Paleontology

Order PRIMATES Linnaeus, 1758.
Suborder HAPLORHINI Pocock, 1918.
Infraorder TARSIIFORMES Gregory, 1915.
Family OMOMYIDAE Trouessart, 1879.
Subfamily MICROCHOERINAE Lydekker, 1887.
Genus PSEUDOLORIS Stehlin, 1916.
PSEUDOLORIS PYRENAICUS, nov. sp. (Figs. 1–4).

Holotype

Fragment of a right mandible with P_4-M_3 (IPS46297) from Sant Jaume de Frontanyà-3C, stored in the Institut Català de Paleontologia (ICP), Sabadell, Spain.

Other referred material

From Sant Jaume de Frontanyà-3C. Three I_1, three C_1, one P_3, four P_4, one mandible fragment with M_1-M_3, three complete and two incomplete M_1, six complete and one incomplete M_2, three complete and one incomplete M_3, six fragments of indeterminated lower molars, four complete and three incomplete I^1, two C^1, three P^2, one P^3, one complete and three incomplete P^4, two complete and five incomplete M^{1-2}, two M^3. Catalogue numbers IPS8448; IPS8628-IPS8632; IPS46289-IPS46296; IPS46298-IPS46343.

From Sant Jaume de Frontanyà-3D. Four I_1, two C_1, three P_4, two complete and two incomplete M_1, one M_2, three fragments of indeterminated lower molars, one I^1, four P^2, one incomplete P^3, four incomplete P^4, six incomplete M^{1-2}, one M^3. Catalogue numbers IPS46344-IPS46377.

Fig. 1. Holotype of *Pseudoloris pyrenaicus* from Sant Jaume de Frontanyà-3C. Fragment of a right mandible with P_4-M_3 (IPS46297) in (**a**) lingual, (**b**) occlusal, and (**c**) labial views. Scale bar = 1 mm.

Type locality, age and other localities. The type locality is Sant Jaume de Frontanyà-3C, Eastern Pyrenees, Spain. MP14–15, Robiacian, middle Eocene. Other localities only include Sant Jaume de Frontanyà-3D.

Diagnosis

Medium sized *Pseudoloris*, larger than *P. parvulus*, *P. isabenae* and *P. saalae*, and smaller than *P. crusafonti*, *P. godinoti* and *Pseudoloris* sp. from Weissenburg 8. Lower molars without distinct paraconid, but with a thickened paracristid. Large, round hypoconulid in the M_3. Very well-developed buccal cingulid in the lower molars. P^3 with an extremely reduced protocone. Hypocone and paraconule reduced in M^1-M^2 and absent in M^3.

Etymology

From the Pyrenees, where the type locality of the new species is placed.

Description of the material from SJF-3C

The described isolated lower and upper incisors are identified as central incisors on the basis of their size. When known, the lateral incisors (or the corresponding alveoli) of *Pseudoloris* and other Microchoerinae are very small when compared with I_1 and I^1 (see, for example, Teilhard de Chardin, 1921; Godinot, 1983; Hooker and Harrison, 2008).

I_1. The crown is shovel-shaped. The labial face is convex. The lingual face is crossed by a cingulid that descends from mesial to distal part. Labial and lingual faces are separated by a cutting blade, which is sharper on the

Fig. 2. *Lower dentition of Pseudoloris pyrenaicus from Sant Jaume de Frontanyà-3C.* (**a**, **b**) Right I_1 (IPS46289) in (a) lingual and (b) distal views. (**c**) Left C_1 (IPS46291) in lingual view. (**d**) Right P_3 (IPS46294) in lingual view. (**e**, **f**) Left P_4 (IPS46295) in labial (e) and occlusal (f) views. (**g**, **h**) Left M_1 (IPS46300) in occlusal (g) and labial (h) views. (**i**, **j**) Left M_2 (IPS46309) in occlusal (i) and labial (j) views. (**k**, **l**) Left M_3 (IPS46317) in occlusal (k) and labial (l) views. (**m**, **n**) Right M_3 (IPS46318) in occlusal (m) and labial (n) views. (**o**, **p**) Right M_2 (IPS46312) in occlusal (o) and labial (p) views. (**q**, **r**) Right M_1 (IPS46302) in occlusal (q) and labial (r) views. Scale bar = 1 mm.

distal part. The root is wide and somewhat compressed mesiodistally.

C_1**.** The occlusal outline is elliptical. The posterocristid is longer than the anterocristid, both reach the base of the crown. A well-developed cingulid surrounds the lingual border.

P_3**.** The crown is lower than in the C_1 and the apex is rounder. The posterocristid is weak and does not reach the base of the crown. The lingual cingulid is well developed and thickens at the distal end of the tooth. The root is narrower than in the canine.

Fig. 3. *Upper dentition of Pseudoloris pyrenaicus from Sant Jaume de Frontanyà-3C.* (**a**) Left I^1 (IPS46321) in medial view. (**b**) Left I^1 (IPS46323) in ligual view. (**c**) Right C^1 (IPS8629) in lingual view. (**d**) Left C^1 (8630) in occusal view. (**e**) Left P^2 (IPS46328) in occlusal view. (**f**) Left P^3 (IPS46330) in occlusal view. (**g**) Right P^4 (IPS46332) in occlusal view. (**h**) Left P^4 (IPS46331) in occlusal view. (**i**) Left M^{1-2} (IPS46335) in occlusal view. (**j**) Right M^3 (IPS46342) in occlusal view. Scale bar = 1 mm.

P_4**.** The protoconid is high. The paracristid thickens at its mesial end, but there is no distinct paraconid. This cristid continues in a well-developed mesiolingual cingulid. There is an incipient metaconid. The well-defined talonid basin is crossed by a longitudinal cristid. There is a thick distal cingulid.

M_1**.** The talonid is notably wider than the trigonid. There is no distinct paraconid, but the paracristid is somewhat thickened at its mesiolingual end. The lingual part of the trigonid is variable. Most specimens have a low cristid, connecting paracristid and metaconid. In one specimen, there is a minuscule cuspule instead of this crest. Finally, in another specimen, the trigonid basin is completely open lingually. The protocristid shows a well-marked trigonid notch. The hypoconulid is low, but very

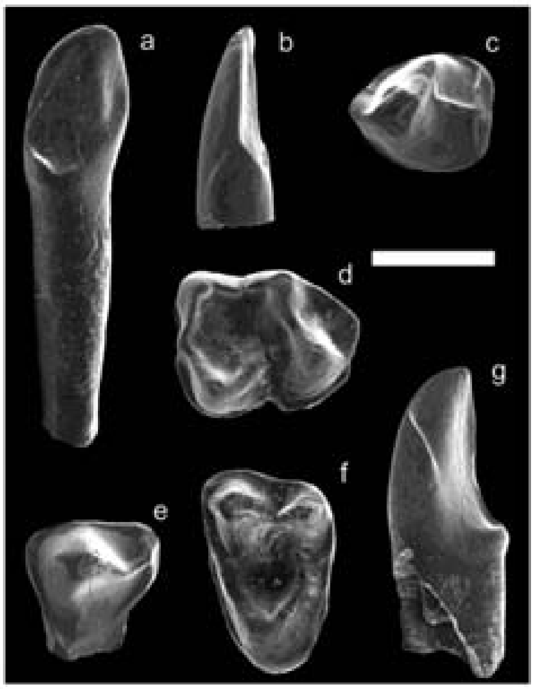

Fig. 4. *Pseudoloris pyrenaicus* from Sant Jaume de Frontanyà-3D. (**a**) Left I_1 (IPS46345) in lingual view. (**b**) Left I_1 (IPS46346) in distal view. (**c**) Left P_4 (IPS46350) in occlusal view. (**d**) Rigth M_1 (IPS46355) in occlusal view. (**e**) Left P^3 (IPS46366) in occlusal view. (**f**) Left M^3 (IPS46377) in occlusal view. (**g**) Left I^1 (IPS46361) in medial view. Scale bar = 1 mm.

prominent. There is a very well-developed cingulid occupying the mesial, buccal and distal borders. It is especially thick on the buccal part.

***M_2*.** The trigonid is shorter and wider than in M_1, so the difference in width between talonid and trigonid is less accentuated. The protoconid is placed in a more buccal position. There is a low crest on the lingual side of the trigonid, connecting paracristid and metaconid. It can be continuous or interrupted by a notch. The rest of characters are those described for the M_1.

***M_3*.** The trigonid is somewhat narrower than the talonid. There is no paraconid. The paracristid continues in a low cristid that reaches The metaconid, closing the trigonid basin. The cristid obliqua joins the trigonid near the protoconid, more buccally positioned than in M_1 and M_2. The hypoconulid is rounded, very large, and prominent. The strong buccal cingulid starts at the mesiobuccal corner of the tooth and ends at the buccal side of the hypoconulid.

***I^1*.** High-crowned tooth, with the apex pointed and upturned backwards. The lateral face is convex. The medial face is faintly concave. A well-developed cingulum occupies the labial border of the medial face, from the middle of the crown height to the enamel base. There is a sharp posterocrista that reaches a well-differentiated talon at the lingual base of the crown. The root is long, laterally compressed.

***C^1*.** Small, conical tooth, with elliptical outline. The apex is pointed. There is no anterocrista. The posterocrista is sharp and reaches the base of the crown. There is a very thick cingulum occupying the entire border of the tooth, which forms a small projection at the distal end.

***P^2*.** The crown is conical, with elliptical outline. The anterocrista is weak and reaches the cingulum. The posterocrista is even weaker and does not reach the crown base. A strong cingulum borders the mesial, lingual and distal parts. At the distal end, this cingulum thickens and delimitates a very narrow and shallow basin.

***P^3*.** The paracone is high. The lingual lobe is broad, showing an extremely reduced protocone. The anterocrista is weak and restricted to the upper portion of the paracone. The posterocrista is well developed. At the middle of the crown height, it curves buccally and reaches the distobuccal corner of the tooth. A thick cingulum occupies the mesial border. There is another short, weak cingulum in the middle part of the distal border.

***P^4*.** The paracone is high. The anterocrista is thin and straight. The posterocrista is thick and curved buccally. Both cristas reach the base of the crown. The lingual lobe is broad and nearly flat. A distinct protocone is present only in one of the three specimens preserving the lingual part. The mesial cingulum is well marked. There is a small parastyle. The distal cingulum does not reach the distobuccal corner of the tooth. There is no metastyle.

***M^{1-2}*.** Paracone and metacone are similar in size. The protocone is lower and placed mesioligually. The hypocone is small and attached to the distal side of the protocone. In some specimens it is a mere thickening at the end of the distal cingulum. There is no postprotocingulum. The paraconule is very reduced, as a weak protuberance on the preprotocrista. The metaconule is well developed, crescentiform, bearing pre and postmetaconule cristas. The mesial and buccal cingula are strong and the distal cingulum is somewhat thinner. Parastyle and metastyle are absent.

***M^3*.** The paracone is notably larger than the metacone. There is neither hypocone, nor paraconule. The metaconule is small but distinct, crescentiform, with pre and postmetaconule cristas. A well-marked preprotocrista reaches the mesiobuccal corner, bordering the paracone and continuing in a low buccal cingulum. The mesial cingulum is thicker than the distal one.

Description of the material from SJF-3D

The material from the level of SJF-3D is very similar to that from SJF-3C described above. The subtle differences we have found are the following: the crown of the I_1 is notably shorter than in SJF-3C. The P_4 are slightly smaller than those from SJF-3C, and have more convex buccal and lingual borders. The talon of the I^1 is somewhat less prominent than that of the specimens from SJF-3C. The only P^3 from SJF-3D has a distinct metastyle. The single P^4 of SJF-3D, which preserves the lingual part, has a high and well-developed protocone. The single M^3 from SJF-3D has less-developed cingula than the specimens from SJF-3C.

The rest of dental elements of these two levels do not show any morphological difference. As in SJF-3C, the

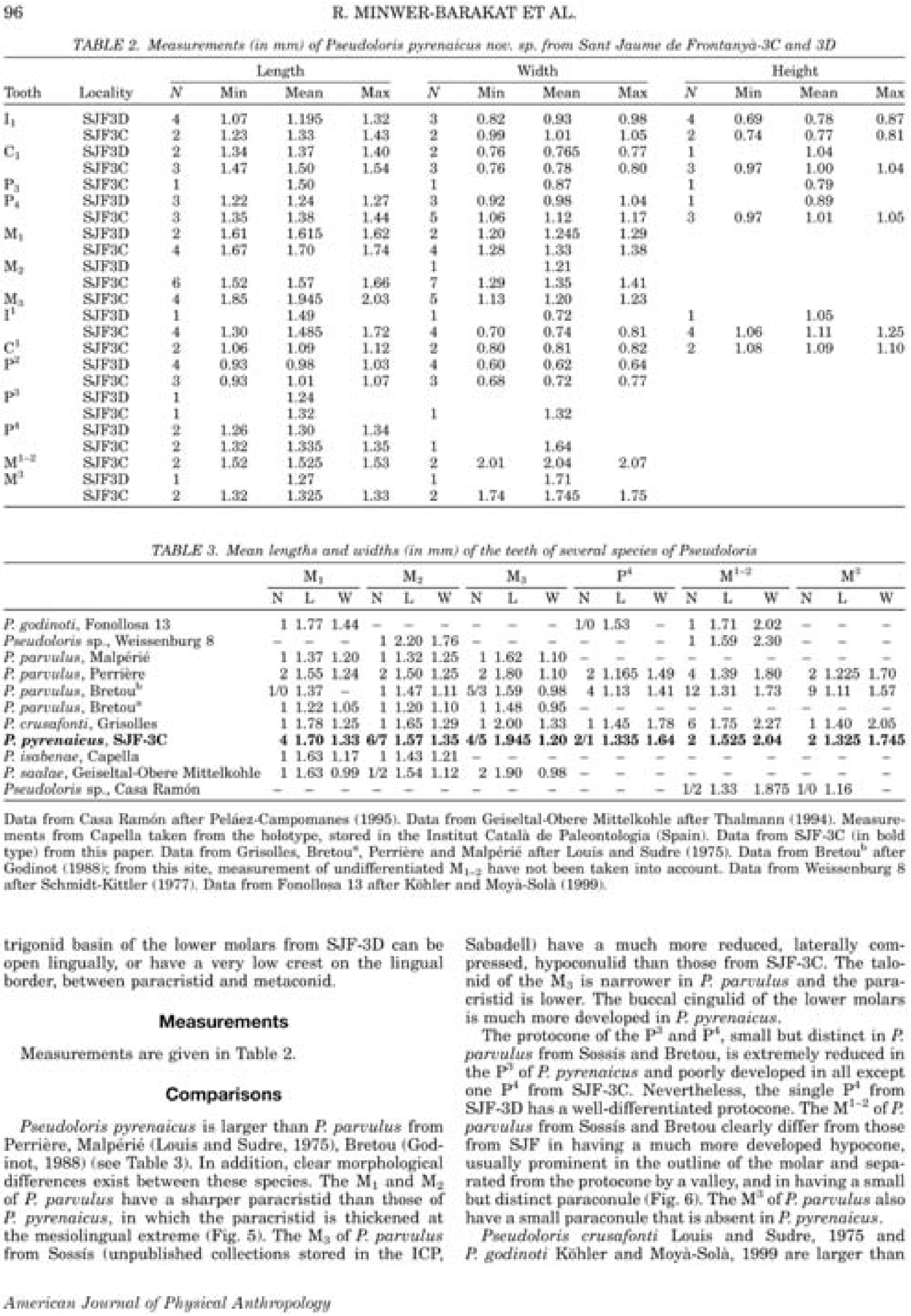

TABLE 2. Measurements (in mm) of Pseudoloris pyrenaicus nov. sp. from Sant Jaume de Frontanyà-3C and 3D

		Length				Width				Height			
Tooth	Locality	*N*	Min	Mean	Max	*N*	Min	Mean	Max	*N*	Min	Mean	Max
I$_1$	SJF3D	4	1.07	1.195	1.32	3	0.82	0.93	0.98	4	0.69	0.78	0.87
	SJF3C	2	1.23	1.33	1.43	2	0.99	1.01	1.05	2	0.74	0.77	0.81
C$_1$	SJF3D	2	1.34	1.37	1.40	2	0.76	0.765	0.77	1		1.04	
	SJF3C	3	1.47	1.50	1.54	3	0.76	0.78	0.80	3	0.97	1.00	1.04
P$_3$	SJF3C	1		1.50		1		0.87		1		0.79	
P$_4$	SJF3D	3	1.22	1.24	1.27	3	0.92	0.98	1.04	1		0.89	
	SJF3C	3	1.35	1.38	1.44	5	1.06	1.12	1.17	3	0.97	1.01	1.05
M$_1$	SJF3D	2	1.61	1.615	1.62	2	1.20	1.245	1.29				
	SJF3C	4	1.67	1.70	1.74	4	1.28	1.33	1.38				
M$_2$	SJF3D					1		1.21					
	SJF3C	6	1.52	1.57	1.66	7	1.29	1.35	1.41				
M$_3$	SJF3C	4	1.85	1.945	2.03	5	1.13	1.20	1.23				
I^1	SJF3D	1		1.49		1		0.72		1		1.05	
	SJF3C	4	1.30	1.485	1.72	4	0.70	0.74	0.81	4	1.06	1.11	1.25
C^1	SJF3C	2	1.06	1.09	1.12	2	0.80	0.81	0.82	2	1.08	1.09	1.10
P^2	SJF3D	4	0.93	0.98	1.03	4	0.60	0.62	0.64				
	SJF3C	3	0.93	1.01	1.07	3	0.68	0.72	0.77				
P^3	SJF3D	1		1.24									
	SJF3C	1		1.32		1		1.32					
P^4	SJF3D	2	1.26	1.30	1.34								
	SJF3C	2	1.32	1.335	1.35	1		1.64					
M$^{1-2}$	SJF3C	2	1.52	1.525	1.53	2	2.01	2.04	2.07				
M^3	SJF3D	1		1.27		1		1.71					
	SJF3C	2	1.32	1.325	1.33	2	1.74	1.745	1.75				

TABLE 3. Mean lengths and widths (in mm) of the teeth of several species of Pseudoloris

	M$_1$			M$_2$			M$_3$			P^4			M$^{1-2}$			M^3		
	N	L	W	N	L	W	N	L	W	N	L	W	N	L	W	N	L	W
P. godinoti, Fonollosa 13	1	1.77	1.44	–	–	–	–	–	–	1/0	1.53	–	1	1.71	2.02	–	–	–
Pseudoloris sp., Weissenburg 8	–	–	–	1	2.20	1.76	–	–	–	–	–	–	1	1.59	2.30	–	–	–
P. parvulus, Malpérié	1	1.37	1.20	1	1.32	1.25	1	1.62	1.10	–	–	–	–	–	–	–	–	–
P. parvulus, Perrière	2	1.55	1.24	2	1.50	1.25	2	1.80	1.10	2	1.165	1.49	4	1.39	1.80	2	1.225	1.70
P. parvulus, Bretou^b	1/0	1.37	–	1	1.47	1.11	5/3	1.59	0.98	4	1.13	1.41	12	1.31	1.73	9	1.11	1.57
P. parvulus, Bretou^a	1	1.22	1.05	1	1.20	1.10	1	1.48	0.95	–	–	–	–	–	–	–	–	–
P. crusafonti, Grisolles	1	1.78	1.25	1	1.65	1.29	1	2.00	1.33	1	1.45	1.78	6	1.75	2.27	1	1.40	2.05
***P. pyrenaicus*, SJF-3C**	**4**	**1.70**	**1.33**	**6/7**	**1.57**	**1.35**	**4/5**	**1.945**	**1.20**	**2/1**	**1.335**	**1.64**	**2**	**1.525**	**2.04**	**2**	**1.325**	**1.745**
P. isabenae, Capella	1	1.63	1.17	1	1.43	1.21	–	–	–	–	–	–	–	–	–	–	–	–
P. saalae, Geiseltal-Obere Mittelkohle	1	1.63	0.99	1/2	1.54	1.12	2	1.90	0.98	–	–	–	–	–	–	–	–	–
Pseudoloris sp., Casa Ramón	–	–	–	–	–	–	–	–	–	–	–	–	1/2	1.33	1.875	1/0	1.16	–

Data from Casa Ramón after Peláez-Campomanes (1995). Data from Geiseltal-Obere Mittelkohle after Thalmann (1994). Measurements from Capella taken from the holotype, stored in the Institut Català de Paleontologia (Spain). Data from SJF-3C (in bold type) from this paper. Data from Grisolles, Bretou^a, Perrière and Malpérié after Louis and Sudre (1975). Data from Bretou^b after Godinot (1988); from this site, measurement of undifferentiated M$_{1-2}$ have not been taken into account. Data from Weissenburg 8 after Schmidt-Kittler (1977). Data from Fonollosa 13 after Köhler and Moyà-Solà (1999).

trigonid basin of the lower molars from SJF-3D can be open lingually, or have a very low crest on the lingual border, between paracristid and metaconid.

Measurements

Measurements are given in Table 2.

Comparisons

Pseudoloris pyrenaicus is larger than *P. parvulus* from Perrière, Malpérié (Louis and Sudre, 1975), Bretou (Godinot, 1988) (see Table 3). In addition, clear morphological differences exist between these species. The M$_1$ and M$_2$ of *P. parvulus* have a sharper paracristid than those of *P. pyrenaicus*, in which the paracristid is thickened at the mesiolingual extreme (Fig. 5). The M$_3$ of *P. parvulus* from Sossís (unpublished collections stored in the ICP, Sabadell) have a much more reduced, laterally compressed, hypoconulid than those from SJF-3C. The talonid of the M$_3$ is narrower in *P. parvulus* and the paracristid is lower. The buccal cingulid of the lower molars is much more developed in *P. pyrenaicus*.

The protocone of the P^3 and P^4, small but distinct in *P. parvulus* from Sossís and Bretou, is extremely reduced in the P^3 of *P. pyrenaicus* and poorly developed in all except one P^4 from SJF-3C. Nevertheless, the single P^4 from SJF-3D has a well-differentiated protocone. The M$^{1-2}$ of *P. parvulus* from Sossís and Bretou clearly differ from those from SJF in having a much more developed hypocone, usually prominent in the outline of the molar and separated from the protocone by a valley, and in having a small but distinct paraconule (Fig. 6). The M^3 of *P. parvulus* also have a small paraconule that is absent in *P. pyrenaicus*.

Pseudoloris crusafonti Louis and Sudre, 1975 and *P. godinoti* Köhler and Moyà-Solà, 1999 are larger than

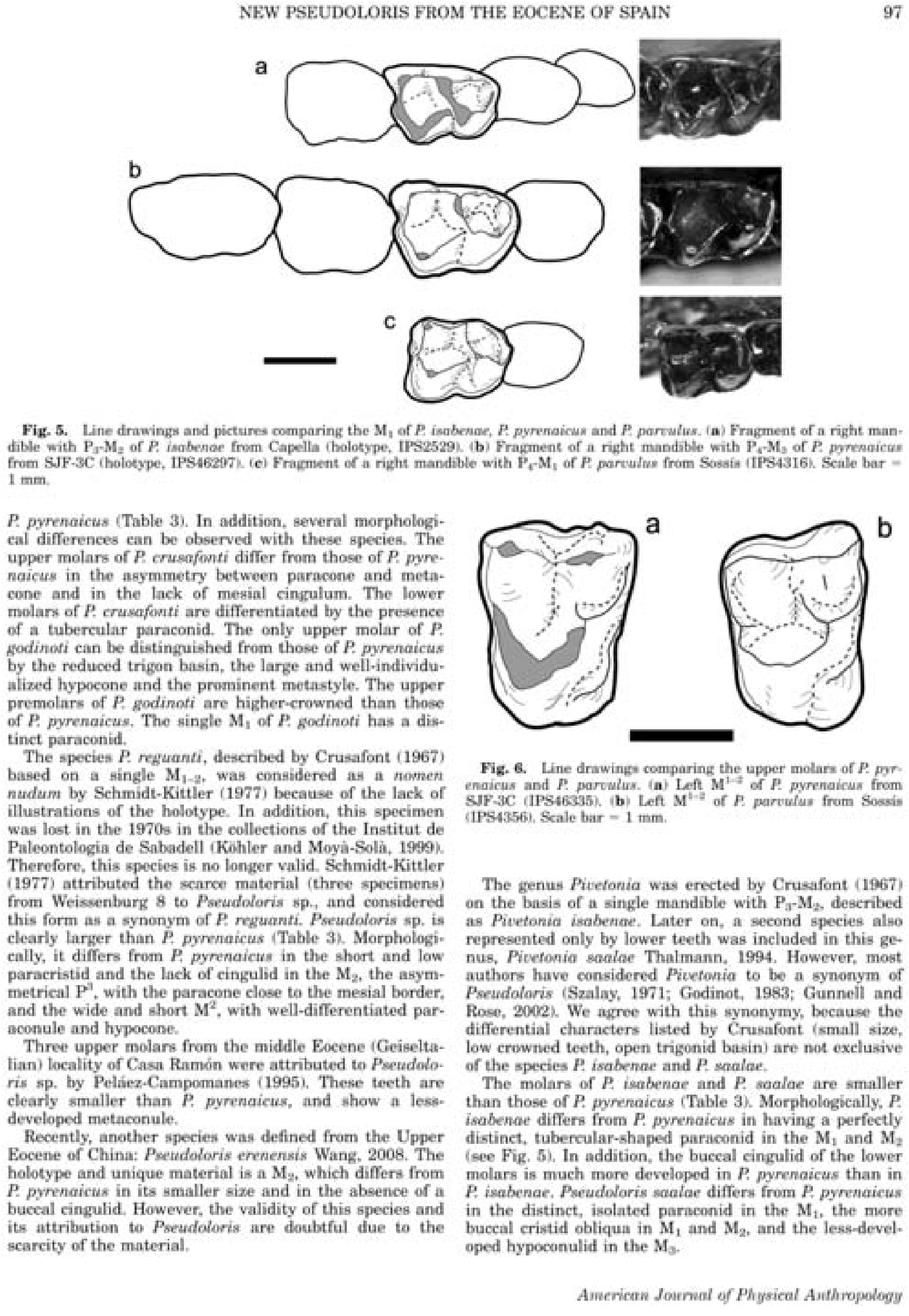

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Fig. 5. Line drawings and pictures comparing the M_1 of *P. isabenae*, *P. pyrenaicus* and *P. parvulus*. (**a**) Fragment of a right mandible with P_3-M_2 of *P. isabenae* from Capella (holotype, IPS2529). (**b**) Fragment of a right mandible with P_4-M_3 of *P. pyrenaicus* from SJF-3C (holotype, IPS46297). (**c**) Fragment of a right mandible with P_4-M_1 of *P. parvulus* from Sossís (IPS4316). Scale bar = 1 mm.

P. pyrenaicus (Table 3). In addition, several morphological differences can be observed with these species. The upper molars of *P. crusafonti* differ from those of *P. pyrenaicus* in the asymmetry between paracone and metacone and in the lack of mesial cingulum. The lower molars of *P. crusafonti* are differentiated by the presence of a tubercular paraconid. The only upper molar of *P. godinoti* can be distinguished from those of *P. pyrenaicus* by the reduced trigon basin, the large and well-individualized hypocone and the prominent metastyle. The upper premolars of *P. godinoti* are higher-crowned than those of *P. pyrenaicus*. The single M_1 of *P. godinoti* has a distinct paraconid.

The species *P. reguanti*, described by Crusafont (1967) based on a single M_{1-2}, was considered as a *nomen nudum* by Schmidt-Kittler (1977) because of the lack of illustrations of the holotype. In addition, this specimen was lost in the 1970s in the collections of the Institut de Paleontologia de Sabadell (Köhler and Moyà-Solà, 1999). Therefore, this species is no longer valid. Schmidt-Kittler (1977) attributed the scarce material (three specimens) from Weissenburg 8 to *Pseudoloris* sp., and considered this form as a synonym of *P. reguanti*. *Pseudoloris* sp. is clearly larger than *P. pyrenaicus* (Table 3). Morphologically, it differs from *P. pyrenaicus* in the short and low paracristid and the lack of cingulid in the M_2, the asymmetrical P^3, with the paracone close to the mesial border, and the wide and short M^2, with well-differentiated paraconule and hypocone.

Three upper molars from the middle Eocene (Geiseltalian) locality of Casa Ramón were attributed to *Pseudoloris* sp. by Peláez-Campomanes (1995). These teeth are clearly smaller than *P. pyrenaicus*, and show a less-developed metaconule.

Recently, another species was defined from the Upper Eocene of China: *Pseudoloris erenensis* Wang, 2008. The holotype and unique material is a M_2, which differs from *P. pyrenaicus* in its smaller size and in the absence of a buccal cingulid. However, the validity of this species and its attribution to *Pseudoloris* are doubtful due to the scarcity of the material.

Fig. 6. Line drawings comparing the upper molars of *P. pyrenaicus* and *P. parvulus*. (**a**) Left M^{1-2} of *P. pyrenaicus* from SJF-3C (IPS46335). (**b**) Left M^{1-2} of *P. parvulus* from Sossís (IPS4356). Scale bar = 1 mm.

The genus *Pivetonia* was erected by Crusafont (1967) on the basis of a single mandible with P_3-M_2, described as *Pivetonia isabenae*. Later on, a second species also represented only by lower teeth was included in this genus, *Pivetonia saalae* Thalmann, 1994. However, most authors have considered *Pivetonia* to be a synonym of *Pseudoloris* (Szalay, 1971; Godinot, 1983; Gunnell and Rose, 2002). We agree with this synonymy, because the differential characters listed by Crusafont (small size, low crowned teeth, open trigonid basin) are not exclusive of the species *P. isabenae* and *P. saalae*.

The molars of *P. isabenae* and *P. saalae* are smaller than those of *P. pyrenaicus* (Table 3). Morphologically, *P. isabenae* differs from *P. pyrenaicus* in having a perfectly distinct, tubercular-shaped paraconid in the M_1 and M_2 (see Fig. 5). In addition, the buccal cingulid of the lower molars is much more developed in *P. pyrenaicus* than in *P. isabenae*. *Pseudoloris saalae* differs from *P. pyrenaicus* in the distinct, isolated paraconid in the M_1, the more buccal cristid obliqua in M_1 and M_2, and the less-developed hypoconulid in the M_3.

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TABLE 4. European sites containing remains of Pseudoloris, referred to the corresponding European Land Mammal Ages (ELMAs) and MP units

ELMA	MP unit	Locality	Species
Suevian	MP22	Fonollosa 13	*Pseudoloris godinoti*
	MP21	Sant Pedor-2	*Pseudoloris godinoti*
Headonian	MP19	Weissenburg 8	*Pseudoloris* sp.
	MP19	Sant Cugat de Gavadons	*Pseudoloris reguanti*
	MP17b	Perrière, Malpérié	*Pseudoloris parvulus*
	MP17a	Sossís, Euzet	*Pseudoloris parvulus*
Robiacian	MP16	Bretou	*Pseudoloris parvulus*
	MP16	Grisolles	*Pseudoloris crusafonti*
	MP15-16	Mazaterón	*Pseudoloris* sp.
	MP14-15	Sant Jaume de Frontanyà-3C, 3D	*Pseudoloris pyrenaicus*
	MP14	Capella, Lissieu	*Pseudoloris isabenae*
Geiseltalian	MP13	Geiseltal-Obere Mittelkohle	*Pseudoloris saalae*
	MP11	Casa Ramón	*Pseudoloris* sp.

Melaneremia bryanti Hooker, 2007 is similar in size to *P. pyrenaicus* but shows clear morphological differences: the teeth are lower crowned, the lower molars have a distinct paraconid, the trigonid basin of the M_3 is open, and the M^1 is more elongated transversely. The rest of genera of Microchoerinae (*Microchoerus*, *Necrolemur*, *Nannopithex*, and *Vectipithex*) can be distinguished from *P. pyrenaicus* mainly by their much larger size and the presence of enamel wrinkling in the cheek teeth. Other differences are the larger hypocone in the upper molars of *Microchoerus* and *Necrolemur*, and the lack of P^2 in *Vectipithex*.

DISCUSSION

The genus *Pseudoloris* is known from several European localities (Table 4) ranging in age between the middle Eocene (Geiseltalian, MP11) and the early Oligocene (Suevian, MP22). Out of Europe, the only mention to this genus is *P. eremensis* from China (Wang, 2008) but, as explained above, its attribution to *Pseudoloris* is doubtful.

The oldest record of the genus is *Pseudoloris* sp. from Casa Ramón (MP11), only represented by one complete M^2, and two fragments of M^1 and M^3 (Peláez-Campomanes, 1995), which are small and have reduced metaconules. Apart from that, the oldest species ascribed to the genus are *P. saalae* from Geiseltal-Obere Mittelkohle (MP13) and *P. isabenae* from Capella (MP14), both of them known only by their lower molars. Godinot (1983) ascribed to *P. isabenae* a single M_2 from Lissieu. The same author indicated that three teeth from Aumelas (P_4, M_3, and M^2) probably belonged to *P. isabenae*, but a definitive attribution was not made. Therefore, the oldest sites where abundant material of both lower and upper teeth of *Pseudoloris* has been recovered are SFJ-3C and 3D (MP14-15).

The best represented species of the genus is *P. parvulus*, known from several middle and late Eocene (MP16-17) sites of Spain and France. Stehlin (1916) and Teilard de Chardin (1921) described some specimens of *P. parvulus* from the phosphorites of Quercy. Later, this species has been identified in Sossís, Euzet (Crusafont, 1967), Perrière, Malpérié (Godinot, 1983) and Bretou (Godinot, 1988). The material from Grisolles (15 isolated teeth) was attributed to *P. crusafonti* by Louis and Sudre (1975). This finding revealed the existence of two different lineages of the genus in the latest middle Eocene, since Grisolles is contemporaneous to Bretou, a site containing *P. parvulus* (Godinot, 1983).

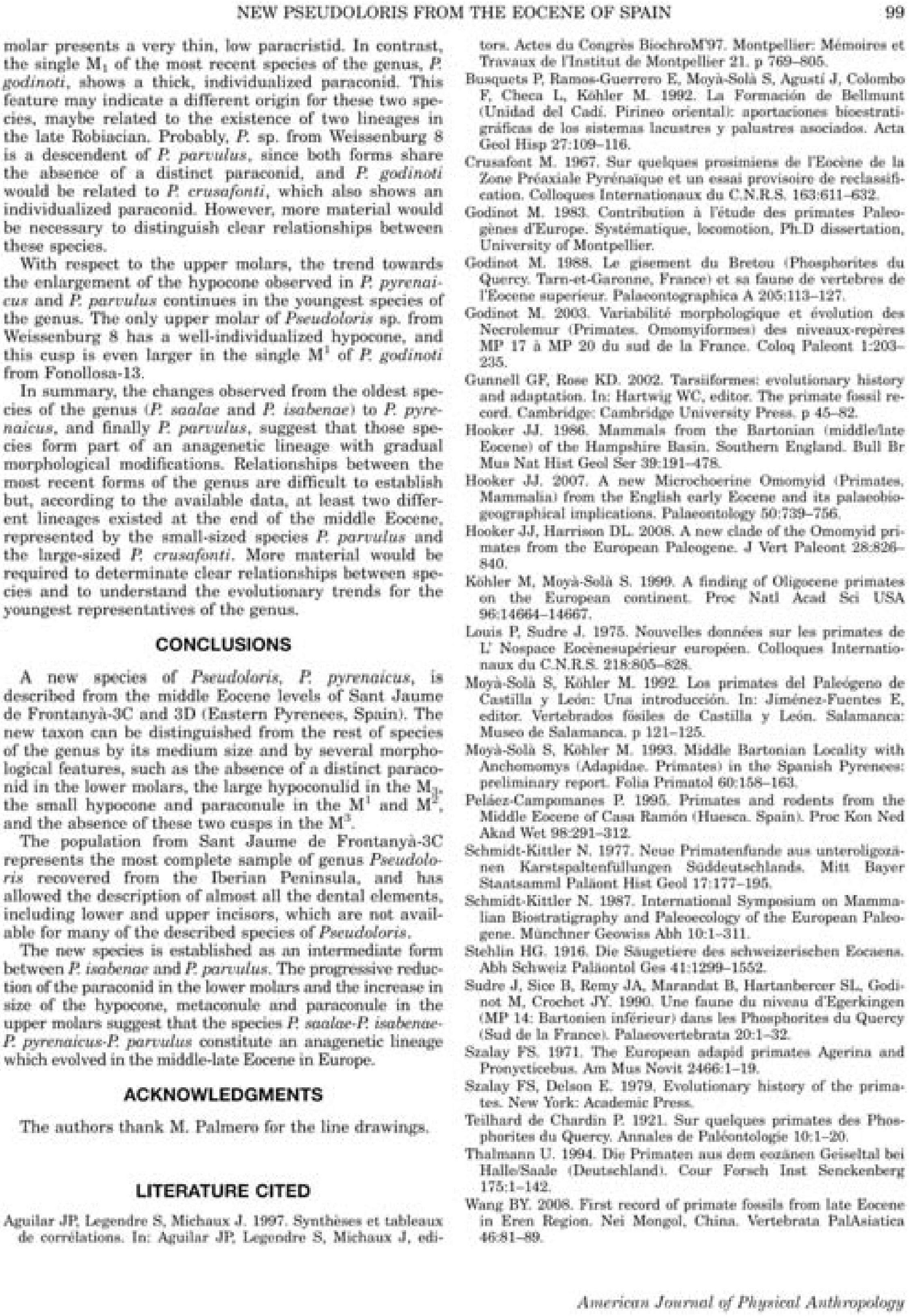
The latest Eocene mentions of the genus are *P. reguanti* from Sant Cugat de Gavadons (a single lost tooth), and the three specimens of *Pseudoloris* sp. from Weissenburg 8 (Schmidt-Kittler, 1977), both sites corresponding to MP19. Finally, *P. godinoti*, known only by six complete teeth and two fragments, is recorded in the Oligocene localities of Santpedor-2 and Fonollosa-13 (MP21 and 22, respectively, Köhler and Moyà-Solà, 1999).

Till now, morphological or biometrical changes in successive populations of this genus were very difficult to observe, because of its very discontinuous record, and to the scarcity of material in almost all the localities in which it has been found. Thus, no clear trend has been described in the evolution of *Pseudoloris*. In this context, the finding of *P. pyrenaicus* from SJF-3C and 3D is particularly interesting. The abundance of material, with almost all the dental elements represented, and its intermediate position between the oldest species of the genus and the well-known *P. parvulus*, allows us to recognize several directional changes in the early evolution of the genus.

In the lower molars, the paraconid becomes less developed through time, changing from a distinct tubercule in *P. saalae* and *P. isabenae* to a sharp cristid in *P. parvulus*. *Pseudoloris pyrenaicus* represents an intermediate step between these two stages. Godinot (1983) examined several populations of *P. parvulus* and indicated the possibility of a trend to the closing of the trigonid basin from oldest (Bretou) to youngest (Perrière and Malpérié) populations of this species. After direct comparison, we have observed that the morphology of the trigonid is quite variable in *P. pyrenaicus* and *P. parvulus* from Sossís. Some lower molars have a crest connecting paracristid and metaconid, closing completely the trigonid. In other teeth, this crest is interrupted by a notch. Other specimens have the trigonid open lingually. Finally, some molars have a tiny tubercule in the lingual part of the trigonid. So, we think that the variability of this character in all the samples with a high number of specimens does not allow observing clear changes through time.

The upper dentition of *P. saalae* and *P. isabenae* remains unknown. When comparing the upper molars of *P. pyrenaicus* and *P. parvulus*, an increase on the size of the hypocone can be observed. The metaconule and paracolule are also larger in the most recent species.

The trends observed in the oldest species of the genus are difficult to evaluate in the most recent ones. The progressive reduction of the paraconid seems to continue in *Pseudoloris* sp. from Weissenburg 8, since the only lower



molar presents a very thin, low paracristid. In contrast, the single M_1 of the most recent species of the genus, *P. godinoti*, shows a thick, individualized paraconid. This feature may indicate a different origin for these two species, maybe related to the existence of two lineages in the late Robiacian. Probably, *P.* sp. from Weissenburg 8 is a descendent of *P. parvulus*, since both forms share the absence of a distinct paraconid, and *P. godinoti* would be related to *P. crusafonti*, which also shows an individualized paraconid. However, more material would be necessary to distinguish clear relationships between these species.

With respect to the upper molars, the trend towards the enlargement of the hypocone observed in *P. pyrenaicus* and *P. parvulus* continues in the youngest species of the genus. The only upper molar of *Pseudoloris* sp. from Weissenburg 8 has a well-individualized hypocone, and this cusp is even larger in the single M^1 of *P. godinoti* from Fonollosa-13.

In summary, the changes observed from the oldest species of the genus (*P. saalae* and *P. isabenae*) to *P. pyrenaicus*, and finally *P. parvulus*, suggest that those species form part of an anagenetic lineage with gradual morphological modifications. Relationships between the most recent forms of the genus are difficult to establish but, according to the available data, at least two different lineages existed at the end of the middle Eocene, represented by the small-sized species *P. parvulus* and the large-sized *P. crusafonti*. More material would be required to determinate clear relationships between species and to understand the evolutionary trends for the youngest representatives of the genus.

CONCLUSIONS

A new species of *Pseudoloris*, *P. pyrenaicus*, is described from the middle Eocene levels of Sant Jaume de Frontanyà-3C and 3D (Eastern Pyrenees, Spain). The new taxon can be distinguished from the rest of species of the genus by its medium size and by several morphological features, such as the absence of a distinct paraconid in the lower molars, the large hypoconulid in the M_3, the small hypocone and paraconule in the M^1 and M^2, and the absence of these two cusps in the M^3.

The population from Sant Jaume de Frontanyà-3C represents the most complete sample of genus *Pseudoloris* recovered from the Iberian Peninsula, and has allowed the description of almost all the dental elements, including lower and upper incisors, which are not available for many of the described species of *Pseudoloris*.

The new species is established as an intermediate form between *P. isabenae* and *P. parvulus*. The progressive reduction of the paraconid in the lower molars and the increase in size of the hypocone, metaconule and paraconule in the upper molars suggest that the species *P. saalae-P. isabenae-P. pyrenaicus-P. parvulus* constitute an anagenetic lineage which evolved in the middle-late Eocene in Europe.

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NEW ANCHOMOMYINI (ADAPOIDEA, PRIMATES) FROM THE MAZATERÓN MIDDLE EOCENE LOCALITY (ALMAZÁN BASIN, SORIA, SPAIN)

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News and Views

New Anchomomyini (Adapoidea, Primates) from the Mazaterón Middle Eocene locality (Almazán Basin, Soria, Spain)

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Robiacian

Introduction

Adapoid primates have been studied since the late 19th century (Rütimeyer, 1890, 1891; Stehlin, 1916; Teilhard de Chardin, 1921, 1922). However, they were not found in the Iberian Peninsula until the 1950's by Crusafont (1958), who reported the first adapoid found in the "Rafaela" mine in the locality of Capella (Huesca) (see also Crusafont, 1965, 1967; Crusafont and Golpe-Posse, 1974). For many years fossil prosimians were only known from the Àger-Tremp and the Isàbena Basins (Catalonia and Huesca) in the Iberian Peninsula. The first finding of an adapoid primate outside these basins was a lower molar found in the Santa Clara fossil site (Zamora) (Peláez-Campomanes et al., 1989). Several Eocene localities from the Duero Basin were discovered by Jiménez and his team from the University of Salamanca, including Caenes (Salamanca) and Mazaterón (Soria), which have yielded some Eocene prosimian remains (Moyà-Solà and Köhler, 1992). In recent decades many other adapoids have been identified from other Iberian fossil sites such as Sant Jaume de Frontanyà, Fonollosa and Santpedor (Moyà-Solà and Köhler, 1993). The genus *Anchomomys* has been documented at the fossil sites of Sossís (Catalonia) (Checa Soler and Casanovas-Cladellas, 1990), Santa Clara (Zamora), Caenes (Salamanca) (Moyà-Solà and Köhler, 1992) and Sant Jaume de Frontanyà-3C (Catalonia) (Moyà-Solà and Köhler, 1993).

The anchomomyins were small prosimians of about 60–500 g (Gingerich, 1980) that radiated slightly later than other cercamoniines (Godinot, 1998). Although for many years many adapoid genera were included in the tribe Anchomomyini, currently the tribe includes only three genera (*Anchomomys*, *Periconodon* and *Buxella*) following Godinot's revisions (1998, 2006).

The Mazaterón fossil site: geological setting, age and faunal content

The site of Mazaterón (WL 75559941) is 2.5 km to the East-Northeast from the village of Mazaterón, 40 km Southeast of Soria (Castilla y León, Spain) (Cuesta and Jiménez Fuentes, 1994). It is situated in the Almazán Basin, which constitutes the eastern sector of the Duero Basin (Fig. 1). Sedimentation in the Almazán Basin began in the middle Eocene, during the uplift of the Iberian Range in the context of the Alpine compression. The Northern and Northeastern sectors of the Almazán Basin are occupied mainly by Paleogene materials, representing fluvial systems, alluvial fans, lacustrine/palustrine systems and evaporitic mudflats (Huerta and Armenteros, 2006). In the southern and western parts, the Paleogene rocks are covered by Neogene deposits. The maximum thickness of the Tertiary succession is estimated to be 3500–4000 m (Huerta et al., 2006). The infill of the basin is divided in four depositional sequences, whose age cannot be established precisely due to the scarcity of paleontological data (Huerta and Armenteros, 2006). Apart from Mazaterón, the only fossil localities recognized in the basin are the upper Eocene site of Deza (Cuesta and Jiménez Fuentes, 1994; Cuesta, 2003), and the lower Miocene localities of Cetina (Álvarez Sierra, 1986) and Ariza (Cuenca, 1991).

Mazaterón is the oldest fossiliferous level identified in this Basin; it is situated in the upper part of the lowest despositional sequence, about 350 m over the base of the Tertiary succession. This level belongs to the Mazaterón Formation, which is composed of limestones, dolostones and marls with lutitic intercalations, and represents a lake system with the central areas permanently inundated (Huerta et al., 2006). The grey marls that contain the vertebrate remains correspond to lacustrine sediments deposited in the central anoxic bottom, and change laterally and vertically to

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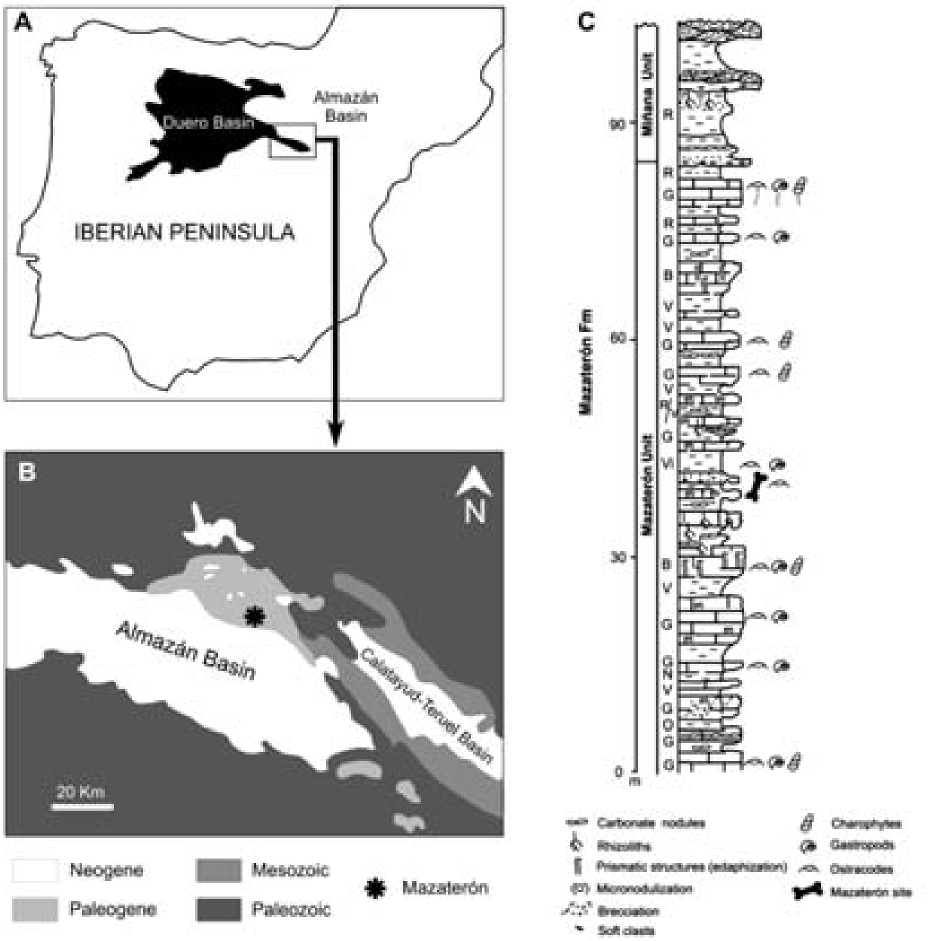

Figure 1. (A) Location of the Almazán Basin in the Iberian Peninsula; (B) Geological context of the Almazán Basin with the situation of the Mazaterón fossil site; (C) Stratigraphic column of the Mazaterón section (Modified from Armenteros, 1994 and Cuesta and Badiola, 2009).

palustrine deposits formed in seasonally exposed areas (Cuesta and Badiola, 2009).

The site of Mazaterón has yielded the richest Eocene continental fauna of the Duero Basin: twenty-seven vertebrate taxa have been identified, including fishes, turtles, crocodiles, squamates, rodents, creodonts, perissodactyls and artiodactyls (Table 1) (Cuesta and Jiménez Fuentes, 1994; Badiola and Cuesta, 2008; Badiola et al., 2009; Cuesta and Badiola, 2009), and primates (Moyà-Solà and Köhler, 1992; Marigó et al., 2009). The mammal assemblage can be assigned to the late Robiacian, corresponding to the MP15-16 Paleogene reference levels (Cuesta, 1991, 1999; Cuesta and Jiménez Fuentes, 1994; Peláez-Campomanes, 1996).

Materials and methods

Studied material

All the fossil remains included in this study are housed at the collections of the Institut Català de Paleontologia in Sabadell (Catalonia, Spain). The fossil remains were recovered in 1991 from Mazaterón (Almazán Basin, Soria, Spain), using both excavation and screen-washing methods. Almost all of the dental elements, including incisors and canines, are represented in the 66 dental pieces that were recovered. Many of the identified pieces are well preserved, although some are only fragments or have some kind of damage (extreme wear or digestion).

Comparative sample

The analyzed material was compared with fossils from other sites on the basis of published descriptions, pictures, drawings and measurements. Casts of material housed in other museums were also used when possible. Moreover, this material was compared to other undescribed material attributed to Anchomomyini from other Iberian sites such as Caenes and Sant Jaume de Frontanyà (Moyà-Solà and Köhler, 1992, 1993) that are also part of the collections of the Institut Català de Paleontologia.

Table 1
Updated faunal list of the Mazaterón fossil site (after Cuesta and Jiménez Fuentes, 1994; Badiola and Cuesta, 2008; Cuesta and Badiola, 2009)

PISCES

Bagridae indet.

REPTILIA

Chelonia
  Testudinidae
    Hadrianus sp.
  Pelomedusidae
    Neochelys sp.
  Trionychidae
    Trionyx sp.
Crocodylia
  Alligatoridae
    Diplocynodon sp.
  Baurusuchidae
    Iberosuchus sp.
  Crocodylia indet.
Squamata
  ? Lacertidae

MAMMALIA

Primates
  Adapoidea
    Mazateronodon endemicus
    cf. *Adapis*
  Omomyidae
    Pseudoloris sp.
Rodentia
  Pseudosciuridae
    Sciuroides cf. *siderolithicus*
  Theridomyidae
    Pseudoltinomys crebrum
    Remys ibericus
Creodonta
  Hyaenodontidae
    Proviverra sp.
Perissodactyla
  Pachynolophidae
    Paranchilophus remyi
    Plagiolophus mazateronensis
    Plagiolophus sp.
    Leptolophus sp.
  Palaeotheriidae
    Palaeotherium giganteum
    Cantabrotherium casanovasae
    Franzenium durense
    Iberolophus jimenezi
Artiodactyla
  Dacrytheriidae
    cf. *Dacrytherium*
    cf. *Leptotheridium*
  Xiphodontidae
    cf. *Dichodon*
  Anoplotheriidae
    Duerotherium sudrei

Dental nomenclature, measurements, micrographs and pictures

The dental nomenclature employed is based on Hooker (1986) and Szalay and Delson (1979). Criteria used for tooth measurements are shown in Fig. 2. Measurements in Table 2 were made using an optic caliper Nikon Measuroscope 10 connected to a Nikon SC112 monitor. Micrographs of upper and lower dentition (Figs. 3 and 5) were taken using a Hitachi S-570 Scanning Electron Microscope. Drawings of mandible fragments (Fig. 4) and dental pieces (Supplemental Online Material) were made using a binocular Leica MZ 6 with a camera lucida. Pictures of mandible fragments (Supplemental Online Material) were taken using a Leica MZ16 A stereomicroscope connected to a computer.

Systematic paleontology

Order Primates Linnaeus, 1758
Suborder Euprimates Hoffstetter, 1977
Infraorder Strepsirrhini Geoffroy Saint-Hilaire, 1812
Superfamily Adapoidea Trouessart, 1879
Family Notharctidae Trouessart, 1879
Subfamily Cercamoniinae Gingerich, 1975
Tribe Anchomomyini Szalay and Delson, 1979 (*sensu* Godinot, 1988)
Mazateronodon gen. nov.

Etymology

"Mazateron-": after the Mazaterón fossil site where this taxon was found; "-odon": meaning "tooth" in Greek.

Generic diagnosis

Lack of P$_1$, single-rooted P$_2$, P$_3$ larger than the P$_4$, P$_3$ and P$_4$ imbricated and highly buccolingually compressed, lower molars lacking paraconid and hypoconulid lobe lingually placed in the M$_3$. Upper molars with reduced paraconule and hypocone, and lacking pericone and metaconule.

Mazateronodon endemicus sp. nov.

Etymology

The species name "endemicus" was chosen because of the endemic character of the Almazán Basin fauna.

Holotype

Left mandible fragment with complete lower canine, alveolus for P$_2$, and complete P$_3$ and P$_4$ (IPS46238).

Hypodigm

Three left I$_{1-2}$ (IPS46207, IPS46208 and IPS46214), five right I$_{1-2}$ (IPS46209-IPS46213), one left I$_2$ (IPS46215), one right lower canine (IPS46216), one left lower canine (IPS46217), one right P$_3$ (IPS46218), one possible left P$_3$ (IPS46219), two left P$_3$ (IPS46220 and IPS46221), two right P$_{3-4}$ (IPS46222 and IPS46224), one left P$_{3-4}$ (IPS46223), two left P$_4$ (IPS46225 and IPS46226), two right P$_4$ (IPS46227 and IPS46228), two right M$_1$ (IPS46229 and IPS46230), two left M$_2$ (IPS46231 and IPS46232), one right M$_2$ (IPS46233), two left M$_3$ (IPS46234 and IPS46235), one right M$_3$ (IPS46236), one right mandible fragment with M$_2$ and M$_3$ (IPS46237), one right mandible fragment with P$_3$ and P$_4$ (IPS46239), one left I^1 (IPS46241), one right I^2 (IPS46240), one right upper canine (IPS46242), one left P^2 (IPS46243), three P^3 (IPS46244-IPS46246), five right P^4 (IPS46247, IPS46248, IPS46252-IPS46254), three left P^4 (IPS46249, IPS46251 and IPS46255), one P^4 (IPS46250), five left M$^{1-2}$ (IPS46256, IPS46257, IPS46259, IPS46260 and IPS46265), four right M$^{1-2}$ (IPS46261-IPS46264), one M$^{1-2}$ (IPS46258), three right M^3 (IPS46266, IPS46270 and IPS46271), four left M^3 (IPS46267-IPS46269 and IPS46272).

Locality and horizon

Mazaterón (Soria, Castilla y León, Spain). Almazán Basin, Mazaterón Formation, late Robiacian (MP 15–16) (Fig. 1).

Description

Only one I$_{1-2}$ specimen is perfectly preserved (IPS46209, see Fig. 3). It has a high crown that narrows mesiodistally to the apex, and is slightly rounded and buccolingually compressed at the end. The crown is slightly curved lingually. A small cingulid crosses the lingual face vertically from nearly the base of the crown to the apex, dividing the lingual side of the crown in two parts; the distal part is wider and more depressed than the mesial part. A small rib encloses the distal depression of the lingual side of the crown, extending distiolingually from the base of the crown to the center. The buccal side is flat and smooth. The I$_{1-2}$ specimen has a single very long and mesiolaterally compressed root. From the base of the crown to the base of the root, the tooth widens and at half-length it starts to narrow mesiodistally. On the mesial and distal sides, a small valley crosses the whole root from top to bottom, making a slight split of the root in two parts. One I$_2$ (IPS46215) presents one contact facet on the mesial side, indicating contact with I$_1$. In the specimens that have the whole or most of the root preserved the roots are not straight. The root-crown complex curvature can be seen in Fig. 3.

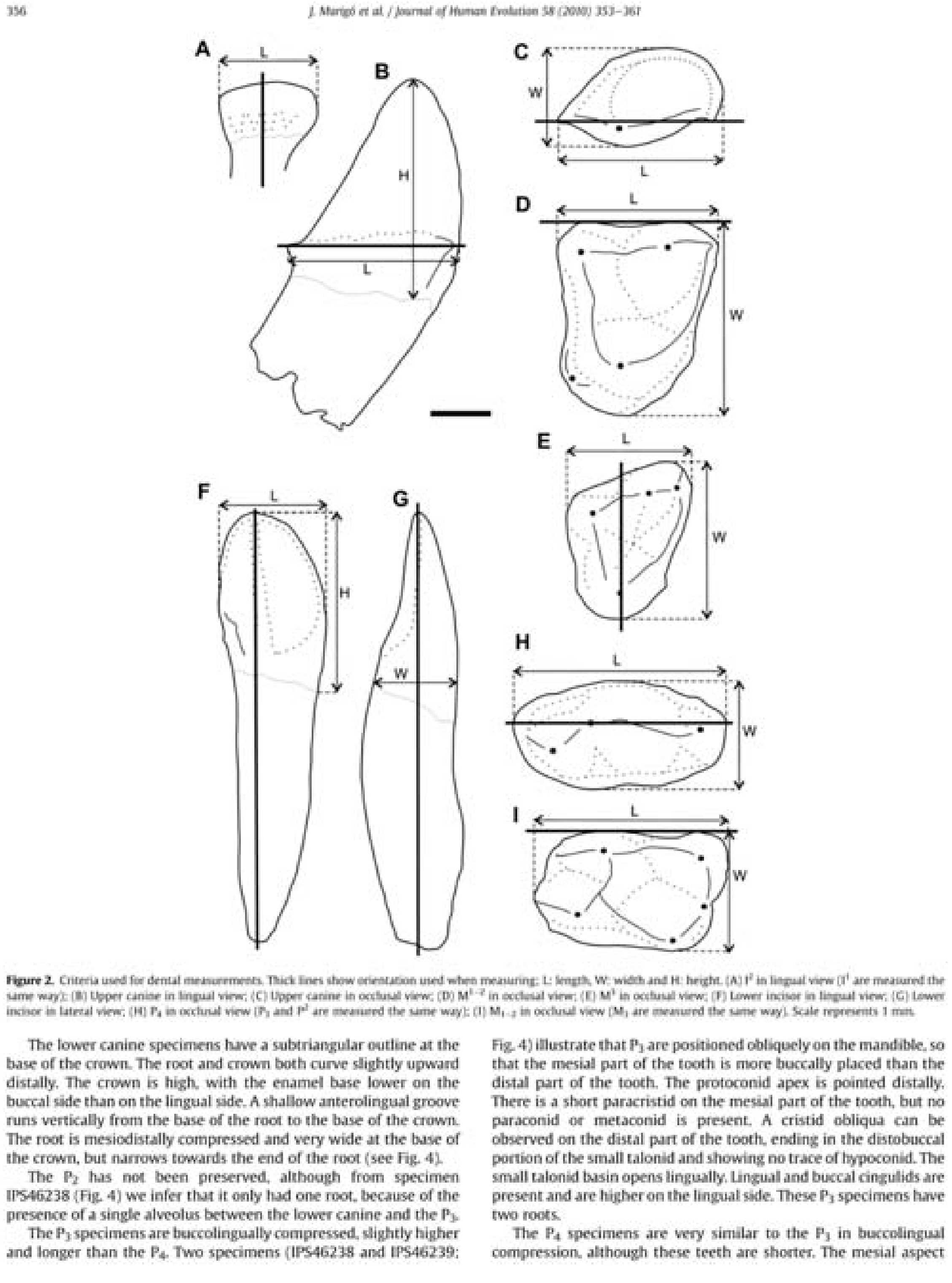

Figure 2. Criteria used for dental measurements. Thick lines show orientation used when measuring; L: length, W: width and H: height. (A) I^2 in lingual view (I^1 are measured the same way); (B) Upper canine in lingual view; (C) Upper canine in occlusal view; (D) M^{1-2} in occlusal view; (E) M^3 in occlusal view; (F) Lower incisor in lingual view; (G) Lower incisor in lateral view; (H) P_4 in occlusal view (P_3 and P^2 are measured the same way); (I) M_{1-2} in occlusal view (M_3 are measured the same way). Scale represents 1 mm.

The lower canine specimens have a subtriangular outline at the base of the crown. The root and crown both curve slightly upward distally. The crown is high, with the enamel base lower on the buccal side than on the lingual side. A shallow anterolingual groove runs vertically from the base of the root to the base of the crown. The root is mesiodistally compressed and very wide at the base of the crown, but narrows towards the end of the root (see Fig. 4).

The P_2 has not been preserved, although from specimen IPS46238 (Fig. 4) we infer that it only had one root, because of the presence of a single alveolus between the lower canine and the P_3.

The P_3 specimens are buccolingually compressed, slightly higher and longer than the P_4. Two specimens (IPS46238 and IPS46239; Fig. 4) illustrate that P_3 are positioned obliquely on the mandible, so that the mesial part of the tooth is more buccally placed than the distal part of the tooth. The protoconid apex is pointed distally. There is a short paracristid on the mesial part of the tooth, but no paraconid or metaconid is present. A cristid obliqua can be observed on the distal part of the tooth, ending in the distobuccal portion of the small talonid and showing no trace of hypoconid. The small talonid basin opens lingually. Lingual and buccal cingulids are present and are higher on the lingual side. These P_3 specimens have two roots.

The P_4 specimens are very similar to the P_3 in buccolingual compression, although these teeth are shorter. The mesial aspect

Table 2
Measurements (mm) of dental elements of *Mazateronodon endemicus*. L: length), W: width, H: height, >: specimens with extreme wear or lacking a small part. Only those specimens where at least one measurement could be taken have been included

Specimen	Dental element	L	W	H
IPS-46207	I_{1-2}	>1.59	>1.09	>2.41
IPS-46208	I_{1-2}	1.53	1.31	–
IPS-46209	I_{1-2}	1.63	1.29	2.40
IPS-46210	I_{1-2}	1.69	1.28	–
IPS-46211	I_{1-2}	1.60	1.21	>2.40
IPS-46215	I_2	1.62	1.22	–
IPS-46218	P_3	> 2.74	> 1.18	
IPS-46220	P_3	–	1.44	
IPS-46223	P_{3-4}	>2.49	>1.05	
IPS-46226	P_4	>2.89	>1.41	
IPS-46228	P_4	–	1.58	
IPS-46229	M_1	3.13	–	
IPS-46232	M_2	2.90	1.84	
IPS-46233	M_2	2.89	1.86	
IPS-46234	M_3	2.74	1.72	
IPS-46237	M_2	3.00	1.94	
	M_3	2.64	1.87	
IPS-46238	P_3	>3.26	>1.58	
	P_4	3.08	1.51	
IPS-46239	P_3	3.63	1.80	
	P_4	> 3.23	1.65	
IPS-46241	I^1	1.53	1.18	>2.45
IPS-46240	I^2	1.58	0.57	>0.94
IPS-46242	Upper C	2.82	1.63	>3.10
IPS-46243	P^2	1.52	1.20	
IPS-46248	P^4	2.35	–	
IPS-46249	P^4	2.26	–	
IPS-46251	P^4	2.48	–	
IPS-46263	M^{1-2}	2.53	3.13	
IPS-46266	M^3	2.08	2.45	
IPS-46267	M^3	>1.97	>2.54	
IPS-46268	M^3	>1.93	>2.65	
IPS-46269	M^3	>1.97	2.67	
IPS-46270	M^3	>1.87	>2.31	
IPS-46271	M^3	>1.88	>2.53	
IPS-46272	M^3	1.89	>2.41	

has a small paraconid followed by a short paracristid. The protoconid is larger but a little bit shorter than in the P_3; it occupies the center of the tooth, pointing distally. No metaconid is present. On the distal part of the tooth a small hypoconid and a short cristid obliqua are present; these are much larger than those of the P_3. The talonid basin is also somewhat broader than that of the P_3, but also opens lingually. Buccal and lingual cingulids are present; the lingual cingulid is higher than the buccal cingulid. These teeth have two roots.

The M_1 teeth are more buccolingually compressed than M_2 teeth. Neither M_1 nor M_2 specimens have a paraconid, just a small paracristid located on the mesial part of the tooth. There is a high protoconid and metaconid, and both are similarly developed. In the M_1 the metaconid is located more distally with respect to the protoconid than in the M_2. A premetacristid and protocristid are present, as well as a well-developed buccal cingulid and a broad talonid basin. The entoconid and hypoconid are similarly developed, although the entoconid is more distally placed. There is a very small hypoconulid directed buccally, closer to the hypoconid than to the entoconid. These specimens have two roots.

The shape of the M_3 trigonid and the orientation of the cristid obliqua are very similar to that of the M_2, although the hypoconid is more buccally placed. The hypoconulid lobe is elongated mesiodistally and lingually placed, very close to the entoconid. The talonid basin is more buccolingually compressed than the M_2. These specimens have two roots.

The specimen IPS46241 is tentatively assigned to an I^1, although the scarcity of comparison material of this group does not allow a conclusive determination. The crown is higher than it is long, and it is curved lingually to the apex. The base of the crown is thick, but thins buccolingually and towards the apex, forming a subtriangular depression in the latter. This specimen is broken at the base of the crown and the root is not preserved.

Similarly, the specimen IPS46240 is tentatively assigned to I^2. The crown is longer than it is high, making it almost rectangular in shape. The buccal side is flat and smooth, but the lingual side has some enamel wrinkling at the center, from the base of the crown halfway up the lingual surface. Where wrinkling is present, the crown is also depressed, whereas on either side of the wrinkled area the crown is thicker, with thinning to the apex. No contact surfaces are noticeable. The apex curves slightly lingually. This specimen presents only one buccolingually compressed root.

Only one upper canine specimen, showing moderate wear, is preserved (IPS46242). The crown and single root are both buccolingually compressed. The crown has an oval outline that is elongated and curved posteriorly and lingually to the apex, which is very pointed. The buccal cingulum is well-developed, and is closer to the apex on the mesial side than on the distal aspect. No lingual cingulum is present.

In the absence of evidence for a P^1, P^2 is judged to have followed the upper canine. Only one specimen was recovered (IPS46243). The tooth is well preserved, even though the tip of the crown is broken. The mesial end is rounded with a pointed distal end. Labial and buccal cingula surround the whole tooth and are higher on lingual side. There is no protocone, but there is a high paracone that is curved distally to the apex, occupying most of the tooth. Postprotocrista are present, ending at a pointed distal tooth-end. There is no metacone. This specimen has a single root.

All P^3 specimens have either a broken crown or extreme wear. They are subtriangular in shape and have a small, but present metastyle and parastyle. The paracone occupies most of the tooth. Preparacrista and postparacrista are present. There is a small lingual extension without a distinct protocone. Buccal and lingual cingula surround the tooth. There are two roots, in anterior and posterior positions.

The paracone of the P^4 is the most prominent cusp, centered on the buccal side. On both sides of the paracone, a small parastyle and a metastyle are present. There is neither a paraconule nor a metaconule. The protocone lobe is buccolingually wide, but mesiodistally short, and the protocone is moderately large on the lingual side of the tooth. Preprotocrista is present, as well as a short crista directed distally from the protocone apex. There is no hypocone and narrow trigon basin. The P^4 has three roots.

The structure of M^{1-2} is essentially tribosphenic. A small hypocone is present. The paracone is slightly larger than the metacone, making the metacone the least prominent of the three main cusps. There is a small paraconule, no metaconule, and a broad trigon basin. The protocone lobe is larger and broader than that of the P^4. A prominent anterocingulum runs from the base of the protocone nearly to the base of the paraconule. There is no pericone. The postcingulum is less prominent than the anterocingulum. There is no mesostyle, but there is a weak metastyle and parastyle. There are three roots.

The M^3 has a subtriangular outline, elongated to the mesiobuccal side. The paracone is prominent, and the metacone is reduced when compared to the paracone and the protocone. Neither a metaconule nor a paraconule is present, but there is a well-developed postcingulum and anterocingulum, the former extending from the lingual base of the protocone to the base of the metacone, and the latter extending from the lingual base of the protocone to the buccal base of the protocone. The M^3 has a broad trigon basin. There is intraspecific variability in the presence/

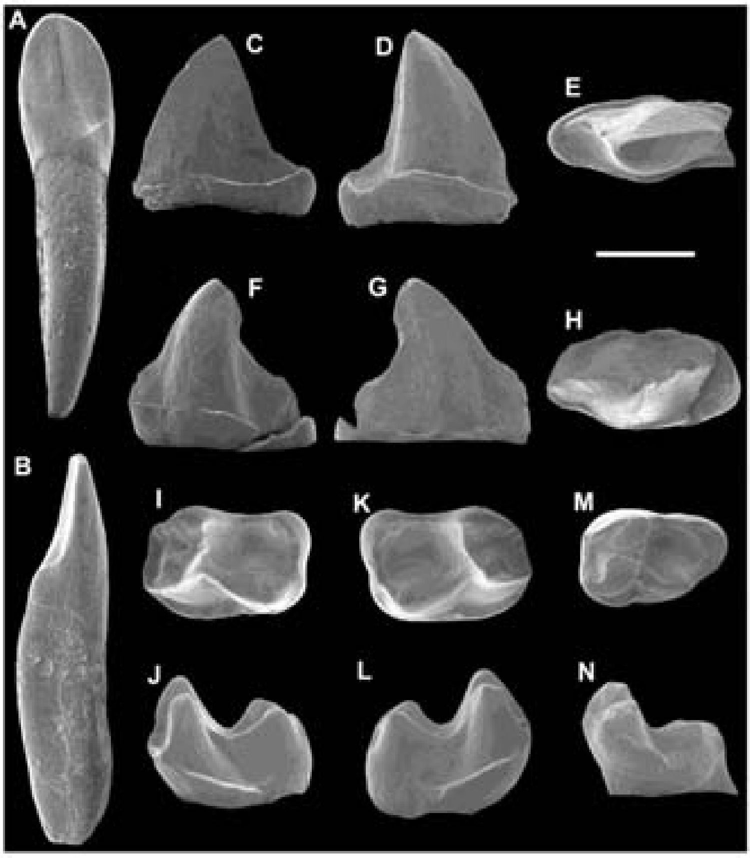

Figure 3. Micrograph of lower dentition of *Mazateronodon endemicus*. (A) Right lower incisor in lingual view (IPS46209); (B) Right lower incisor in lateral view (IPS46209); (C) Left P_3 in labial view (IPS46220); (D) Left P_3 in lingual view (IPS46220); (E) Left P_3 in occlusal view (IPS46220); (F) Right P_4 in lingual view (IPS46227); (G) Right P_4 in labial view (IPS46227); (H) Right P_4 in occlusal view (IPS46227); (I) Left M_2 in occlusal view (IPS46232); (J) Left M_2 in labial view (IPS46232); (K) Right M_2 in occlusal view (IPS46233); (L) Right M_2 in labial view (IPS46233); (M) Left M_1 in occlusal view (IPS46234); (N) Left M_1 in labial view (IPS46234). Scale represents 1.5 mm.

absence of a postparaconule crista. Of the specimens available, one has a postparaconule crista (IPS46269), another one does not have it (IPS46266) and the rest show such extreme wear that presence or absence cannot be determined. There are three roots.

Comparisons

All the members of the tribe Anchomomyini share a small hypocone, lack a distinct metaconule, and show the presence of the entoconid more distolingual to the hypoconid than that of the Microadapini (Szalay and Delson, 1979). They also have narrow premolars (although P_4 extends posteriorly), and a low degree of molarization (Godinot, 2006), so the new taxon can be attributed to this tribe.

Mazateronodon differs from all the species of the genus *Periconodon* because it lacks a pericone, has a considerably reduced hypocone, no trace of an incipient metaconule, and more lingually placed hypoconulid lobe on the M_3. Regarding the P_4, *P. huerzeleri* has a less developed paraconid and the hypoconid is almost aligned with the mesiodistal axis of the tooth, whereas *Mazateronodon* specimens have a much more buccally placed hypoconid and a broader talonid basin. Moreover, the M_1 of *P. huerzeleri* have an incipient or small paraconid and all lower molars present a better-developed paracristid. The cristid obliqua extends more lingually, to the base where protoconid and metaconid cusps meet. When compared to *P. huerzeleri*, *Mazateronodon* lower molars have a more lingually placed hypoconulid and a more mesially placed hypoconid. The material of *Periconodon huerzeleri* shows smaller P_4 and larger upper and lower molars than *Mazateronodon* specimens.

Mazateronodon can be distinguished from *Buxella* because it lacks a pericone, has a much more reduced hypocone, a more buccal cristid obliqua, a much more lingual hypoconulid lobe, a less developed premetacristid and it lacks a paraconid in the M_1. The hypoconulid lobe in *Buxella prisca* is located on the mesiodistal axis of the tooth. Despite an overall smaller size, P_3 of *Buxella prisca* is less buccolingually compressed than those of *Mazateronodon*. Lower molars of *Mazateronodon* are closer in size to those of *B. prisca*, although they are relatively narrower.

In fact, the most similar genus to *Mazateronodon* is *Anchomomys*, a taxon created by Stehlin (1916) with *A. quercyi* as type species, sharing the absence of the metaconule and the pericone,

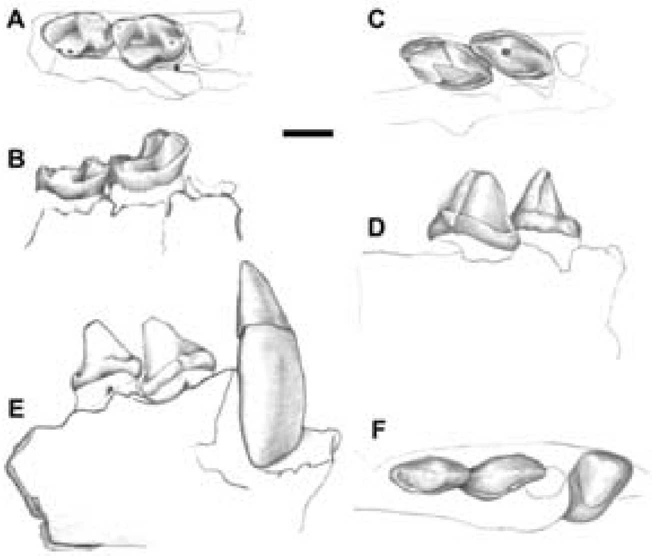

Figure 4. Drawings of mandible fragments of *Mazateronodon endemicus*. (A) Right mandible fragment with distal alveolus for M_1, and complete M_2 and M_3 in occlusal view (IPS46237); (B) Right mandible fragment with distal alveolus for M_1, and complete M_2 and M_3 in buccal view (IPS46237); (C) Right mandible fragment with alveolus for P_2, and complete P_3 and P_4, plus mesial alveolus for M_1 in occlusal view (IPS46239); (D) Right mandible fragment with alveolus for P_2, and complete P_3 and P_4, plus mesial alveolus for M_1 in lingual view (IPS46239); (E) Left mandible fragment with lower canine, alveolus for P_2, and complete P_3 and P_4 in lingual view (IPS46238); (F) Left mandible fragment with lower canine, alveolus for P_2, and complete P_3 and P_4 in occlusal view (IPS46238). Scale represents 2 mm.

and the reduction or absence of the paraconid. However, it differs from *Anchomomys* in the peculiar morphology of the lower premolars. The P_3 is larger than the P_4, the premolars are extremely buccolingually compressed, highly imbricated with overlapping crowns, and both buccal and lingual cingulids. Moreover, it also differs from *Anchomomys* in the overall shape of the upper molars, the reduced metacone and hypocone, the presence of a single root in the P^2, as well as its overall large size. The lower molars of *Mazateronodon* resemble those of *A. gaillardi*, although they are much larger and have a less developed paraconule and hypocone. Additionally, the protoconid is less developed, the cristid obliqua and the hypoconulid are more buccally placed, and the M_3 of *Mazateronodon* show a shorter talonid with a poorly differentiated and lingually placed hypoconulid lobe, whereas the hypoconulid lobe of *A. gaillardi* is huge and centered in the mesiodistal axis of the tooth.

Moyà-Solà and Köhler (1993) assigned the adapoid found in the fossil site Sant Jaume de Frontanyà-3C (SJF-3C) to *Anchomomys* nov. sp., and stated it was closely related to *A. pygmaeus* from Egerkingen. *Anchomomys* from SJF-3C is much smaller than *Mazateronodon*, has a small but distinct paraconid on M_1, a more mesial cristid obliqua in M_1 and M_2, a more mesially placed hypoconulid, and a narrower talonid basin in the lower molars. M^{1-2} from SJF-3C have a more developed paraconule and a less developed paracone than *Mazateronodon*. There is also an incipient metaconule in the better-preserved specimens from SJF-3C. In general, cusps of the upper molars from SJF-3C look sharper than those of *Mazateronodon*.

Another adapoid (not yet described) from the Caenes fossil site is housed in the Institut Català de Paleontologia and was assigned to the genus *Anchomomys* by Moyà-Solà and Köhler (1992). The only material attributed to this taxon is a mandible fragment with alveolus for P_2 and P_3, a partial P_4, a partial M_1, a complete M_2 and alveolus for M_3 (IPS46288). The *Anchomomys* from Caenes has a double-rooted P_2, inferred from the alveolus, and this differs from *Mazateronodon*. The material from Caenes is not very well preserved, although it is much smaller than *Mazateronodon*. The P_4 specimens from Caenes are much less laterally compressed, much more symmetric and have a less-developed hypoconid than the specimens of *Mazateronodon*. Moreover, the talonid basin is even broader than in *Mazateronodon*. Not much can be seen of the M_1 from Caenes, since only the protoconid is preserved. The M_2 differs from *Mazateronodon* because the metaconid is better developed than the protoconid and the hypoconulid and cristid obliqua are more mesially placed.

Certain similarities, in particular the overall lower molar shape, the more distally placed entoconid compared to the hypoconid and lack of a paraconid on M_2, seem to exist between the new genus and the material assigned to *Anchomomys* from Caenes (Duero Basin) and SJF-3C (Pyrenean Basin), although this material is not yet described in full detail.

Paleobiogeographic implications

The specific morphological characters of *Mazateronodon* have interesting biogeographic implications. Crusafont et al. (1954) first noticed that Iberian Peninsula Eocene faunas presented a certain degree of endemism when compared to those of Europe (see also Crusafont, 1961; Casanovas-Cladellas and Santafé-Llopis, 1987; Cuesta, 1988; Jiménez et al., 1989). Casanovas-Cladellas and Santafé-Llopis (1989, 1991) suggested the existence of a western region in the Iberian Peninsula (WRIP) that presented high endemism during the Eocene. They proposed that the isolation phase might have taken place during the Eocene marine transgression, connecting the Cantabric and the Mediterranean seas, isolating the WRIP from the Pyrenean Basins and the rest of Europe. The WRIP was formerly defined as the Western Iberian Bioprovince by Cuesta (1991). Endemism of other taxa (e.g., Perissodactyla and Artiodactyla [Cuesta, 1991; Badiola and Cuesta, 2008; Cuesta and Badiola, 2009])

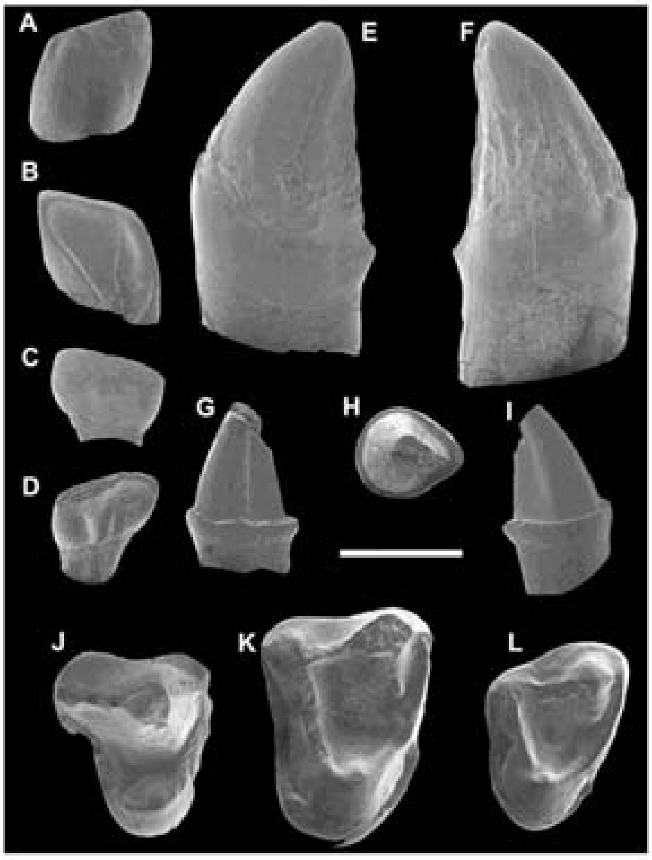

Figure 5. Micrograph of upper dentition of *Mazateronodon endemicus*. (A) Specimen tentatively assigned to left I^1 in buccal view (IPS46241); (B) Specimen tentatively assigned to left I^1 in lingual view (IPS46241); (C) Specimen tentatively assigned to right I^2 in buccal view (IPS46240); (D) Specimen tentatively assigned to right I^2 in lingual view (IPS46240); (E) Right upper canine in labial view (IPS46242); (F) Right upper canine in lingual view (IPS46242); (G) Left P^2 in lingual view (IPS46243); (H) Left P^2 in occlusal view (IPS46243); (I) Left P^2 in labial view (IPS46243); (J) Right P^4 in occlusal view (IPS46254); (K) Right M^{1-2} in occlusal view (IPS46263)); (L) Right M^3 in occlusal view (IPS46266). Scale represents 1.5 mm.

suggests that the unique characteristics of *Mazateronodon*, compared to all other previously described anchomomyins from the rest of Europe, could be explained by the isolation of the Duero Basin during the Eocene. Some similarities with the material of *Anchomomys* from Caenes (Salamanca) and SJF-3C (Barcelona) confirm an autochthonous origin of the genus *Mazateronodon*.

Summary and conclusions

A new genus and species from the fossil site of Mazaterón (Robiacian, Middle Eocene) is assigned to the tribe Anchomomyini. Almost all the dental elements are described, and for the first time the anterior dentition (upper and lower canines and incisors) are available for a member of the Anchomomyini. The material of the new genus and species presented here is the richest Eocene primate assemblage from the Western Iberian Bioprovince described until now. *Mazateronodon* differs morphologically and biometrically from all the other members of the tribe Anchomomyini. It shows extremely buccolingually compressed P_3 and P_4, a P_3 that is larger than the P_4, highly imbricated premolars, with overlapping crowns, and both buccal and lingual cingulids. Some similarities with the material assigned to *Anchomomys* from Caenes (Duero Basin) and SJF-3C (Pyrenean Basin) strongly suggest an Iberian origin of this taxon. In accordance, the unique features of *Mazateronodon* support the idea that the Eocene fauna of the Duero Basin is highly endemic as a consequence of the Eocene marine transgression connecting the Cantabric and the Mediterranean seas, isolating the WRIP (Western Iberian Bioprovince) from the rest of Europe.

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Appendix. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.jhevol.2010.01.011.

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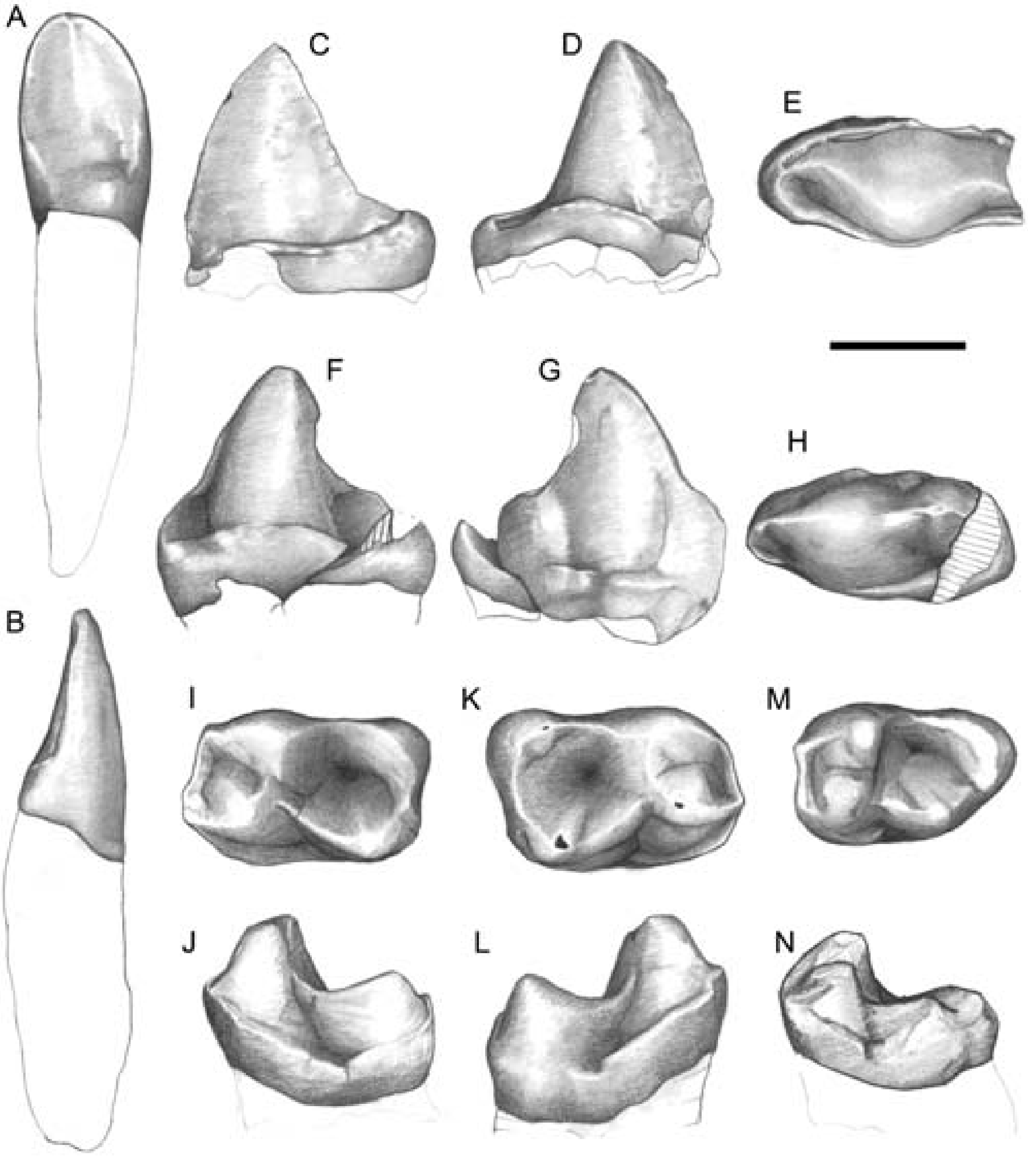
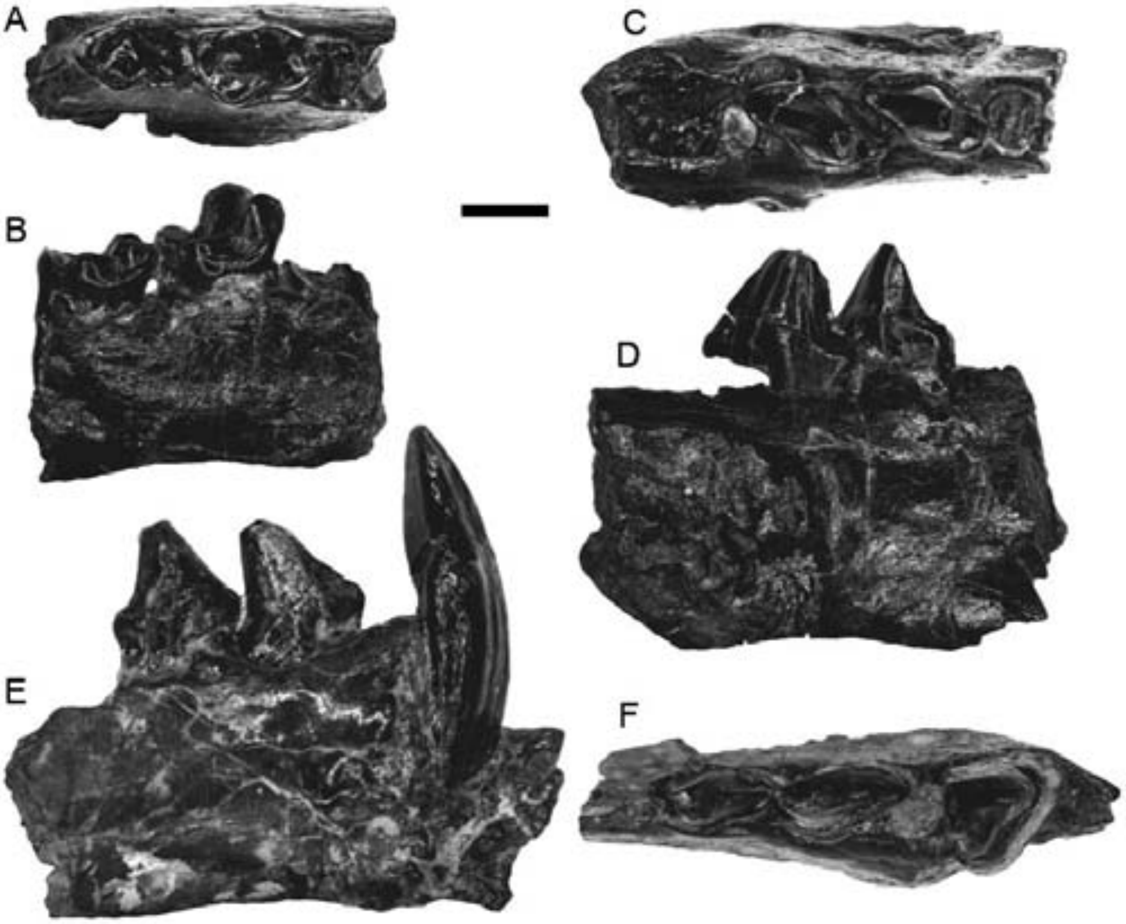
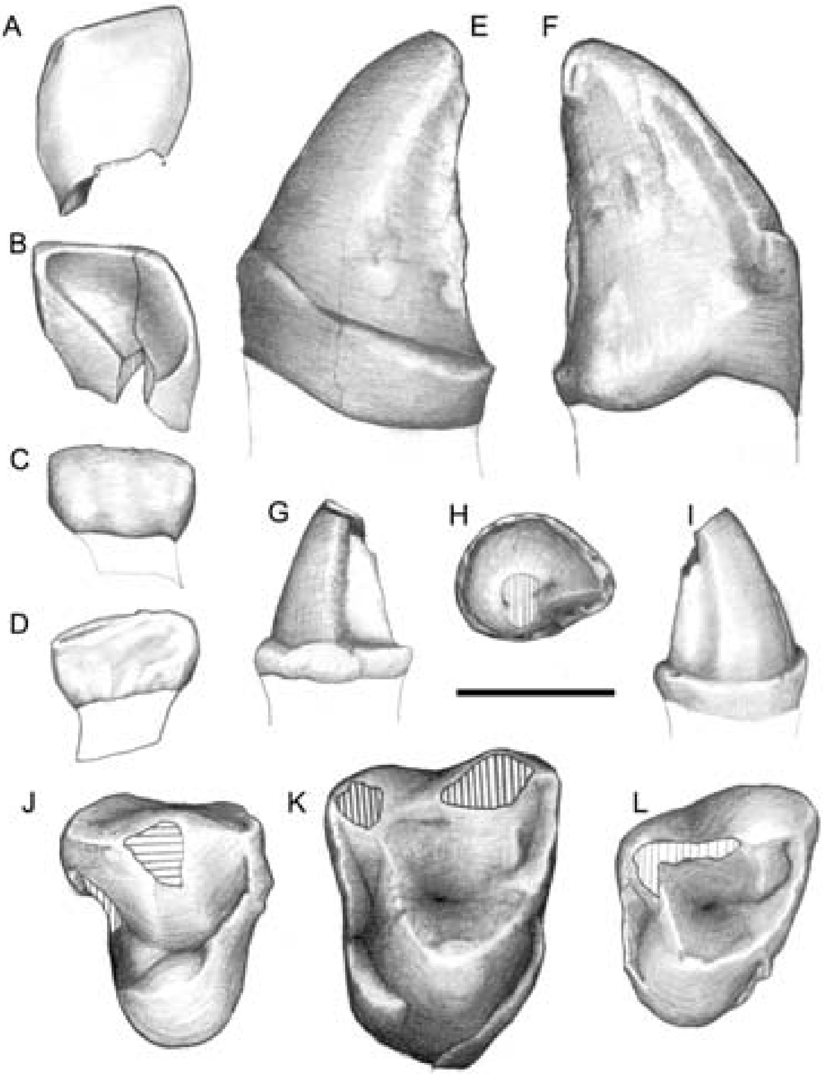
Supplementary data (Supplemental Online Material):



Drawings of lower dentition of *Mazateronodon endemicus*. (A) Right lower incisor in lingual view (IPS46209); (B) Right lower incisor in lateral view (IPS46209); (C) Left P_3 in labial view (IPS46220); (D) Left P_3 in lingual view (IPS46220); (E) Left P_3 in occlusal view (IPS46220); (F) Right P_4 in lingual view (IPS46227); (G) Right P_4 in labial view (IPS46227); (H) Right P_4 in occlusal view (IPS46227); (I) Left M_2 in occlusal view (IPS46232); (J) Left M_2 in labial view (IPS46232); (K) Right M_2 in occlusal view (IPS46233); (L) Right M_2 in labial view (IPS46233); (M) Left M_3 in occlusal view (IPS46234); (N) Left M_3 in labial view (IPS46234). Scale represents 1.5 mm.



Pictures of mandible fragments of *Mazateronodon endemicus*. (A) Right mandible fragment with distal alveolus for M_1, and complete M_2 and M_3 in occlusal view (IPS46237); (B) Right mandible fragment with distal alveolus for M_1, and complete M_2 and M_3 in buccal view (IPS46237); (C) Right mandible fragment with alveolus for P_2, and complete P_3 and P_4, plus mesial alveolus for M_1 in occlusal view (IPS46239); (D) Right mandible fragment with alveolus for P_2, and complete P_3 and P_4, plus mesial alveolus for M_1 in lingual view (IPS46239); (E) Left mandible fragment with lower canine, alveolus for P_2, and complete P_3 and P_4 in lingual view (IPS46238); (F) Left mandible fragment with lower canine, alveolus for P_2, and complete P_3 and P_4 in occlusal view (IPS46238). Scale represents 2 mm.



Drawing of upper dentition of *Mazateronodon endemicus*. (A) Right I^1 in labial view (IPS46240); (B) Right I^1 in lingual view (IPS46240); (C) specimen tentatively assigned to left I^2 in labial view (IPS46241); (D) specimen tentatively assigned to left I^2 in lingual view (IPS46241); (E) Right upper canine in labial view (IPS46242); (F) Right upper canine in lingual view (IPS46242); (G) Left P^2 in lingual view (IPS46243); (H) Left P^2 in occlusal view (IPS46243); (I) Left P^2 in labial view (IPS46243); (J) Right P^4 in occlusal view (IPS46254); (K) Right M^{1-2} in occlusal view (IPS46263)); (L) Right M^3 in occlusal view (IPS46266). Scale represents 1.5 mm.

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PSEUDOLORIS CUESTAI, A NEW MICROCHOERINE (PRIMATES, OMOMYIDAE) FROM THE MIDDLE EOCENE OF THE IBERIAN PENINSULA

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ARTICLE

PSEUDOLORIS CUESTAI, A NEW MICROCHOERINE (PRIMATES, OMOMYIDAE) FROM THE MIDDLE EOCENE OF THE IBERIAN PENINSULA

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ABSTRACT—A new species of *Pseudoloris* (Primates, Microchoerinae, Omomyidae) is described from the middle Eocene (Robiacian) locality of Mazaterón (Almazán Basin, Spain). *Pseudoloris cuestai* is characterized by its medium size, high and thick paracristid and absence of a distinct paraconid in the lower molars, large hypoconulid in the m3, well-developed protocone in the P3 and P4, reduced hypocone and presence of a weak postprotocingulum in the M1–2, and especially by the lower incisor, with a buccolingually enlarged crown and a very wide, anteroposteriorly compressed root. The material from Mazaterón constitutes the only record of the subfamily Microchoerinae in the Western Iberian Bioprovince, and is clearly different from the species of *Pseudoloris* that appear in the middle and late Eocene in the Pyrenean basins (*P. isabenae* from Capella, *P. parvulus* from Sossís, and the recently described *P. pyrenaicus* from Sant Jaume de Frontanyà). This discovery reinforces the endemic nature of the mammal faunas from this bioprovince, already observed in other groups such as Perissodactyla, Artiodactyla, Rodentia, and also evidenced in adapoid primates, with the recent description of the genus *Mazateronodon*.

INTRODUCTION

Omomyid primates represent some of the earliest members of the order, which were abundant and diverse in the Northern Hemisphere during the Eocene. They were small-bodied primates, similar to living galagids in form and locomotor adaptations (Gunnell and Rose, 2002). Compared to their contemporaries the adapoids, omomyids usually differ in being smaller, nocturnal, and incorporating more insects into their diets (see Tornow, 2008, and references therein). The family Omomyidae is currently divided into three subfamilies: the Omomyinae and Anaptomorphinae, found in North America, Europe, and Asia, and the Microchoerinae, limited to the European continent from early to late Eocene, with some genera (e.g., *Pseudoloris* Stehlin, 1916) lasting into the Oligocene (Köhler and Moyà-Solà, 1999). Representatives of this latter subfamily are scarce in the fossil record; however, very recent findings have contributed to increase the knowledge about Microchoerinae (Hooker, 2007; Hooker and Harrison, 2008).

Pseudoloris is a very small microchoerine, similar in some morphological features to the living *Tarsius* Storr, 1780, sharing strong dental convergences (Szalay and Delson, 1979). Its geographic distribution is limited to Spain, France, England, and Germany, and its remains are, in general, very scarce in the sites where it is identified, so the knowledge of the dental morphology of the genus remains incomplete. The incisors have been only figured for *P. parvulus* (Filhol, 1890) from Perrière (Godinot, 1983) and for *P. pyrenaicus* Minwer-Barakat, Marigó, and Moyà-Solà, 2010, from Sant Jaume de Frontanyà.

In the Iberian Peninsula, *Pseudoloris* has been recognized in several localities: Crusafont (1967) mentioned the presence of the genus in Spain for the first time, with the identification of *Pseudoloris parvulus* from Sossís, and the definition of two new species: *P. reguanti* Crusafont, 1967, from Sant Cugat de Gavadons and *P. isabenae* (Crusafont, 1967), originally ascribed to *Pivetonia*, from Capella. *Pseudoloris godinoti* Köhler and Moyà-Solà, 1999, was recognized in the Oligocene deposits from Fonollosa, representing the only microchoerine that survived the climatic deterioration of the Eocene–Oligocene boundary. Recently, Minwer-Barakat et al. (2010) described a new species of the genus from the Robiacian site of Sant Jaume the Frontanyà: *Pseudoloris pyrenaicus*. There are also some mentions to *Pseudoloris* without specific ascription (Peláez-Campomanes, 1995). All the mentioned sites are situated in the southern Pyrenean basins.

Several bioprovinces have been described in the European continent during the late Eocene, on the basis of regional differences in some groups of mammals, mainly rodents, primates, artiodactyls, and perissodactyls (e.g., Hartenberger, 1973; Sudre, 1978; Vianey-Liaud, 1991; Hooker, 1992). This faunal differentiation is especially marked between the western part of the Iberian Peninsula and the rest of Europe. During the middle and late Eocene, the mammal faunas from the western and central Iberian basins were clearly different to those from the southern Pyrenean basins (northeastern Iberia), these latter being similar to those from the southern part of the Central European Island, well represented in southern France and Switzerland (e.g., Casanovas and Santafé, 1987; Cuesta, 1991, 1999, 2003; Casanovas and Moyà-Solà, 1992; Peláez-Campomanes, 1993). On the basis of this faunal differentiation, Cuesta (1991) hypothesized the existence of the Western Iberian Bioprovince, which included several western and central Iberian basins (Duero, Almazán, and Oviedo basins) with middle Eocene mammal faunas different from those of the southern Pyrenean basins. Further detailed studies on different mammal groups, such as Rodentia, Artiodactyla, and, especially, Perissodactyla, have reinforced this hypothesis (Peláez-Campomanes, 1996; Peláez-Campomanes and López-Martínez, 1996; Cuesta, 1999; Badiola and Cuesta, 2008; Badiola et al., 2009; Cuesta and Badiola, 2009; among others). There is evidence that this bioprovince existed from the late middle Eocene to the late Eocene, because the perissodactyls found in the late

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Eocene beds of Zambrana (Miranda-Trebiño Basin; Headonian, MP18) are related to endemic forms from the late middle Eocene (Robiacian, MP15/16 and MP16) of the Duero, Almazán, and Oviedo basins (Badiola, 2004).

Contrarily to the abundance and diversity of perissodactyls (five genera and 16 species of equoids and five taxa of lophiodonts, which are unknown elsewhere in Europe, have been identified to date in the Western Iberian Bioprovince; Badiola and Cuesta, 2008), the record of Primates from this bioprovince is quite scarce and poorly known: there exist some mentions of Adapiformes from Caenes and Santa Clara in the Duero Basin (Moyà-Solà and Köhler, 1992), but the most diverse Primate assemblage of the bioprovince is that from Mazaterón in the Almazán Basin.

The site of Mazaterón has yielded three different forms of Primates, presented in two preliminary notes by Moyà-Solà and Köhler (1992) and Marigó et al. (2009), in which no specific determination was given. The most abundant is a small adapiform assigned to the tribe Anchomomyini, recently described as the new genus and species *Mazateronodon endemicus* Marigó, Minwer-Barakat, and Moyà-Solà, 2010. A second form corresponds to a larger adapiform only represented by a mandible fragment with m1–m3, tentatively assigned to *Adapis* Cuvier, 1821. Finally, 22 isolated teeth attributed to the genus *Pseudoloris* are described in detail for the first time in the present paper.

This finding represents the only mention of the subfamily Microchoerinae from the Western Iberian Bioprovince, and the westernmost record of the genus *Pseudoloris* known up to now. Therefore, the description of this new species has a great paleobiogeographical interest, contributing to understand the endemic nature of the faunas from this bioprovince, and the relationships with the taxa from other European areas.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The site of Mazaterón is placed near the village of Mazaterón, 40 km southeast of Soria (Castilla y León, Spain). It is situated in the Almazán Basin (Fig. 1), which constitutes the eastern sector of the Duero Basin and limits to the north with the Cameros Massif, to the northeast with the Aragonian branch of the Iberian Range, and to the south with the Castilian Branch of the Iberian Range.

The sedimentation in the Almazán Basin started in the middle Eocene, during the uplift of the Iberian Range in the context of the Alpine compression. The northern and northeastern sectors of the Almazán Basin are occupied mainly by Paleogene materials, representing fluvial systems, alluvial fans, lacustrine/palustrine systems, and evaporitic mudflats (Huerta and Armenteros, 2006). In the southern and western parts, the Paleogene rocks are covered by Neogene deposits. The maximum thickness of the Tertiary succession is estimated in 3500–4000 m (Huerta et al., 2006). The infill of the basin is divided in four depositional sequences, whose age cannot be established precisely due to the scarcity of paleontological data (Huerta and Armenteros, 2006).

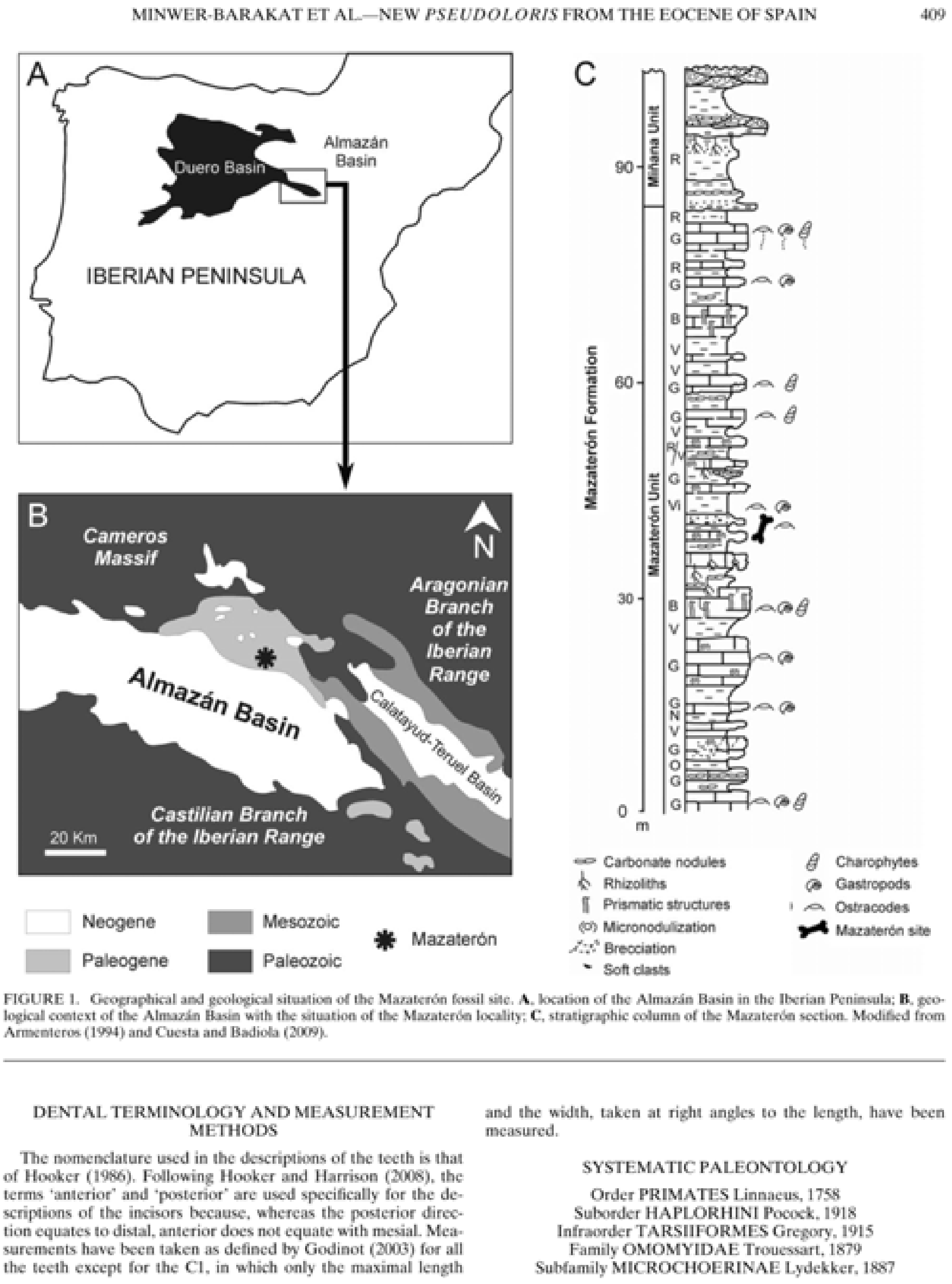
The site of Mazaterón, situated in the upper part of the lowest despositional sequence, about 350 m over the base of the Tertiary succession, is the oldest fossiliferous level identified in this basin. This level belongs to the Mazaterón Formation, which is composed by limestones, dolostones, and marls with lutitic intercalations, and represents a lake system with the central areas permanently inundated (Huerta et al., 2006). The grey marls that contain the vertebrate fossil remains correspond to lacustrine sediments deposited in the central anoxic bottom, and change laterally and vertically to palustrine deposits formed in seasonally exposed areas (Cuesta and Badiola, 2009).

TABLE 1. Updated faunal list of Mazaterón.[a]

- PISCES
    - Bagridae indet.
- REPTILIA
    - Chelonia
        - Testudinidae
            - *Hadrianus* sp.
        - Pelomedusidae
            - *Neochelys* sp.
        - Trionychidae
            - *Trionyx* sp.
    - Crocodylia
        - Alligatoridae
            - *Diplocynodon* sp.
        - Baurusuchidae
            - *Iberosuchus* sp.
        - Crocodylia indet.
    - Squamata
        - ? Lacertidae
- MAMMALIA
    - Primates
        - Notharctidae
            - *Mazateronodon endemicus*
        - Adapidae
            - cf. *Adapis*
        - Omomyidae
            - *Pseudoloris cuestai*, sp. nov.
    - Rodentia
        - Pseudosciuridae
            - *Sciuroides* cf. *siderolithicus*
        - Theridomyidae
            - *Pseudoltinomys crebrum*
            - *Remys ibericus*
    - Creodonta
        - Hyaenodontidae
            - *Proviverra* sp.
    - Perissodactyla
        - Pachynolophidae
            - *Paranchilophus remyi*
        - Palaeotheriidae
            - *Plagiolophus mazateronensis*
            - *Plagiolophus* sp.
            - *Leptolophus* sp.
            - *Iberolophus jimenezi*
            - *Palaeotherium medium*
            - *Cantabrotherium casanovasae*
            - *Franzenium durense*
        - Lophiodontidae
            - *Lophiodon* sp.
    - Artiodactyla
        - Dacrytheriidae
            - cf. *Dacrytherium*
            - cf. *Leptotheridium*
        - Xiphodontidae
            - cf. *Dichodon*
        - Anoplotheriidae
            - *Duerotherium sudrei*

[a]After Peláez-Campomanes, 1996; Cuesta, 1999; Cuesta, 2003; Badiola and Cuesta, 2008; Cuesta and Badiola, 2009; and Marigó et al., 2010.

Mazaterón has yielded the richest Eocene continental fauna of the Duero Basin: 27 vertebrate taxa have been identified, including fishes, turtles, crocodiles, saurians, primates, rodents, creodonts, perissodactyls, and artiodactyls (Cuesta and Jiménez-Fuentes, 1994; Cuesta, 1999, 2003). The mammal fossil assemblage can be assigned to the MP15–16 Paleogene reference level (Cuesta, 1991; Cuesta and Jiménez-Fuentes, 1994; Peláez-Campomanes, 1996), corresponding to the late Robiacian, which is roughly equivalent to the late Lutetian–Bartonian stages (for correlations see Luterbacher et al., 2004, and references therein). Table 1 shows an updated vertebrate faunal list of the locality.



MINWER-BARAKAT ET AL.—NEW *PSEUDOLORIS* FROM THE EOCENE OF SPAIN 409

FIGURE 1. Geographical and geological situation of the Mazaterón fossil site. **A**, location of the Almazán Basin in the Iberian Peninsula; **B**, geological context of the Almazán Basin with the situation of the Mazaterón locality; **C**, stratigraphic column of the Mazaterón section. Modified from Armenteros (1994) and Cuesta and Badiola (2009).

DENTAL TERMINOLOGY AND MEASUREMENT METHODS

The nomenclature used in the descriptions of the teeth is that of Hooker (1986). Following Hooker and Harrison (2008), the terms 'anterior' and 'posterior' are used specifically for the descriptions of the incisors because, whereas the posterior direction equates to distal, anterior does not equate with mesial. Measurements have been taken as defined by Godinot (2003) for all the teeth except for the C1, in which only the maximal length and the width, taken at right angles to the length, have been measured.

SYSTEMATIC PALEONTOLOGY

Order PRIMATES Linnaeus, 1758
Suborder HAPLORHINI Pocock, 1918
Infraorder TARSIIFORMES Gregory, 1915
Family OMOMYIDAE Trouessart, 1879
Subfamily MICROCHOERINAE Lydekker, 1887

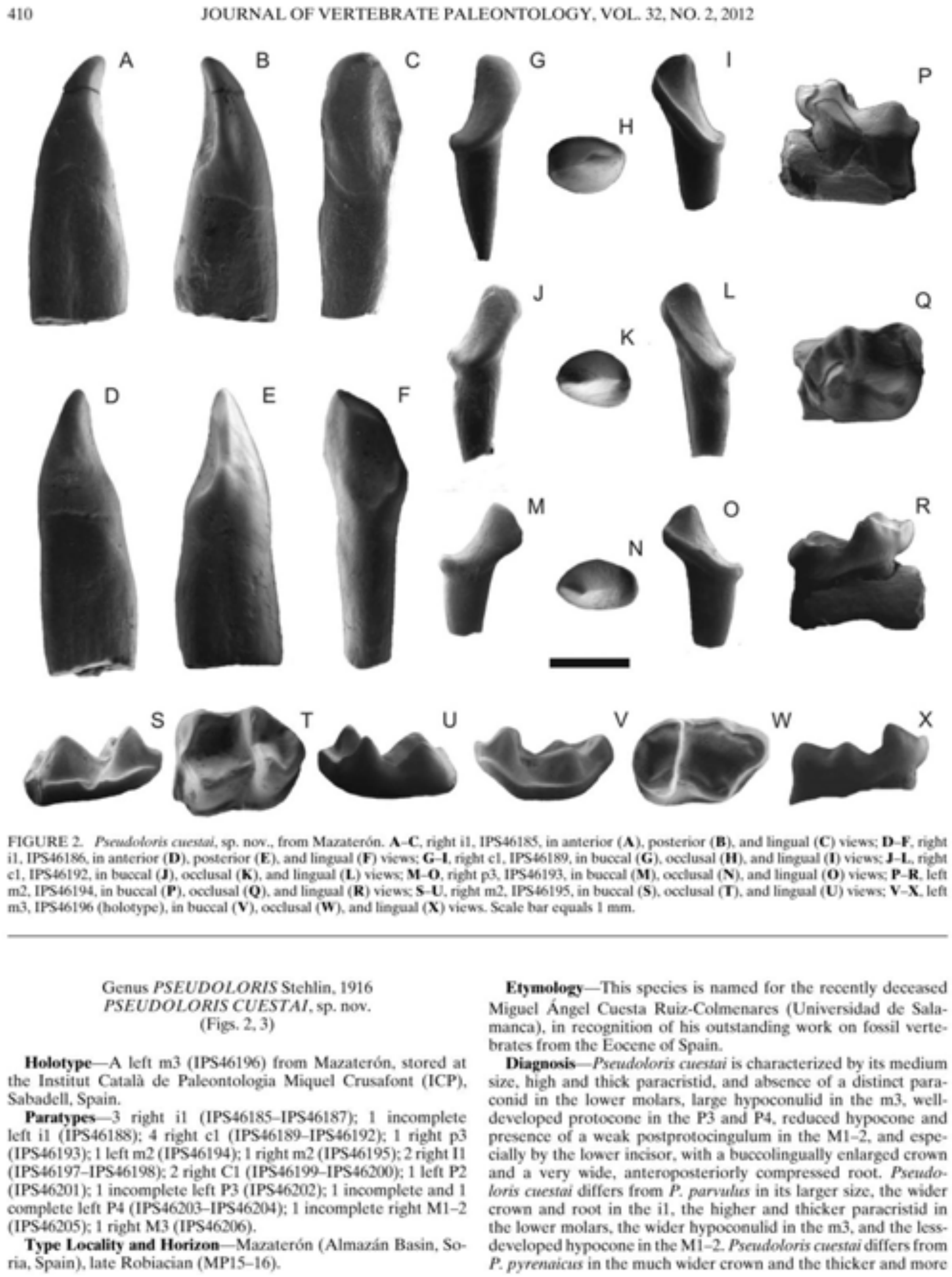


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FIGURE 2. *Pseudoloris cuestai*, sp. nov., from Mazaterón. **A–C**, right i1, IPS46185, in anterior (**A**), posterior (**B**), and lingual (**C**) views; **D–F**, right i1, IPS46186, in anterior (**D**), posterior (**E**), and lingual (**F**) views; **G–I**, right c1, IPS46189, in buccal (**G**), occlusal (**H**), and lingual (**I**) views; **J–L**, right c1, IPS46192, in buccal (**J**), occlusal (**K**), and lingual (**L**) views; **M–O**, right p3, IPS46193, in buccal (**M**), occlusal (**N**), and lingual (**O**) views; **P–R**, left m2, IPS46194, in buccal (**P**), occlusal (**Q**), and lingual (**R**) views; **S–U**, right m2, IPS46195, in buccal (**S**), occlusal (**T**), and lingual (**U**) views; **V–X**, left m3, IPS46196 (holotype), in buccal (**V**), occlusal (**W**), and lingual (**X**) views. Scale bar equals 1 mm.

Genus *PSEUDOLORIS* Stehlin, 1916
PSEUDOLORIS CUESTAI, sp. nov.
(Figs. 2, 3)

Holotype—A left m3 (IPS46196) from Mazaterón, stored at the Institut Català de Paleontologia Miquel Crusafont (ICP), Sabadell, Spain.

Paratypes—3 right i1 (IPS46185–IPS46187); 1 incomplete left i1 (IPS46188); 4 right c1 (IPS46189–IPS46192); 1 right p3 (IPS46193); 1 left m2 (IPS46194); 1 right m2 (IPS46195); 2 right I1 (IPS46197–IPS46198); 2 right C1 (IPS46199–IPS46200); 1 left P2 (IPS46201); 1 incomplete left P3 (IPS46202); 1 incomplete and 1 complete left P4 (IPS46203–IPS46204); 1 incomplete right M1–2 (IPS46205); 1 right M3 (IPS46206).

Type Locality and Horizon—Mazaterón (Almazán Basin, Soria, Spain), late Robiacian (MP15–16).

Etymology—This species is named for the recently deceased Miguel Ángel Cuesta Ruiz-Colmenares (Universidad de Salamanca), in recognition of his outstanding work on fossil vertebrates from the Eocene of Spain.

Diagnosis—*Pseudoloris cuestai* is characterized by its medium size, high and thick paracristid, and absence of a distinct paraconid in the lower molars, large hypoconulid in the m3, well-developed protocone in the P3 and P4, reduced hypocone and presence of a weak postprotocingulum in the M1–2, and especially by the lower incisor, with a buccolingually enlarged crown and a very wide, anteroposteriorly compressed root. *Pseudoloris cuestai* differs from *P. parvulus* in its larger size, the wider crown and root in the i1, the higher and thicker paracristid in the lower molars, the wider hypoconulid in the m3, and the less-developed hypocone in the M1–2. *Pseudoloris cuestai* differs from *P. pyrenaicus* in the much wider crown and the thicker and more

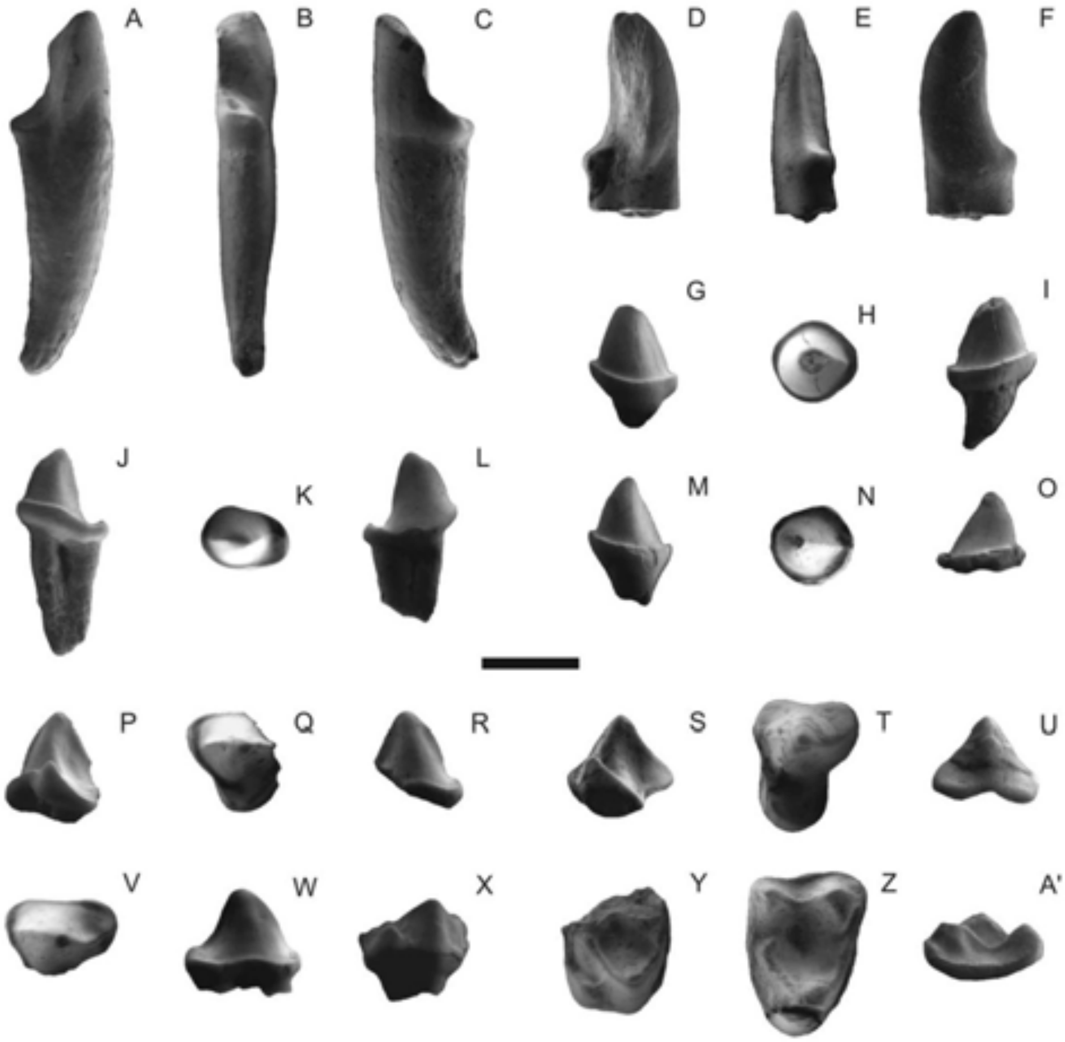


FIGURE 3. *Pseudoloris cuestai*, sp. nov., from Mazaterón. **A–C**, right I1, IPS46197, in lingual (**A**), posterior (**B**), and buccal (**C**) views; **D–F**, right I1, IPS46198, in lingual (**D**), posterior (**E**), and buccal (**F**) views; **G–I**, right C1, IPS46199, in lingual (**G**), occlusal (**H**), and buccal (**I**) views; **J–L**, left P2, IPS46201, in lingual (**J**), occlusal (**K**), and buccal (**L**) views; **M–O**, right C1, IPS46200, in lingual (**M**), occlusal (**N**), and buccal (**O**) views; **P–R**, left P3, IPS46202, in lingual (**P**), occlusal (**Q**), and buccal (**R**) views; **S–U**, left P4, IPS46204, in lingual (**S**), occlusal (**T**), and buccal (**U**) views; **V–W**, left P4, IPS46203, in occlusal (**V**) and buccal (**W**) views; **X–Y**, right M1–2, IPS46205, in lingual (**X**) and occlusal (**Y**) views; **Z–A'**, right M3, IPS46206, in occlusal (**Z**) and buccal (**A'**) views. Scale bar equals 1 mm.

anteroposteriorly compressed root of the i1, in the smaller c1 and p3, in the longer I1, in the more developed protocone in the P3 and P4, in the presence of a weak postprotocingulum, and in the more developed hypocone in the M1–2. *Pseudoloris cuestai* differs from *P. godinoti* in the smaller size, the less-developed hypocone in the M1–2, and the absence of a distinct paraconid in the lower molars. It differs from *P. crusafonti* in the smaller size, especially in the P4 and upper molars, the better developed buccal cingulid in the lower molars, the less individualized hypoconulid lobe in the m3, the more anteroposteriorly compressed lingual lobe in the P4, and the presence of a weak postprotocingulum in the M1–2. *Pseudoloris cuestai* differs from *P. saalae* and *P. isabenae* in the larger size, the absence of a distinct paraconid, and the better-developed buccal cingulid in the lower molars.

Description

i1—The crown is robust, markedly enlarged buccolingually. The buccal face is convex; the lingual one is slightly concave.

There is a well-marked crest on the posterior face that, near the base of the crown, curves towards the lingual side, continuing in a lingual cingulid. The root, notably long in relation with the crown height, is also very enlarged buccolingually and compressed anteroposteriorly.

c1—The occlusal outline is elliptical. The enamel base rises notably at the mesial side. A thin posterocristid crosses the distal face. There is a small protuberance at the distal end of the tooth. A well-marked cingulid occupies the lingual border. There is a single root, relatively short.

p3—This tooth is shorter than the lower canine. The enamel-dentine boundary rises mesially. The posterocristid is weak and does not reach the base of the crown. The lingual cingulid is less marked than in the canine. There is a single root, relatively short.

m2—The trigonid is shorter than the talonid, and similar in width to it. There is no distinct paraconid, but the paracristid thickens slightly at its mesiolingual part. There is a low cristid in the lingual border of the trigonid, connecting paracristid and metaconid; it is interrupted by a notch. The protoconid is slightly higher than the metaconid. The cristid obliqua is straight. The hypoconulid is small and low, as a distal salient of the posterocristid. There is a well-developed cingulid that starts at the middle of the mesial face, surrounds the entire buccal border, and ends at the level of the hypoconulid. There is no cingulid on the lingual border. There are two roots in mesial and distal positions.

m3—The trigonid is somewhat narrower than the talonid. There is no distinct paraconid. The paracristid is low, and continues in a thin cristid that reaches de metaconid, closing the trigonid basin. The protoconid is slightly higher than the metaconid. The cristid obliqua joins the trigonid near the protoconid. The hypoconulid is rounded, large, and prominent. The buccal cingulid is well developed; it runs from the mesiobuccal end of the tooth to the buccal face of the hypoconulid. There are two roots, the distal one very elongated in mesiodistal direction.

I1—The crown is high, and the apex is pointed. The lingual (mesial) face is slightly concave; the buccal one is slightly convex, nearly flat. The cingulum on the anterior part of the lingual face is weak. There is a small but protruding talon. The root is long, laterally compressed.

C1—Small canine, with nearly rounded occlusal outline. The apex is pointed. The enamel base rises faintly in the mesial part. A sharp posterocrista reaches the cingulum, which is very thick and surrounds the entire border of the tooth. There is a single root.

P2—Premolar with elliptic outline and a single, pointed cusp. The anterocrista is weak; the posterocrista is sharp and does not reach the base of the crown. The cingulum is weak on the buccal face, well marked on the mesial and lingual borders, and thicker at the distal face of the tooth. There are two fused roots.

P3—The single specimen is broken at its distal part. The paracone is high and acute. The posterocrista is thicker than the anterocrista. There is a very small, pointed protocone, placed in mesiolingual position. A well-developed cingulum occupies the mesial border and reaches the protocone. There is no distinct parastyle. The metastyle, if existed, cannot be observed because the distal end of the tooth is missing.

P4—The single complete specimen has the enamel very badly preserved, probably due to digestion; the incomplete specimen corresponds to the buccal part of the tooth. The paracone is high. The anterocrista is weak and straight. The posterocrista is well marked and curved buccally. There is a distinct, relatively high protocone, located in mesiolingual position. The incomplete specimen has a broad metastyle. There are three roots: mesiobuccal, distobuccal, and lingual.

M1–2—The single fragment corresponds to the lingual part of the tooth. The protocone is high. The hypocone is small but well differentiated. A weak, short postprotocingulum connects the hypocone to the distal face of the protocone. The preprotocrista and postprotocrista thicken towards the buccal part, but the existence or absence of metaconule and paraconule cannot be noted, due to the lack of the buccal part of the tooth. The fragment preserves part of the precingulum and the postcingulum; both are narrow but well marked.

TABLE 2. Measurements (in mm) of *Pseudoloris cuestai*, sp. nov., from Mazaterón.

Catalogue number	Tooth	Length	Width	Height
IPS46185	i1	1.72	1.07	1.09
IPS46186	i1	1.65	1.12	1.12
IPS46187	i1		1.09	1.08
IPS46189	c1	1.38	0.73	0.71
IPS46190	c1	1.44		
IPS46191	c1	1.38	0.69	
IPS46192	c1	1.31	0.74	0.61
IPS46193	p3	1.19	0.66	0.65
IPS46195	m2	1.76	1.35	
IPS46196	m3	1.82	1.14	
IPS46197	I1		0.66	1.06
IPS46198	I1	1.68	0.64	1.06
IPS46199	C1	0.95	0.87	
IPS46200	C1	0.91	0.88	
IPS46201	P2	1.02	0.69	
IPS46202	P3		1.06	
IPS46203	P4	1.22		
IPS46204	P4	1.13	1.39	
IPS46206	M3	1.27	1.66	

Only those specimens where at least one measurement could be taken have been included.

M3—The enamel of the only specimen is damaged, so probably the lack of some structures may be due to the bad preservation of the tooth. The paracone is larger than the metacone. There is neither hypocone, nor paraconule. The preprotocrista is high, thick, and reaches the mesiobuccal corner of the tooth, continuing in a short parastyle. The metaconule is hardly a minuscule protuberance on the postprotocrista. There is no metastyle. The precingulum is well developed, the ectocingulum is weaker, and the postcingulum is poorly marked.

Measurements—See Table 2.

Comparisons—The molars and premolars of *Pseudoloris cuestai* from Mazaterón are clearly larger than those of *P. parvulus* from Perrière, Malpérié (Louis and Sudre, 1975), Bretou (Louis and Sudre, 1975; Godinot, 1988), and Sossís (Crusafont, 1967, and unpublished material stored at the Institut Català de Paleontologia Miquel Crusafont, Spain); differences are specially marked in the m2. Measurements of the incisors of *P. parvulus* are only available from Bretou (Godinot, 1988); these teeth are also much smaller than in *P. cuestai*. The lower canines of *P. parvulus* from Sossís are slightly smaller than those of *P. cuestai* from Mazaterón, but have longer roots (direct comparison).

The m2 of *P. parvulus* from Sossís differ from those of *P. cuestai* from Mazaterón in having a lower and sharper paracristid; the m3 of *P. parvulus* have a narrower talonid basin and a notably more buccolingually compressed hypoconulid than the specimen of *P. cuestai* from Mazaterón. The development of the buccal cingulid of the lower molars is quite variable in the sample of *P. parvulus* from Sossís but, in general terms, this cingulid is less developed than in the specimens of *P. cuestai* from Mazaterón.

The M1–2 of *P. parvulus* from Sossís have a larger hypocone than the only fragment of *P. cuestai* from Mazaterón, usually very prominent in the outline of the molar and well-separated from the protocone by a valley; on the contrary, the specimen from Mazaterón shows a weak postprotocingulum. The precingulum is better developed in *P. parvulus*. The M3 of *P. parvulus* from Sossís have a well-differentiated, crescentiform metaconule; this cusp is poorly developed in the specimen of *P. cuestai* from

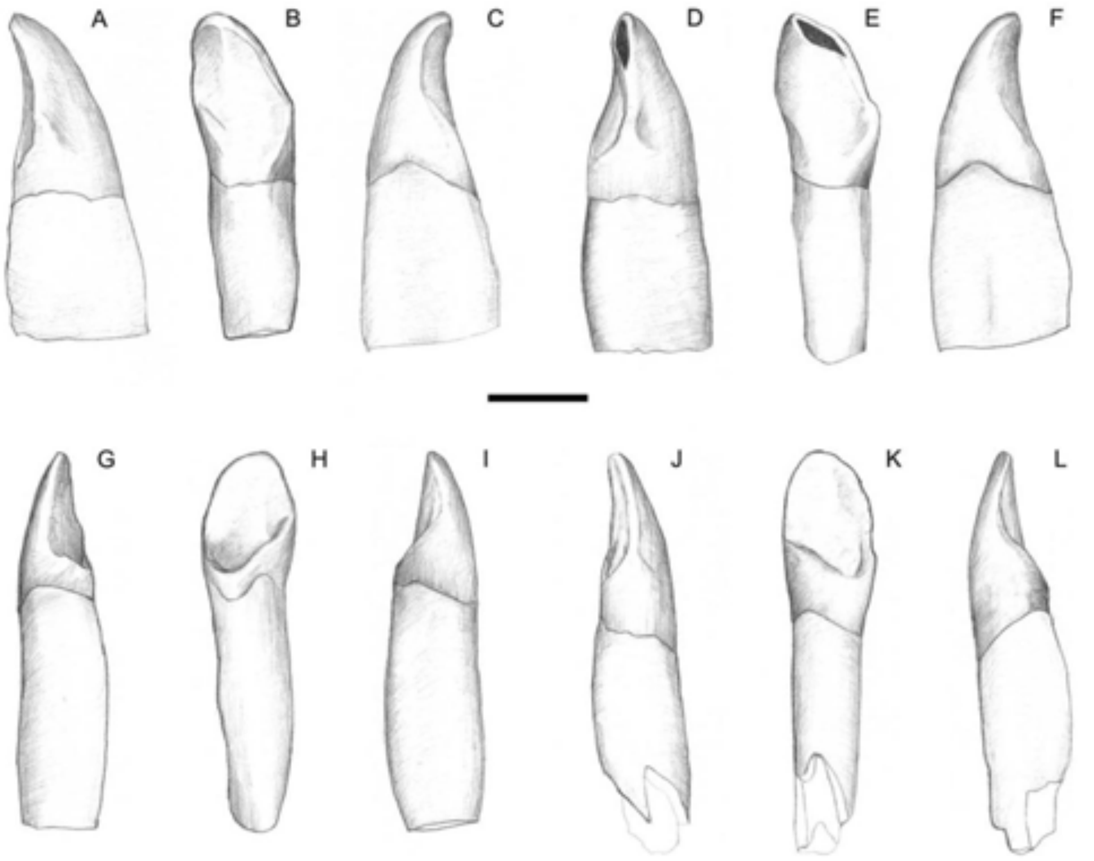


FIGURE 4. Comparison of the lower incisors of *Pseudoloris cuestai*, sp. nov., from Mazaterón and *Pseudoloris pyrenaicus* Minwer-Barakat, Marigó, and Moyà-Solà, 2010, from Sant Jaume de Frontanyà. **A–C**, right i1 of *P. cuestai* from Mazaterón, IPS46185; **D–F**, right i1 of *P. cuestai* from Mazaterón, IPS46186; **G–I**, left i1 of *P. pyrenaicus* from Sant Jaume de Frontanyà 3D, IPS46345; **J–L**, right i1 of *P. pyrenaicus* from Sant Jaume de Frontanyà 3C, IPS46289. **A**, **D**, **G**, **J**, posterior view; **B**, **E**, **H**, **K**, lingual view; **C**, **F**, **I**, **L**, anterior view. Scale bar equals 1 mm.

Mazaterón, although, as explained above, it may be due to the bad preservation of the enamel.

Anyhow, the main morphological difference between *P. cuestai* and *P. parvulus* is the shape of the lower incisors. No i1 has been recovered from Sossís, but the specimen from Perrière figured by Godinot (1983) is clearly different from those of *P. cuestai* from Mazaterón in having a much more buccolingually compressed crown and a notably thinner root.

The canines, premolars, and molars of *P. cuestai* from Mazaterón are smaller than those of *Pseudoloris pyrenaicus* from Sant Jaume de Frontanyà (Minwer-Barakat et al., 2010), with the exception of the m2, larger in Mazaterón, and the P2, very similar in size in both species. On the contrary, the incisors are notably larger in *P. cuestai* from Mazaterón. The most remarkable difference is the shape of the i1, which is notably wider in Mazaterón, giving a much more robust aspect to the lower incisors of *P. cuestai*. The root of the i1 is also different in both species: it is much thicker in relation to the crown in *P. cuestai* than in *P. pyrenaicus* and, in addition, much more anteroposteriorly compressed and buccolingually enlarged (Fig. 4). In contrast, the c1 and p3 of *P. cuestai* from Mazaterón are notably smaller than those of *P. pyrenaicus* from Sant Jaume de Frontanyà and have much shorter roots. Moreover, the distal border of the crown, which is nearly parallel to the root in *P. pyrenaicus*, is inclined in *P. cuestai* from Mazaterón.

The lower molars of *P. cuestai* and *P. pyrenaicus* are similar in shape, although subtle differences exist: the buccal cingulid is somewhat lower in *P. cuestai* from Mazaterón, the metaconid is placed in a more distal position, and the hypoconulid is less prominent, especially in the m3. The scarcity of material from Mazaterón does not allow observing the variability in the morphology of the lingual part of the trigonid that exists in *P. pyrenaicus* from SJF-3C (Minwer-Barakat et al., 2010).

The upper incisors of *P. cuestai* from Mazaterón are longer than those of *P. pyrenaicus*; the cingulum and the talon are less marked than in the specimens from Sant Jaume de Frontanyà, but this may be due to the bad preservation of the two specimens from Mazaterón. The C1 of *P. cuestai* from Mazaterón are smaller and have a rounder outline than those of *P. pyrenaicus*.

FIGURE 5. Comparison between *Pseudoloris cuestai*, sp. nov., from Mazaterón (**A–E**) and *Pseudoloris crusafonti* from Grisolles (**F–I**). **A**, right m2 (reversed for comparison), IPS46195; **B**, left m3, IPS46196 (holotype of *P. cuestai*); **C**, left P4, IPS46204; **D**, right M1–2, IPS46205; **E**, right M3, IPS46206; **F**, fragment of left mandible with m2 and m3, Gri1014; **G**, left P4, Gri445; **H**, right M2, Gri443 (holotype of *P. crusafonti*); **I**, right M3, Gri444. All teeth are represented in occlusal view. Scale bar equals 1 mm.

The P3 and P4 of *P. cuestai* differ from those of *P. pyrenaicus* in having a clearly more developed protocone.

The only fragment of M1–2 of *P. cuestai* from Mazaterón can be distinguished from those of *P. pyrenaicus* by the better-differentiated hypocone and the presence of a weak postprotocingulum. The single M3 from Mazaterón has a weaker metaconule than those of *P. pyrenaicus* but, as explained in the description, this feature may be due to the bad preservation of the enamel.

Pseudoloris godinoti Köhler and Moyà-Solà, 1999, is much larger than *P. cuestai* from Mazaterón. In addition, some morphological differences exist. The upper premolars of *P. godinoti* are higher crowned than those of *P. cuestai.* The M1 of *P. godinoti* from Fonollosa-13 has a better-developed hypocone than the fragment of M1–2 from Mazaterón. The m1 of *P. godinoti* differs from the lower molars of *P. cuestai* in having a distinct paraconid and a small protuberance on the lingual border of the trigonid, which is absent in the teeth from Mazaterón.

According to the published measurements, the teeth of *Pseudoloris crusafonti* Louis and Sudre, 1975, are notably larger than those of *P. cuestai*. These differences are very marked in the m3 (1.82 × 1.14 mm in *P. cuestai*; 2.00 × 1.33 mm in *P. crusafonti*), the P4 (1.13 × 1.39 mm in the complete specimen of *P. cuestai*; 1.45 × 1.78 mm in *P. crusafonti*), and the M3 (1.27 × 1.66 mm in *P. cuestai*; 1.40 × 2.05 mm in *P. crusafonti*; see data in Louis and Sudre, 1975). With respect to the m2, Louis and Sudre (1975) just published the measurements of a single specimen of *P. crusafonti* (1.65 × 1.29 mm), which are smaller than those of the only measured m2 of *P. cuestai* (1.76 × 1.35 mm). We have compared the material from Mazaterón with the collection of *P. crusafonti* from Grisolles stored at the Muséum National d'Histoire Naturelle (Paris, France), observing the existence of two m2: one of them isolated, and the other located in a mandibular fragment, together with the m3. The first (Gri447), which most probably corresponds to the measurements given by Louis and Soudre, is slightly shorter than the specimen from Mazaterón, but similar in width. The second (Gri1014) is larger than the specimen from Mazaterón (Fig. 5). Therefore, we can affirm that, with the exception of one isolated m2, all the specimens of *P. crusafonti* from Grisolles are clearly larger than those of *P. cuestai* from Mazaterón.

Morphologically, *P. cuestai* can be distinguished from *P. crusafonti* by several features, evidenced after direct comparison of the material from Mazaterón with the collection of *P. crusafonti* from Grisolles. The lower molars are somewhat lower crowned in *P. cuestai*, and have clearly better-developed buccal cingulids. In the m2, the posthypocristid and postentocristid are less concave distally in *P. cuestai* than in *P. crusafonti*. In the m3, the hypoconulid lobe is better differentiated in the single specimen of *P. crusafonti* than in that of *P. cuestai*. Apart from the very strong difference in size, the P4 of *P. crusafonti* shows a broader lingual lobe, less compressed mesiodistally than in *P. cuestai*. The single specimen of *P. crusafonti* also displays a well-developed cingulum on the distal border, which is absent in the complete specimen of *P. cuestai*, but this may be due to the bad preservation of the latter. Regarding the upper molars, the only M1–2 from Mazaterón is fragmentary, preserving only the lingual part; despite the absence of measurements, we can verify that the specimen from *P. cuestai* is much smaller than those of *P. crusafonti* (see comparison with the holotype of the latter species in Fig. 5). Moreover, the fragment from Mazaterón shows a weak but evident postprotocingulum connecting the hypocone to the distal part of the protocone. The precingulum, narrow but well-marked in the single piece of *P. cuestai*, is absent in one specimen of *P. crusafonti* (Gri442), as stated by Louis and Sudre (1975) in the original description of this species, but this may be due to the bad preservation of the enamel in that tooth. On the contrary, the other two specimens from Grisolles (Gri443 and Gri1015) display a distinct precingulum, so we do not consider the presence of this structure as a specific difference. Finally, the single M3

from Mazaterón has no paraconule and a very weak metaconule, although, as explained in the description, this may be due to the bad preservation of the enamel. Contrarily, the three specimens of *P. crusafonti* from Grisolles have well-developed paraconules and metaconules.

Pseudoloris reguanti Crusafont, 1967, was considered a nomen nudum by Schmidt-Kittler (1977) because of the lack of illustrations of the holotype and unique material of the species, an isolated lower molar. Unfortunately, as pointed out by Köhler and Moyà-Solà (1999), this specimen was lost in the 1970s in the collections of the Institut de Paleontologia de Sabadell (currently named Institut Català de Paleontologia Miquel Crusafont). Therefore, it is impossible to illustrate the previous holotype, and also to designate a new type for this species, which is no longer valid. Schmidt-Kittler (1977) attributed the scarce material (three specimens) from Weissenburg 8 to *Pseudoloris* sp., and considered this form as a synonym of *P. reguanti.* The teeth from this German locality differ from those from Mazaterón mainly in their much larger size. Regarding to morphology, *Pseudoloris* sp. from Weissenburg 8 differs from *P. cuestai* in the shorter and lower paracristid and the lack of buccal cingulid in the m2, in the more separated protocone and hypocone in the M2, and in the more mesial paracone in the P3.

The species *Pseudoloris isabenae* (Crusafont, 1967) and *P. saalae* (Thalmann, 1994) were ascribed originally to the genus *Pivetonia*. However, most authors have considered *Pivetonia* to be a synonym of *Pseudoloris* (Szalay, 1971; Godinot, 1983; Gunnell and Rose, 2002). We agree with this synonymy, because the differential characters listed by Crusafont (1967) in the description of *Pivetonia* (small size, low crowned teeth, open trigonid basin) are not exclusive of the species *P. isabenae* and *P. saalae*. Both *P. isabenae* and *P. saalae* are defined on the basis of lower teeth. *Pseudoloris isabenae* from Capella is notably smaller than *P. cuestai* from Mazaterón, as far as the scarce material allows comparison. The p3, m2, and one of the m3 of *P. saalae* from Geiseltal-Obere Mittelkohle are notably smaller than the corresponding teeth from Mazaterón; the other m3 is longer than the specimen from Mazaterón, but narrower. Morphologically, the main difference is the presence of a well-individualized tubercular paraconid in the lower molars of *P. isabenae* and *P. saalae*. In addition, the buccal cingulid of the lower molars of *P. cuestai* is much more developed than in *P. isabenae*. The cristid obliqua is placed in a more buccal position in the lower molars of *P. saalae* than in those of *P. cuestai.*

Pseudoloris erenensis Wang, 2008, from the late Eocene of China is defined on the basis of a single m2, which differs from those of *P. cuestai* in its smaller size and in the absence of a buccal cingulid. However, the validity of this species and its attribution to *Pseudoloris* are doubtful due to the scarcity of the material.

The middle Eocene (Geiseltalian) site of Casa Ramón (Peláez-Campomanes, 1995) has yielded two fragments of M1 and M3 and a complete M2 ascribed to *Pseudoloris* sp. The only measured parameter that we can compare is the length of the M3, smaller in Casa Ramón (1.16 mm) than in the specimen from Mazaterón. Morphological comparisons with the material from Mazaterón are difficult, because there are no common complete dental elements in both sites. The M1 from Casa Ramón has a similar-sized hypocone than the upper molar from Mazaterón, but lacks the short postprotocingulum present in *P. cuestai.*

The p3 of *Melaneremia bryanti* Hooker, 2007, is smaller than that of *P. cuestai*, but the molars are similar in size in both species. However, there are clear morphological differences: the teeth of *Melaneremia* are lower crowned, the lower molars have a distinct paraconid, the trigonid basin of the m3 is open, and the upper molars are more elongated transversely than those of *P. cuestai.*

Indusius kaliae Gunnell, Gingerich, Ul-Haq, Bloch, Khan, and Clyde, 2008, from the early Eocene of Pakistan is represented only by a m2 and a M2. The m2 is much smaller than those of *P. cuestai*; the site of Mazaterón has not yielded any complete M2, but the specimen of *I. kaliae* is even smaller than the M3 of *P. cuestai.* Morphologically, *I. kaliae* differs from *P. cuestai* mainly in the tubercular paraconid of the m2 and in the much more buccal protocone and the less developed hypocone of the M2.

The rest of the genera of Microchoerinae (*Microchoerus* Wood, 1846; *Necrolemur* Filhol, 1873; *Nannopithex* Stehlin, 1916; and *Vectipithex* Hooker and Harrison, 2008) can be distinguished from *P. cuestai* mainly by their much larger size and by the presence of enamel wrinkling in the cheek teeth. Other important differences are the notably larger hypocone in the upper molars of *Microchoerus* and *Necrolemur*, and the lack of P2 in *Vectipithex*.

DISCUSSION

The fossil site of Mazaterón has yielded a diverse Eocene continental vertebrate assemblage, including 20 different mammal taxa, and represents one of the most complete middle Eocene vertebrate fossil assemblages from the Western Iberian Bioprovince. The mammalian fauna (mainly perissodactyls but also rodents and artiodactyls) from this bioprovince is characterized by its endemic nature: many of the genera and species described in some central and western Iberian basins included into that bioprovince (Duero, Almazán, Oviedo, and Miranda-Trebiño basins) are unknown elsewhere in Europe (Badiola and Cuesta, 2008; Badiola et al., 2009). The Primates from Mazaterón (Almazán Basin) were also considered to be different from all the other species previously described in the literature (Moyà-Solà and Köhler, 1992; Badiola et al., 2009), but a detailed study of the material has not been made until now. The most abundant primate from Mazaterón, belonging to the tribe Anchomomyini, has been very recently described as a new genus and species, *Mazateronodon endemicus*, which shows clear morphological and biometrical differences with all the other representatives of this tribe (Marigó et al., 2010). Regarding *Pseudoloris*, the remains from Mazaterón are described and figured for the first time in the present paper.

The genus *Pseudoloris* is known from several European sites from the middle Eocene (Geiseltalian, MP11) to the early Oligocene (Suevian, MP22). Out of Europe, the only mention of this genus is *Pseudoloris eremensis* from China (Wang, 2008), but the generic ascription of the single molar from this locality is doubtful. The oldest record of the genus is *Pseudoloris* sp. from Casa Ramón (MP11), only represented by three teeth (Peláez-Campomanes, 1995). Apart from that, the oldest species ascribed to the genus are *Pseudoloris saalae* from Geiseltal-Obere Mittelkohle (MP13) and *Pseudoloris isabenae* from Capella (MP14), both of them known only by their lower teeth. Recently, the species *P. pyrenaicus* from Sant Jaume de Frontanyà (MP14–15) was described on the basis of a quite abundant material, including almost all the dental elements (Minwer-Barakat et al., 2010). The best-represented species of the genus is *P. parvulus*, known from several middle and late Eocene (MP16–17) sites of Spain and France: the phosphorites of Quercy (Stehlin, 1916; Theilard de Chardin, 1921), Sossís, Euzet (Crusafont, 1967), Perrière, Malpérié (Godinot, 1983), and Bretou (Godinot, 1988). The material from Grisolles was attributed to *Pseudoloris crusafonti* by Louis and Sudre (1975), evidencing the existence of two different lineages of the genus in the latest middle Eocene, because Grisolles is contemporaneous to Bretou, a site containing *P. parvulus* (Godinot, 1983). The latest Eocene mentions of the genus are *P. reguanti* from Sant Cugat de Gavadons (a single disappeared tooth), and the three specimens of *Pseudoloris* sp. from Weissenburg 8 (Schmidt-Kittler, 1977), both sites corresponding to MP19. Finally, *P. godinoti* is recorded in the early Oligocene localities of Santpedor-2 and Fonollosa-13 (MP21 and 22, respectively;

Köhler and Moyà-Solà, 1999). The summary of the European sites containing remains of *Pseudoloris*, referred to the corresponding European Land Mammal Age (ELMA) and MP unit, can be also consulted in Minwer-Barakat et al. (2010).

The scarcity of material in most localities in which *Pseudoloris* has been identified and its very discontinuous record make the observation of morphological or biometrical trends in successive populations difficult. However, recent findings have allowed the recognition of several directional changes in the early evolution of the genus (Minwer-Barakat et al., 2010): the progressive reduction of the paraconid in the lower molars (changing from a distinct tubercle to a sharp cristid) and the increase in the size of the hypocone, metaconule, and paraconule in the upper molars, among other characters, lead to the suggestion of the existence of an anagenetic lineage formed by the species *P. saalae*, *P. isabenae*, *P. pyrenaicus*, and *P. parvulus*. Such trends are difficult to evaluate in the most recent species of the genus (*P. crusafonti*, *P. godinoti*, *Pseudoloris* sp. from Weissenburg 8), whose phylogenetic relationships are unclear (Minwer-Barakat et al., 2010).

Pseudoloris cuestai from Mazaterón has an intermediate age between *P. pyrenaicus* and *P. parvulus*, and shows several dental features in between those of these two species. For example, the buccal cingulid of the lower molars is less developed than in *P. pyrenaicus*, but stronger than in *P. parvulus*; the hypoconulid of the m3 is narrower than in *P. pyrenaicus*, but wider than in *P. parvulus*; the hypocone of the M1–2 is larger than in *P. pyrenaicus* and smaller than in *P. parvulus*. The paracristid of the lower molars is similar to that of *P. pyrenaicus*, but thicker and higher than in *P. parvulus*.

Nevertheless, the most remarkable differences between *P. cuestai* and the species *P. parvulus* and *P. pyrenaicus* are in the anterior dentition: the lower incisors of *P. cuestai* are much larger and robust than those of *P. parvulus* and *P. pyrenaicus* (see Fig. 4). On the contrary, the lower canines and the p3 of *P. cuestai* are smaller than those of *P. pyrenaicus* (Minwer-Barakat et al., 2010) and only slightly larger than those of *P. parvulus* from Sossis (direct comparison). The upper incisors are also clearly larger than those of *P. parvulus* from Perrière, and longer than those of *P. pyrenaicus*, but similar in height and width. It is particularly interesting the shape and size of the root of the lower incisors of *P. cuestai*, which is thick, notably enlarged laterally and compressed anteroposteriorly. This implies that the mandible must have been wider than in the other species whose incisors are known (*P. parvulus* and *P. pyrenaicus*, the two closest species geographically and temporally). Moreover, the roots of the lower canine and p3 are shorter in *P. cuestai* than in *P. pyrenaicus* and *P. parvulus*, which may be in fact related to the larger root of the incisor. These morphological traits, different to those of the older (*P. pyrenaicus*) and younger (*P. parvulus*) species of the genus, may be the result of a geographic isolation from the lineage present in the Pyrenean basins and France.

The isolation of the Iberian Peninsula from Central Europe until the late Lutetian (Meulenkamp et al., 2000), although with intermittent exchanges with the rest of Europe, has been suggested to be the cause of the endemism of the Eocene mammal faunas from the Western Iberian Bioprovince (Badiola and Cuesta, 2008; Badiola et al., 2009). Moreover, the existence of special ecological conditions, with more open environments and a more arid climate than in the rest of the European continent at least since the middle Eocene could have contributed to the differentiation of the mammal faunas from this bioprovince (Badiola and Cuesta, 2007). The paleoecological analysis of the middle and late Eocene mammal fossil assemblages from Mazaterón (Almazán Basin) and Zambrana (Miranda-Trebiño Basin) suggests that the change from a complex forest habitat to a more open environment observed in the late Eocene in several regions of Europe could have started earlier in the Western Iberian Bioprovince, influencing its faunal composition (Badiola, 2004; Badiola et al., 2009).

In relation to such distinct paleoecological conditions, the peculiar dental morphology of *P. cuestai* (with unusually large lower incisors with very broad roots and relatively small lower canines and p3) may suggest some particularities in its diet. Although the dentition of Omomyidae is relatively well represented in the fossil record, the dietary habits of these primates have been described only in the broadest terms. They are considered to be faunivorous and/or frugivorous, mainly on the basis of the estimations of their body size. Some studies have used the shearing potential on the molar dentition for discriminating between these two dietary specializations (Kay, 1975; Covert, 1986; Strait, 1993, 1997). The only available quantitative study about the dietary habits of *Pseudoloris*, which analyzed several molars of *P. parvulus*, concluded that this taxon was primarily faunivorous (Strait, 2001), supporting previous qualitative dietary reconstructions for this genus (Covert, 1986; Fleagle, 1999). This interpretation is also coherent with the high resemblance in dental morphology between *Pseudoloris* and the extant *Tarsius*, which also has a faunivorous diet, based mainly on insects.

However, the mentioned studies are based only in the shape of the molars. The relationship between the morphology of the anterior dentition and the dietary habits has not been studied for omomyids. As explained in the present work, the main differences between the new species *Pseudoloris cuestai* and the previously defined representatives of the genus are found in the anterior dentition. For this reason, the paleobiological meaning of these anatomical differences, i.e., the relation of the particular morphology of the incisors of *P. cuestai* with a concrete type of nutrition, cannot be known in detail.

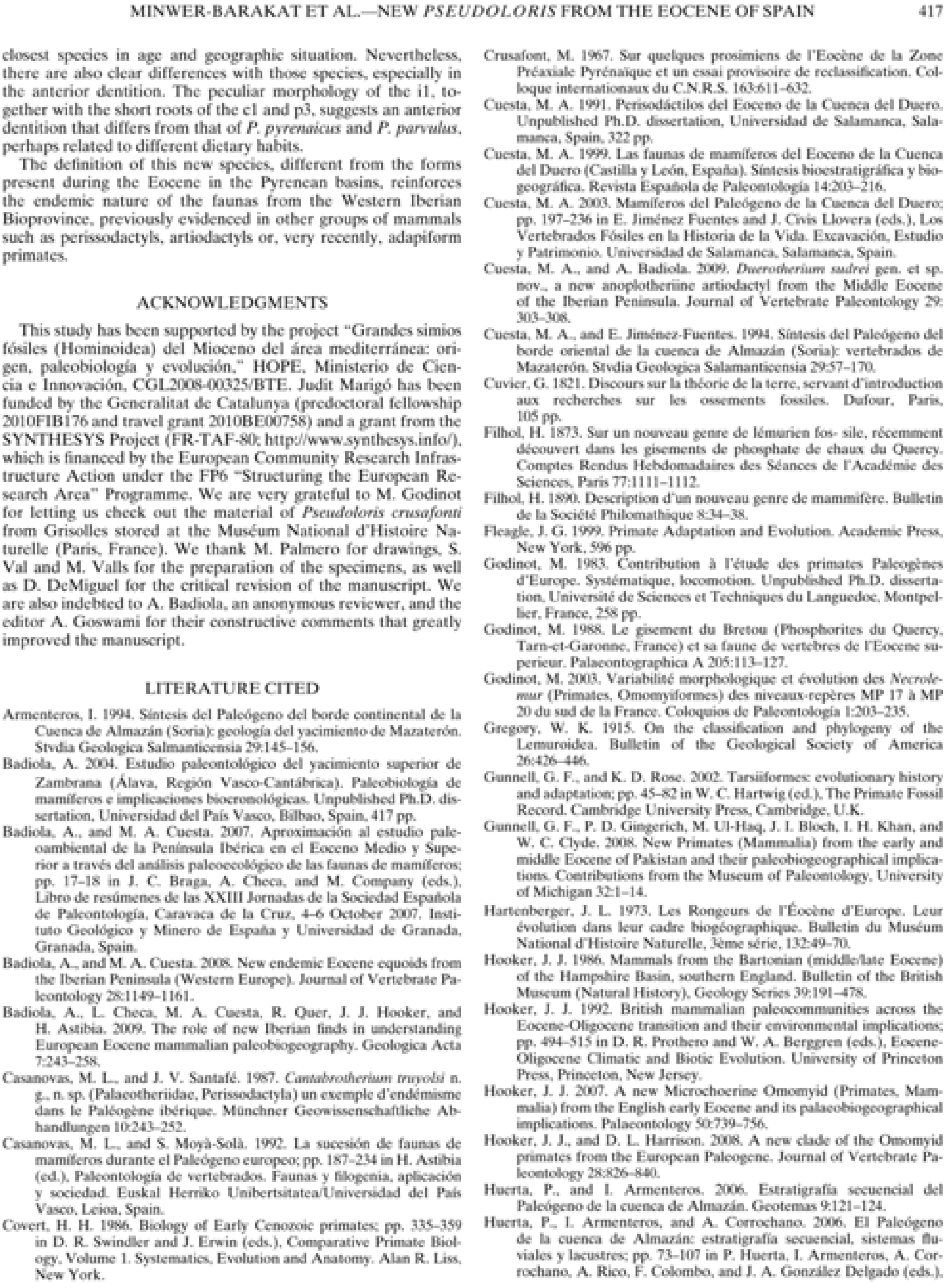
Badiola (2004) and Badiola et al. (2009) pointed out that some dental characters observed in the perissodactyls and rodents from the Western Iberian Bioprovince (such as the reduction of the premolar series combined with large and hypsodont molars) could be interpreted as adaptations to chewing tough plants associated with the increasingly more arid conditions in this region. The low species diversity of the rodent fauna from Mazaterón and other localities of this bioprovince (Miñana, Zambrana) also suggests the existence of less densely forested areas than in the rest of the continent (Peláez-Campomanes, 1993, 1996; Badiola, 2004). In this context, it is likely that the diet of *P. cuestai* could have been different from that of other species of the genus, probably representing an adaptation to the insect prey present in a more arid environment. Nevertheless, more material would be necessary to interpret the concrete nutritional requirements of the new species.

Therefore, although the record of Primates is very scarce in the Western Iberian Bioprovince, the detailed study of two of the three forms present in Mazaterón reveals that they correspond to new taxa, the adapiform *Mazateronodon endemicus* and the microchoerine *P. cuestai*, showing significant differences with their correlatives in the Pyrenean basins. Thus, this study reinforces the endemic nature of the mammal faunas from this bioprovince.

CONCLUSIONS

The new species *Pseudoloris cuestai* is described from the middle Eocene (MP15–16) site of Mazaterón (Almazán Basin, Spain). *Pseudoloris cuestai* can be distinguished from the rest of the species of the genus by its medium size, absence of a distinct paraconid in the lower molars, large hypoconulid in the m3, well-developed protocone in the P3 and P4, small hypocone in the upper molars, and especially for its particular lower incisors, with a large, buccolingually enlarged crown and a thick root.

This finding represents the only citation of a Microchoerinae in the Western Iberian Bioprovince. It shows several similarities with the species *P. pyrenaicus* and *P. parvulus*, which are the



closest species in age and geographic situation. Nevertheless, there are also clear differences with those species, especially in the anterior dentition. The peculiar morphology of the i1, together with the short roots of the c1 and p3, suggests an anterior dentition that differs from that of *P. pyrenaicus* and *P. parvulus*, perhaps related to different dietary habits.

The definition of this new species, different from the forms present during the Eocene in the Pyrenean basins, reinforces the endemic nature of the faunas from the Western Iberian Bioprovince, previously evidenced in other groups of mammals such as perissodactyls, artiodactyls or, very recently, adapiform primates.

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10

NIEVESIA SOSSISSENSIS, A NEW ANCHOMOMYIN (ADAPIFORMES, PRIMATES) FROM THE EARLY LATE EOCENE OF THE SOUTHERN PYRENEES (CATALONIA, SPAIN)

Nievesia sossisensis, a new anchomomyin (Adapiformes, Primates) from the early Late Eocene of the Southern Pyrenees (Catalonia, Spain)

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Abstract

A new genus and species attributed to the tribe Anchomomyini is described from the early Late Eocene locality of Sossís (MP17a), one of the most important Paleogene fossil sites from the Iberian Peninsula. *Nievesia sossisensis* is characterized by its buccolingually compressed P^4, its upper molars with no pericone, medium-sized hypocone, straight postcingulum and minuscule mesostyle, and the extremely reduced metacone in the M^3. Its lower dentition presents a P_4 with an enlargement of the enamel suggesting a minuscule metaconid, lower molars with no paraconid and a premetacristid closing the trigonid basin, and M_3 with the trigonid wider than the talonid. The performed phylogenetic analyses suggest a close relationship between *Nievesia* and *Mazateronodon,* although the new genus is also related to *Anchomomys* and, to a lesser extent, *Buxella* and *Periconodon*. These analyses, which also include djebelemurines, no longer relate European anchomomyins with crown strepsirhines, and suggest their

closer relationship with asiadapines and sivaladapids.

Introduction

Eocene continental deposits are well represented in several Iberian basins constituting one of the most complete primate fossil records from Europe. The study of this group of mammals in Spain was started in the 1960's by Crusafont (1965, 1967), who developed preliminary studies of the primates found in several Pyrenean localities. After several decades of interruption, this research line was reopened and has already given very interesting results (Marigó et al., 2010, 2011, 2012; Minwer-Barakat et al., 2010, 2012). Recent studies of the previously recovered collections of Eocene mammals from Spain have permitted the description of several new taxa ascribed to the tribe Anchomomyini, helping to clarify the phylogenetic relationships within this group of primates.

In this paper we present a new anchomomyin genus from the locality of Sossís, the first site discovered in the Late Eocene of the area of La Pobla de Segur (Lleida, Spain). This fossil site, together with Roc de Santa, is one of the most important localities of the Catalan continental prepyrenean Eocene due to its rich fossil assemblage (Casanovas Cladellas, 1998), which has provided very important paleontological and biostratigraphical information, and has allowed correlation with other Paleogene European basins (López Martínez, 1998).

This site (see Figure 1) is located in the village of Sossís (Conca de Dalt, Lleida Province), in the La Pobla de Segur sub-basin (Tremp-Grauss Basin, Southern Pyrenees). Geologically, the site belongs to the Sossís Member of the Collegats Formation (Cuesta et al., 2006), whose age was established as Late Eocene by Crusafont et al. (1954, 1956) thanks to the micromammal assemblage of Sossís. The lithological succession of the Collegats Formation is fundamentally conglomeratic with lutitic intercalations, with a total thickness of 1000 m and, in this area, lies discordantly over Late Cretaceous marine deposits (López Martínez, 1998). From a sedimentological point of view, these materials are interpreted as alluvial fan and deltaic deposits with lacustrine intercalations, consisting of limestones, lutites and lignites (Robles and Ardévol, 1984, 1985). The lowest of these intercalations is the Sossís Member, with a thickness of 100 m, where the Sossís fossil site is located (López Martínez, 1998). The sampled levels of this fossil site correspond to grey and black marls embedded in white marls, 15 cm over the lignite deposits that were exploited in the past as mining galleries (López Martínez, 1998).

The Sossís fossil site was correlated with the gypsum deposits of Montmartre (France), corresponding to the Headonian (European Land Mammal Ages), MP17a Paleogene reference levels (Sigé, 1997), which corresponds approximately to 37 Ma (Luterbacher et al., 2004). This correlation was possible due to the presence of the rodent species *Theridomys euzetensis*. The genus *Theridomys* is recorded from the Late Eocene-Oligocene of Europe and, due to the rapid evolutionary rate of its species, it is considered excellent for the construction of biochronological scales and determining the relative age of the sites where its remains are identified (Peláez-Campomanes, 1998).

In this fossil site several genera of marsupials, insectivores, rodents, carnivores, perissodactyls, artiodactyls and primates have been identified (see Table 1). Although some of them were studied in detail in several previous works (Thaler, 1966; Golpe, 1971; Crochet, 1978; Hartenberger, 1973; Sigé, 1976; Sudre, 1977; Checa, 1994), there is still a lot of material poorly studied and even unpublished. Paleoherpetofauna of this fossil site is still under study, although preliminary results on the lizard assemblage can be found in Bolet and Evans (2012). Regarding primates, various microchoerines as well as a large adapine from the Sossís fossil site were identified by Crusafont (1965, 1967). Moreover, the study of further material recovered back then has allowed the identification of the new anchomomyin presented in this paper.

Materials and methods

All the fossil remains included in this study are housed in the collections of the Institut Català de Paleontologia Miquel Crusafont in Sabadell (Catalonia, Spain). The comparisons made in this paper are based on original material and casts of fossil primates from other localities. The nomenclature used for the description of the teeth is that of Szalay and Delson (1979). Measurements of *Nievesia sossisensis* were made using an optic caliper “Nikon measuroscope 10” connected to a monitor “Nikon SC112”, using the criteria described in Marigó et al. (2010). Other measurements were taken from the literature. Micrographs of upper and lower dentition were taken using the Environmental Scanning Electron Microscope (ESEM) of the Universitat de Barcelona (UB).

In order to test more systematically the phylogenetic relationships between the members of the Anchomomyini clade, and with other adapiforms and crown strepsirrhines, two phylogenetic analyses have been run using *PAUP** 4.0b10 (Swofford, 1998), on the basis of the matrix provided by Seiffert et al. (2010). We have included the information given by the rich assemblage of dental specimens of *Nievesia sossisensis*, as well as the recently described Iberian Anchomomyin taxa (Marigó et al., 2010, 2011), taking into account the modifications to the coding of the type species *A. gaillardi* and the addition of taxa made by Marigó et al. (2011), and the addition of the coding for *Anchomomys milleri* and *Djebelemur martinezi* (Boyer et al., 2010). For more information regarding the data matrix used in the phylogenetic analyses presented in this paper, see Supplementary Online Material 1.

The resulting matrix (361 morphological characters scored for each species, including 103 living and extinct taxa) was analyzed under maximum parsimony with random addition sequence and the tree bisection and reconnection branch swapping algorithm across 5000 replicates, following two different hypotheses. For hypothesis 1, no premolar reacquisition was allowed, and some multistate characters were ordered and scaled (following Seiffert et al., 2010) so that any single change within a character could only contribute a maximum of one step to the tree length. For hypothesis 2, some multistate characters were also ordered and scaled, but premolar reacquisition was allowed following an earlier loss (following Seiffert et al., 2010). Polymorphisms were scored as an intermediate character state in all cases. In the two analyses, the monophyly of Malagasy lemurs and an *Arctocebus-Perodictius* clade was enforced, as supported by abundant DNA sequence and SINE data, following Seiffert et al. (2010), and specimen NMMP20 was not assigned to *Poundaungia cotteri*. All tree lengths were recalculated after networks were re-rooted with *Tupaia* spp. For more information regarding the original matrix, character scaling or how the analyses are made, see Seiffert et al. (2009, 2010). For results of these phylogenetic analyses, see the Discussion section.

The character-coding for *Nievesia sossisensis* is as follows:

?????????? ?????????? ?????41042 0224211013
010002?300 ?00011A862 0-02202334 24225-2022
244400040- 1200021000 0????????? ??????????
?????????? 0000000000 0002?0?012 000-000010
0200000202 020010?0?? ?????????? ??????????
?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??????????
?

Systematic Paleontology

Order Primates Linnaeus, 1758

Suborder Euprimates Linnaeus, 1758

Infraorder Strepsirrhini Geoffroy Saint-Hilaire, 1812

Superfamily Adapoidea Trouessart 1879

Family Notharctidae Trouessart, 1879

Subfamily Cercamoniinae Gingerich, 1975

Tribe Anchomomyini Szalay and Delson, 1979 (*sensu* Godinot, 1988a)

Nievesia gen. nov.

Etymology

This genus is named after the recently deceased Dr Nieves López Martínez, in recognition of her remarkable studies on Cretaceous and Cenozoic fossil mammals from the Pyrenees, and of her outstanding work in the Sossís fossil site.

Generic diagnosis

Medium-sized anchomomyin larger than most *Anchomomys* and smaller than *Mazateronodon*, *Periconodon* and *Buxella.* Also smaller than the sivaladapids *Hoanghonius* and *Rencunius,* and the asiadapine *Asiadapis,* and similar in size to the asiadapine *Marcgodinotius*. It presents no wrinkled enamel unlike *Buxella magna* and *Periconodon jaegeri*. Its buccolingually compressed P^4 resembles no other anchomomyin neither *Asiadapis* or *Rencunius*. Upper molars with no pericone unlike *Anchomomys pygmaeus, Buxella prisca, Periconodon, Hoanghonius* and *Rencunius*, medium-sized hypocone similar to that of *Anchomomys quercyi* and *Mazateronodon*, larger than in *Marcgodinotius* and *Asiadapis*, and smaller than in *Periconodon* and *Buxella,* straighter postcingulum than most *Anchomomys, Marcgodinotius*, *Hoanghonius* and *Rencunius*. It also presents an extremely reduced metacone in the M^3 unlike any other anchomomyin and *Marcgodinotius,* a shorter anterocingulum than *Anchomomys*, *Mazateronodon*, *Periconodon*, *Asiadapis*, *Hoanghonius* and *Rencunius*, and no lingual cingulum in the upper molars unlike *Anchomomys, Buxella*, *Hoanghonius* and *Rencunius*.

Lower premolars with no paraconid unlike most *Anchomomys* and discontinuous buccal and lingual cingulids unlike all other anchomomyins. Lower molars with no paraconid unlike most *Anchomomys, Buxella, Periconodon jaegeri,* the asiadapines *Asiadapis* and *Marcgodinotius* and the sivaladapid *Rencunius,* and presenting a premetacristid joining the paracristid and the metaconid, closing the trigonid basin, unlike any other anchomomyin but *Mazateronodon,* and also unlike *Rencunius* and the asiadapines *Marcgodinotius* and *Asiadapis*.

Nievesia sossisensis sp. nov. Figures 2, 3 and 4.

Etymology

After Sossís, the fossil site where the primate material described in this work was found, and one of the villages of the Conca de Dalt municipality, second home of Nieves López Martínez.

Specific diagnosis

Same as for genus.

Holotype

Specimen IPS-57271 (right maxilla fragment with M^2 and M^3), from Sossís, stored in the collections of the Institut Català de Paleontologia Miquel Crusafont.

Hypodigm

Upper dentition: one complete right P^4 (IPS-57269), one incomplete right M^1 (IPS-57273), one complete right M^2 (IPS-57270), one incomplete right M^2 (IPS-57272).

Lower dentition: one complete right dP_4 (IPS-57274), two incomplete right P_3 (IPS-57277 and IPS-57278), two complete right P_4 (IPS-57279 and IPS-57280), four complete right M_1 or M_2 (IPS-57281, IPS-57282, IPS-57284 and IPS-57287), three complete left M_1 or M_2 (IPS-57283, IPS-57285 and IPS-57286), one complete right M_3 (IPS-57289).

Locality and horizon

Sossís (Conca de Dalt, Catalonia, NE Spain). Sossís Member, Collegats Formation, Headonian (MP17a), Late Eocene.

Descriptions of maxillary teeth

The P^4 has a high paracone and a distinct parastyle, and no anterocingulum. A well-developed protocone, smaller than the paracone, is located on the lingual side, centered on the narrow protocone lobe. The preprotocrista connects the protocone and the parastyle. A poorly-developed postcingulum runs distally, from the distal base of the protocone to the distal end of the postparacrista. No postprotocrista is present. This tooth has three roots in mesiobuccal, distobuccal and lingual positions.

Two incomplete and two complete M^1 or M^2 are available. Regarding the two complete specimens, one of them is undoubtedly an M^2 (IPS-57271) because it is attached to a maxilla fragment with its M^3 on one side. The other complete specimen (IPS-57270), almost identical, is also interpreted as a M^2. One of the incomplete specimens (IPS-57272), consisting only of the mesial part of the tooth (paracone, paraconule, protocone, anterocingulum) and the hypocone, may also represent an M^2 because of its proportions. The other incomplete specimen (IPS-57273) consists of the buccal part of the tooth, and it is probably an M^1 because of the proportions of the paracone and the metacone, which are closer in size in this specimen, presenting less reduction of the metacone compared to the protocone than in the M^2, making this tooth longer than the others. However, because of the scarcity of material and their resemblance, they will be described all together as M^1 or M^2.

The M^1 or M^2 is tribosphenic, and has a paracone that exceeds the metacone in size and height. The protocone is very broad. Both metastyle and parastyle are weak, and there is an minuscule mesostyle. A small paraconule is present. No distinct metaconule is present, although a slight enlargement of the enamel in the position of this cusp is visible. The anterocingulum is well marked but very short, only occupying the mesial base of the protocone. There is no pericone, and the hypocone is medium-sized and isolated. The postcingulum, running from the hypocone to the metastyle, is straight and more prominent than the anterocingulum.

The subtriangular M^3 has large paracone and protocone, but an extremely reduced metacone. The paracone is inflated and protrudes markedly on the buccal border. There is a protuberance between protocone and metacone, constituting a minuscule metaconule. An minuscule paraconule is also present. There is a small anterocingulum from the lingual base of the protocone to the buccal base of the paraconule. The postcingulum is more prominent and extends from the lingual base of the protocone to the metacone; this cingulum bears several enamel bulges, which are thicker in the posterolingual part of the tooth, although there is no distinct hypocone. No metastyle is present. The parastyle, if present, cannot be observed because the only M^3 is attached to a maxilla fragment with the M^2, which overlaps with the mesiobuccal side of the M^3. All upper molars have three roots.

Descriptions of mandibular teeth

In the dP_4, the trigonid represents almost half of the tooth length. The paracristid is well developed and it bears a small paraconid. It defines a moderately large basin mesial to the protoconid. The trigonid is not closed lingually because no premetacristid is present. The metaconid is located distal to the protoconid. The cristid obliqua reaches the buccal base of the metaconid, very close to the point where protoconid and metaconid meet. The buccal cingulid starts at the paraconid and reaches the distal base of the hypocone; it becomes thinner at the buccal bases of the protoconid and hypoconid. The entoconid is located distal to the hypoconid, and there is a small but distinct hypoconulid at the distal end of the talonid, slightly closer to the hypoconid than to the entoconid.

Both P_3 recovered from Sossís have their mesial part broken. These teeth are buccolingually compressed, with a large protoconid. Although the mesial part cannot be observed properly, there is no sign of a paraconid. The buccal and lingual cingulids are restricted to the distal part of the tooth; the latter delimits a very narrow talonid basin. From the protoconid there is a cristid obliqua running distally, and a protocristid, shorter and less marked, running lingually. The tooth presents two roots.

The P_4 is very similar to the $P_\mathbf{3}$ in buccolingual compression and overall shape, although larger and more complex. It has no paraconid, and the protoconid, situated slightly mesially, is large and pointed. Distolingual to the protoconid, there is an enlargement of the enamel, suggesting the presence of a minuscule metaconid. In one of the specimens there is a cristid running distally from the metaconid. In both specimens there is a cristid obliqua ending in a small hypoconid. The talonid basin is broader than on the $P_\mathbf{3}$. In one of the specimens the buccal cingulid is continuous, whereas the lingual one is interrupted. In the other specimen both cingulids are discontinuous, restricted to the mesial and distal parts of the tooth. The tooth has two roots.

The M_1 or M_2 lacks a paraconid. High protoconid and metaconid are present, connected by a protocristid, being the metaconid located distally with respect to the protoconid. Premetacristid and paracristid meet at the mesial part of the tooth, closing the trigonid basin. In three out of seven specimens the buccal cingulid is restricted to the base of the protoconid. In the other four teeth, this cingulid is discontinuous, present on the buccal base of the protoconid, interrupted on the buccal base of the hypoconid and present again on the distal base of the hypoconid. The talonid basin is broad. The cristid obliqua extends to the lingual portion of the base of the protoconid in some specimens, and to the point where protoconid and metaconid meet in some others. The entoconid and the hypoconid are similarly developed, although the entoconid is more distally placed. The hypoconulid is well defined and placed buccally, closer to the hypoconid than to the entoconid.

The M_3 is longest and generally narrower than the M_1 or M_2. There is no paraconid. The metaconid is more distally placed than the protoconid, but not so distally as in the M_1 or M_2. The cristid obliqua is notably more buccally placed than in the M_1 or M_2. The hypoconulid lobe is prominent, centered and elongated distally. The two roots are very close to each other, almost in contact, although not fused, and the distal one is much larger and mesiodistally elongated than the mesial one. All lower molars are double-rooted.

Measurements

See Table 2.

Comparisons

Nievesia is considered an anchomomyin due to several features that distinguish the members of this tribe from other cercamoniine adapoids such as the small size, narrow and simple lower premolars and relatively small hypocones in the upper molars. Comparisons with all the genera included in the Tribe Anchomomyini have been made for each known dental specimen (See Table 3 and Supplementary Online Material 2). However, due to the lack of material for several species, comparisons with some dental elements are not possible. For size comparisons see Figure 5.

Comparisons with Anchomomys

Nievesia is larger than *Anchomomys gaillardi* (type species of this genus). The M^1 or M^2 of *Nievesia* differ from those of *A. gaillardi* in the larger hypocone and the more subquadrate shape, with a straighter postcingulum. Moreover, they show a shorter anterocingulum, a minuscule mesostyle, and have the paracone more developed when compared to the metacone. The only M^3 of *Nievesia* has its metacone so extremely reduced that it is almost absent as an isolated cusp. This makes this M^3 shorter than all *Anchomomys* M^3 (only the M^3 of *A. gaillardi* and *A. frontanyensis* are known), although its buccally expanded paracone makes it wider. Moreover, the M^3 of *Nievesia* differs from that of *A. gaillardi* in that it has no anterocingulum, in having a more inflated buccal part of the paracone protruding buccally and in having a longer postcingulum that reaches the distolingual base of the protocone. Because of the reduction of the metacone in *Nievesia,* the protocone is the second of the molar cusps in size and is placed more distally than the metacone, unlike in *A. gaillardi*. Regarding the M_1 and M_2, those of *A. gaillardi* are way smaller than those of *Nievesia*. The mesial part of the buccal cingulid is better developed and extends more distally in *A. gaillardi* although its distal part is better marked in *Nievesia*. Moreover, *A. gaillardi* further differs from *Nievesia* in having a more lingual cristid obliqua in the M_1, a less developed hypoconulid and no premetacristid, which in *Nievesia* closes the trigonid lingually. The M_3 of *A. gaillardi* differs from that of *Nievesia* in the lack of a well-developed premetacristid, it has a more aligned metaconid and protoconid, the cristid obliqua is much more lingual, the entoconid and the hypoconid are similarly developed and almost at the same level mesiodistally, and the hypoconulid lobe is more developed and centered in the mesiodistal axis of the tooth.

When compared to *A. quercyi,* the upper dentition of *Nievesia* differs from it in having a much smaller P^4 (in fact, the smallest known anchomomyin P^4). In *Nievesia*'s P^4, the buccal side is much shorter than that of *A. quercyi,* although the lingual side, mainly the protocone lobe, is much more buccolingually compressed in *Nievesia* than in *A. quercyi,* giving the whole tooth a more compressed aspect. Moreover, the protocone is centered on the protocone lobe in *Nievesia*, unlike in that of *A. quercyi,* where the protocone is more mesially placed. *Nievesia*'s P^4 has no anterocingulum, and it has a straighter postcingulum than any *Anchomomys* P^4. *Nievesia*'s M^1 or M^2 are close in size to that of *A.* cf. *quercyi* from Le Bretou, although slightly larger, and when compared to *A. quercyi* and *A.* cf. *quercyi* they present a similarly developed hypocone located more buccally, a more developed paracone when compared to the metacone, and a straighter postcingulum that makes the tooth more subquadrate in shape. Moreover, the specimens from Sossís present a short anterocingulum such as *A.* cf. *quercyi*, unlike *A. quercyi*.

The P_3 of *Nievesia* are smaller than the single specimen of *A.* cf. *quercyi*. Morphologically the P_3 of *Nievesia* differ from *A.* cf. *quercyi* in the absence of a complete lingual cingulid. The P_4 of *Nievesia* are larger than that of *Anchomomys* cf. *quercyi*, contrarily to the P_3 specimens. The P_4 of *A.* cf. *quercyi* is similar to that of *Nievesia* due to the presence of an enlargement of the enamel suggesting a minuscule metaconid and the discontinuous lingual and buccal cingulids. However, in *Nievesia*, the hypoconid is more developed than in *A.* cf. *quercyi*, whereas the minuscule metaconid is more developed in the latter. The smaller M_1 or M_2 specimens of *Nievesia* resemble in size the M_1 of *Anchomomys* cf. *quercyi*. However, the mesial part of the buccal cingulid of the specimens of *Nievesia* extends more distally, and it does reappear at the distal part of some teeth (whereas in *A.* cf. *quercyi* it does not). The cristid obliqua of *A.* cf. *quercyi* is a little bit more lingual than in *Nievesia*, and the paracristid is more marked in the latter. Regarding the M_2 of *A.* cf. *quercyi*, it has the metaconid and the protoconid more aligned than most specimens of *Nievesia*, the cristid obliqua is more buccal and the buccal cingulid is shorter mesially and it does not appear again at the distal part of the tooth. As in the M_1, the M_2 of *A.* cf. *quercyi* has a less marked paracristid than the specimens of *Nievesia*, and this tooth it is much smaller than all the *Nievesia* specimens.

When compared to *Anchomomys frontanyensis*, *Nievesia*'s P^4 has the buccal side closer in size to that of the former, although the lingual side, mainly the protocone lobe, is much more buccolingually compressed in *Nievesia* than in *A. frontanyensis*, giving the whole tooth a more compressed aspect. The specimen from Sossís has a much higher paracone than *A. frontanyensis*, and a more cuspidate parastyle. *Nievesia*'s P^4 has no anterocingulum, and it has a straighter postcingulum. The M^1 or M^2 of *Nievesia* are longer than the specimens of *A. frontanyensis* for similar widths. However, those of *A. frontanyensis* present a longer anterocingulum that runs past the base of the paraconule, whereas those of *Nievesia* present a very short anterocingulum that never reaches past the base of this cuspule. The hypocone is slightly smaller and less bulbous in *A. frontanyensis*, and only one specimen of *A. frontanyensis* presents a trace of a mesostyle. *Nievesia* also bears a straighter postcingulum, and the weak lingual cingulum that is present in some specimens of *A. frontanyensis* is absent in *Nievesia*. The M^3 of *Nievesia* differs from *A. frontanyensis* in the extremely reduced metacone that makes this tooth the shorter and wider M^3 of all anchomomyins. Moreover, the M^3 of *Nievesia* differs from *A. frontanyensis* in having no anterocingulum and in having a more inflated buccal part of the paracone that protrudes buccally. It resembles some M^3 *A. frontanyensis* specimens in the reduction of the metacone (although it is more pronounced in *Nievesia),* so that the protocone is the second of the molar cusps in size and is placed more distally than the metacone, and in that the postcingulum reaches the distolingual base of the protocone. The P_3 of *Nievesia* fall into the range of *A. frontanyensis* regarding length, although they are narrower. Morphologically the P_3 of *Nievesia* differ from *A. frontanyensis* in having the protoconid more buccolingually compressed, in the presence of lingual and buccal cingulids only below the talonid, and in the broader talonid basin. The P_4 of *Nievesia* are larger than those of *A. frontanyensis*, contrarily to the P_3 specimens. This tooth has similar width than the larger specimens of *A. frontanyensis*, although it is a bit longer. The P_4 of *Nievesia* differ from those of *A. frontanyensis* in their less marked lingual and buccal cingulids (which sometimes are discontinuous), in their less developed paraconid, in their less straight cristid obliqua, in their more buccal hypoconid, and in the enlargement of the enamel suggesting the presence of a minuscule metaconid in the distolingual part of the protoconid. The M_1 or M_2 specimens of *Nievesia* resemble in size the M_2 of *A. frontanyensis*. Morphologically, the specimens of *Nievesia* resemble more the M_2 than the M_1 of that species. The M_1 or M_2 attributed to *Nievesia* show no trace of a paraconid (present in the M_1 of *A. frontanyensis*), they present a shorter mesial part of the buccal cingulid, and usually a more buccal cristid obliqua than the M_1 but similar to that of the M_2 of *A. frontanyensis*. The M_1 or M_2 of *Nievesia* present a better-developed premetacristid, poorly marked in some specimens of *A. frontanyensis*, and absent in most of them. Apart from the paraconid, another small bulge is present in the paracristid of some *A. frontanyensis* M_1 specimens, which is never observed in the M_1 or M_2 of *Nievesia*. Concerning the M_3, those of *Nievesia* are larger than those of *A. frontanyensis* because many *A. frontanyensis* specimens are mesiodistally compressed; contrarily, the M_3 of *Nievesia* presents an elongated hypoconulid lobe and is not mesiodistally compressed. Moreover, the M_3 of *A. frontanyensis* present accessory cuspids in the talonid that are absent in any other anchomomyin. The cristid obliqua of the *Nievesia* M_3 specimen is similarly oriented as in *A. frontanyensis*. However, a well-developed premetacristid is present in *Nievesia*, unlike in *A. frontanyensis*, completely closing the trigonid. The hypoconulid lobe is closer to the entoconid, similarly to the largest (not mesiodistally compressed) *A. frontanyensis* specimens. Moreover, the hypoconid is larger than the entoconid in the

M_3 of *Nievesia,* and it is located more mesially than in *A. frontanyensis*.

When compared to *Anchomomys pygmaeus*, the M^1 or M^2 of *Nievesia* are smaller. *Nievesia*'s M^1 or M^2 resemble the smallest specimen of *A. pygmaeus* (Ef 372) morphologically more than any other *Anchomomys* species regardless of size. When compared to the type specimen of *A. pygmaeus*, *Nievesia*'s M^1 or M^2 are much smaller, they present a smaller hypocone, a shorter anterocingulum, and no lingual cingulum. The P_4 of *A.* cf. *pygmaeus* from Egerkingen Y is smaller than the specimens attributed to *Nievesia*; it differs from them in the well-developed paraconid, very small in *Nievesia,* and in the slightly more buccal hypoconid, although it is similarly developed than in the latter. Moreover, the P_4 of *A.* cf. *pygmaeus* presents continuous lingual and buccal cingulids, whereas the former is always discontinuous and the latter is sometimes discontinuous in *Nievesia*. In addition, the P_4 of *A.* cf. *pygmaeus* has no trace of a metaconid, whereas that of *Nievesia* presents a slight enlargement of the enamel in this position. Considering the M_1 or M_2 of *Anchomomys* cf. *pygmaeus*, the specimens of *Nievesia* are larger and have a more buccal cristid obliqua. Moreover, they present no trace of a paraconid and they have a less developed buccal cingulid. Concerning the M_3, those of *Nievesia* present a cristid obliqua more buccal than in *A.* cf. *pygmaeus.* A well-developed premetacristid completely closing the trigonid is present in *Nievesia*, as well as an hypoconulid lobe close to the entoconid, contrarily to *A.* cf. *pygmaeus*.

When compared to *Anchomomys crocheti*, the M^1 or M^2 of *Nievesia* are much smaller. Besides, *Nievesia*'s M^1 or M^2 present a smaller hypocone, a shorter anterocingulum, and no lingual cingulum. Moreover, *A. crocheti* presents a premetaconule crista absent in *Nievesia*, and the specimens attributed to the latter show a minuscule mesostyle. Regarding the lower dentition, the dP_4 of *Nievesia,* smaller than that of *A. crocheti,* is very similar to it in morphology, although the paraconid is less developed and more buccal, the buccal cingulid reappears at the distal end of the tooth and the cristid obliqua is a bit more buccal in *Nievesia*. Moreover, the P_3 of *Nievesia* are similar in width but longer than the specimen of *A. crocheti,* which is not fully erupted. Morphologically the P_3 of *Nievesia* differ from *A. crocheti* in the lack of cingulids in the mesial part of the tooth. In many *Nievesia* M_1 or M_2 specimens, the cristid obliqua is a bit more buccal than in the M_1 of *A. crocheti*; moreover, the teeth of *Nievesia* do not have a buccally enlarged paracristid and they present no trace of a paraconid.

Comparisons with Buxella

The M^1 and M^2 of *Buxella* differ from *Nievesia* in being much larger. Further differences of M^1 or M^2 of *B. prisca* with those of *Nievesia* are that they present no trace of a mesostyle, the absence of a postparaconule crista and the presence of a pericone. The M^3 of the genus *Buxella* are only represented by a single *B. prisca* specimen, which differs from the M^3 of *Nievesia* in being much larger, in presenting no reduction of the metacone, in the enlargement of the lingual cingulum suggesting the presence of a pericone, in the presence of a well-developed paraconule, in the large hypocone, in the well-developed postcingulum and in the absence of a buccally-protruding buccal side of the paracone. The P_3 of *Buxella* are represented by a single specimen of *B. prisca* that differs from those of *Nievesia* in the larger size, in the presence of complete buccal and lingual cingulids, and in the absence of a protocristid. One M_1 of *Buxella prisca* (specimen 6-12), is similar to those of *Nievesia* in size and overall morphology although the *Buxella* specimen does not present a premetacristid joining the paracristid and the metaconid, and it does present a small paraconid that is absent in *Nievesia*. Moreover, the other two M_1 specimens attributed to *B. prisca* are much larger than the M_1 or M_2 of *Nievesia*, and they present a more developed buccal cingulid, a paraconid, no premetacrisitd, and one of them (specimen 80-69) a more lingual cristid obliqua and a more differentiated hypoconulid. Regarding the single M_2 specimen of *B. prisca*, it differs from the M_1 or M_2 of *Nievesia* in the more developed buccal cingulid, in the presence of a small paraconid, and in the absence of a premetacristid. The only M_3 known for *B. prisca* presents some similarities with the M_3 of *Nievesia* in overall talonid morphology, although it is much larger, its paracristid does not join the metaconid by means of a complete premetacristid, its buccal cingulid is more developed, and its cristid obliqua is more lingually placed.

Differences of M^1 or M^2 of *Buxella magna* with those of *Nievesia* are the less straight postcingulum, the larger hypocone, the presence of a postparaconule crista, a lingual cingulum, and a small prehypocrista. The single M_1 of *B. magna* differs from those of *Nievesia* in the presence of a paraconid, the more developed buccal cingulid, the absence of a premetacristid, and the presence of some enamel wrinkling in the talonid. The single M_2 of *B. magna* resembles *Nievesia* in the presence of a premetacristid that joins the paracristid and the metaconid and in the absence of a paraconid. However, it differs from *Nievesia* in the much larger size, in the more developed buccal cingulid, and in the presence of enamel wrinkling in the talonid.

Comparisons with Periconodon

The type and only material of *Periconodon helveticus* (type species of this genus) is a maxilla fragment with P^3, M^1 and M^2. Its upper molars differ from *Nievesia* in being larger, in the presence of a well-developed pericone, a large hypocone and a prehypocrista, in having no trace of a mesostyle, and in the broader talon basin.

Regarding the species *Periconodon huerzeleri,* its M^1 or M^2 are much larger than those of *Nievesia*, they present a pericone, a longer anterocingulum, a more developed hypocone, and no trace of a mesostyle. The P_4 of *P. huerzeleri* is similar in size to those of *Nievesia*, even though those of *Nievesia* present a discontinuous buccal cingulid, an enlargement of the enamel suggesting a minuscule metaconid and a protocristid, together with a more buccal location of the hypoconid. The M_1 or M_2 of *P. huerzeleri* are twice the size of those of *Nievesia*. Moreover, they present a small paraconid in some of the M_1, a more lingual cristid obliqua, a more mesial position of the entoconid, and a total absence of a premetacristid. The M_3 of *P. huerzeleri* differs from that of *Nievesia* by the absence of a premetacristid joined with the paracristid completely closing the trigonid basin, the longer and more developed buccal cingulid and the more lingual hypoconulid lobe.

Periconodon jaegeri is the only species of this genus for which the P^4 is known. As stated before, *Nievesia* has the smaller anchomomyin P^4, smaller than the one attributed to *P. jaegeri*. The lingual side of the *Nievesia* specimen, mainly the protocone lobe, is much more buccolingually compressed than in *P. jaegeri*, giving the whole tooth a more compressed aspect. The specimen from Sossís has no anterocingulum, and it has a straighter postcingulum than the P^4 attributed to *P. jaegeri*. The M^1 or M^2 of *P. jaegeri* differ from *Nievesia* in being larger, in the presence of a large pericone and a metaconule, in the presence of a prehypocrista, and in the crenulated enamel. *Nievesia*'s M^3 differs from that of *P. jaegeri* in being smaller, in the absence of a pericone, in the extremely reduced metacone, and in having no crenulated enamel. The M_1 or M_2 of *P. jaegeri* differ from those of *Nievesia* in their larger size, in the crenulated enamel, in the paracristid not joining the tip of the metaconid, in the more buccal cristid obliqua, and in the more developed buccal cingulid. The M_3 of *P. jaegeri* differ from those of

Nievesia in being larger, in the presence of crenulated enamel, in the more developed buccal cingulid, and in the absence of a premetacristid joining the paracristid and the metaconid.

Comparisons with Mazateronodon

The buccal side of *Nievesia*'s P^4 is much shorter than that of *Mazateronodon* and the lingual side, mainly the protocone lobe, is much more buccolingually compressed in *Nievesia*, giving the whole tooth a more compressed aspect. Moreover, the protocone is centered on the protocone lobe, unlike in *Mazateronodon*, where the protocone is more mesially placed. The specimen attributed to *Nievesia* has a paracone close in height to that of *Mazateronodon*, although it has no anterocingulum, and it presents a straighter postcingulum than the one attributed to *Mazateronodon*. When compared to *Mazateronodon*, the M^1 or M^2 of *Nievesia* are much smaller, although they have similar proportions of the main cusps and thus similar morphology. However, the specimens of *Nievesia* present a more developed ectocingulum in the buccal side of the paracone, a trace of a mesostyle, and a less developed and shorter anterocingulum. The M^3 of *Mazateronodon* are larger than the *Nievesia* specimen, with a more subtriangular shape due to the more developed metacone, which is extremelly reduced in the specimen from Sossís. Moreover, the M^3 of *Mazateronodon* has more developed anterocingulum and postcingulum, and a less protruding lingual side of the paracone. The P_3 of *Mazateronodon* are larger than the P_4, unlike the specimens of *Nievesia*. Regardless of the size differences (*Mazateronodon* is larger than *Nievesia*), the specimens from Mazaterón are proportionally longer and more buccolingually compressed. Moreover, the specimens of *Nievesia* do not have continuous buccal and lingual cingulids, and present both a protocristid and a cristid obliqua, whereas those of *Mazateronodon* only have the latter. The P_4 of *Nievesia* differ from those of *Mazateronodon* in being larger than the P_3, in having no paraconid, and in the presence of a protocristid and an enlargement of the enamel suggesting a minuscule metaconid. Moreover, the lingual cingulid is more discontinuous in *Nievesia* than in *Mazateronodon.* The M_1 or M_2 of *Mazateronodon*, apart from being much larger than those of *Nievesia*, resemble them in the presence of a paracristid without a differentiated paraconid, and in the presence of a premetacristid connecting the paracristid and the metaconid. However, the premetacristid in the specimens of *Nievesia* is more marked, and the paracristid is more smooth and rounded. Moreover, the specimens of *Nievesia* further differ from those of *Mazateronodon* in the less-developed and discontinuous buccal cingulid, in the better-developed hypoconulid, and in the more lingual cristid obliqua. The M_3 of *Nievesia* differ from those of *Mazateronodon* in being much smaller, in the more smooth and rounded paracristid, the less developed buccal cingulid, the more developed and differentiated entoconid, and the more centered hypoconulid lobe.

Discussion

The only anchomomyin found until now in the Late Eocene of Europe is the genus *Anchomomys* with the species *A. quercyi* (MP17a). All the other already known members of the tribe are not found after the Middle Eocene. Thus, the new anchomomyin genus *Nievesia* described in this paper increases the record of anchomomyins from the early Late Eocene of Spain.

Looking at the results of the phylogenetic analysis we can observe that in all of the most parsimonious trees that were recovered (following hypotheses 1 and 2, see Figure 6A and 6B respectively) all the anchomomyins, including the new genus presented in this paper, fall within the same group, which appears as the sister-group of all other adapoids except for *Donrussellia*.

In the analysis performed by Marigó et al. (2011), which included the same anchomomyins as this one except for the new genus *Nievesia*, anchomomyins appeared either as being closely related to extant Lemuroidea and Lorisoidea (following hypothesis 1), or more closely related to the Subfamily Asiadapinae (*Asiadapis* and *Marcgodinotius*; following hypothesis 2).

Even though there are some differences between the analyses obtained this time (depending on whether reacquisition of previously lost premolars was permitted or not), after the addition of '*Anchomomys' milleri* and *Djebelemur martinezi*, anchomomyins appear to be closely related only to asiadapines, although this must be regarded with caution due to the scarcity of material for some of the coded taxa.

After the addition of '*Anchomomys' milleri* and *Djbelemur martinezi* in the analyses made this time, all anchomomyins are shown to be more closely related to asiadapines (*Asiadapis* and *Marcgodinotius*) and sivaladapids (*Hoanghonius* and *Rencunius*) than to extant Lemuroidea and Lorisoidea. We added these two taxa because djebelemurids are now considered the primitive sister group of crown strepsirrhines (Seiffert et al., 2003, 2005; Godinot, 2006).

For hypothesis 1, we observe crown strepsirrhines with some extinct taxa such as *Donrussellia, Djebelemur* and *'Anchomomys' milleri* forming the sister group of adapoids, which in turn are subdivided in two other groups, one corresponding to notharctids and adapids, and the other one including European anchomomyins, sivaladapids and asiadapines. For hypothesis 2 we find an unresolved position for *Donrussellia provincialis*. *Donrussellia gallica* and djebelemurines fall outside the clade that joins crown strepsirrhines and adapoids together. In this analysis we also find *Nosmips* and *Plesiopitheus* closely related to crown strepsirrhines. However, if we look at the adapoid group, it is again subdivided in two clades, one including European anchomomyins, asiadapines and sivaladapids, and the other one including all other adapiforms, even though the arrangements within the sivaladapids + Asiadapinae + Anchomomyini clade are different for the two hypotheses. In both hypotheses *Marcgodinotius* and *Asiadapis* are outside the clade formed by sivaladapids and anchomomyins. The only relationship that changes within this group is the one between *Nievesia* and *Mazateronodon*, which in hypothesis 1 are sister taxa, but not in hypothesis 2, where they are nested successively closer to *Anchomomys gaillardi* and *Anchomomys frontanyensis*.

The clade formed by asiadapines, anchomomyins and sivaladapids in our analyses is supported by some characters that are considered to be apomorphies, and that exclude this clade from being in the group of the other adapiforms. However, if we look closer at those characters, more than 50% are related to postcranial material. None of the anchomomyins coded for the analyses include postcranial information. Thus, this relationship suggested by our analyses must be treated with extreme caution. Regarding the apomorphies related with dentition, only 50% of the characters are considered to be unambiguous, and from the rest, most of the characters have been considered primitive for adapiforms, such as reduced or absent metaconids on lower fourth premolars, absence of metastylids on the lower molars, and the subtriangular shape of the upper molars (Szalay and Delson, 1979). The only derived character found is the reduction of paraconids on the lower molars, which could represent a convergence.

Nevertheless, anchomomyins are considered to be closely related in our analysis, and the new genus presented here appears to be more closely related to *Mazateronodon* than to any other anchomomyin at least in one of our analyses, which was also observed in our comparisons due to some dental similarities between the two taxa.

Conclusions

In this paper we present a new anchomomyin genus and species from the fossil site of Sossís, one of the most important fossil-bearing early Late Eocene (MP17a) continental sites from the Iberian Peninsula. *Nievesia* differs from all the other members of this tribe in presenting no enamel wrinkling, in its buccolingually compressed P^4, upper molars with no pericone, medium-sized hypocone, straight postcingulum and minuscule mesostyle, and the extremely-reduced metacone in the M^3, lower premolars with no paraconid and discontinuous buccal and lingual cingulids, hypoconid present in the P_4 together with a trace of a metaconid. Its lower molars bear no paraconid and present a premetacristid joining the paracristid and the metaconid, closing the trigonid basin, and its M_3 has a centered and elongated hypoconulid lobe, and the trigonid wider than the talonid.

The new genus *Nievesia* appears to be more closely related to *Mazateronodon* than to any other anchomomyin at least in one of the two phylogenetic analyses we have developed, even though the new taxon presents significant differences from *Mazateronodon*, and it shares some other features with *Anchomomys*, more than with *Buxella* or *Periconodon*.

The addition of *Nievesia* in our analyses, together with the inclusion of djebelemurines, no longer allows linking European anchomomyins with crown strepsirhines, and it also suggests a closer relationship of European anchomomyins with asiadapines and sivaladapids than to other adapiforms. However, these results need to be taken with caution due to the lack of postcranial information for some taxa, and the impossibility of evaluating the true phylogenetic signal of the characters uniting the members of some groups.

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Figures and tables

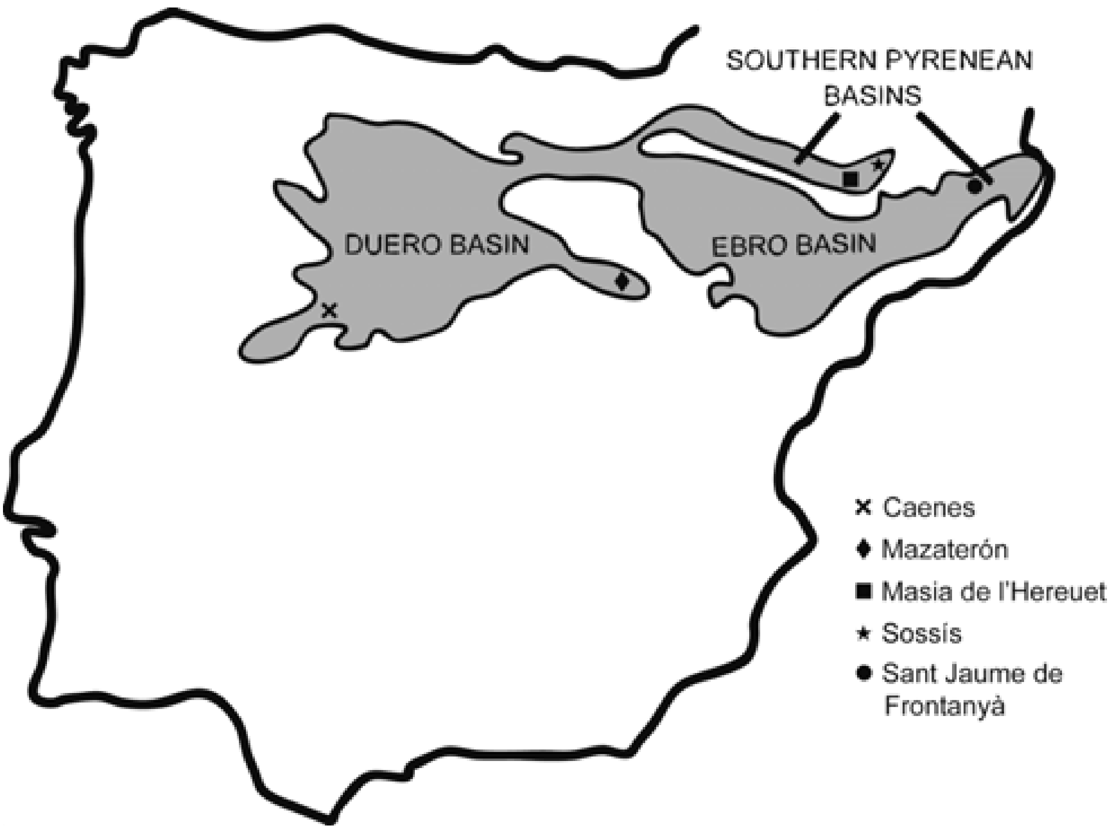

Figure 1. Map of the Iberian Peninsula showing the main Paleogene Basins and some outstanding fossil sites that have yielded primate remains (modified from Antunes et al., 1997 and Badiola et al., 2009).

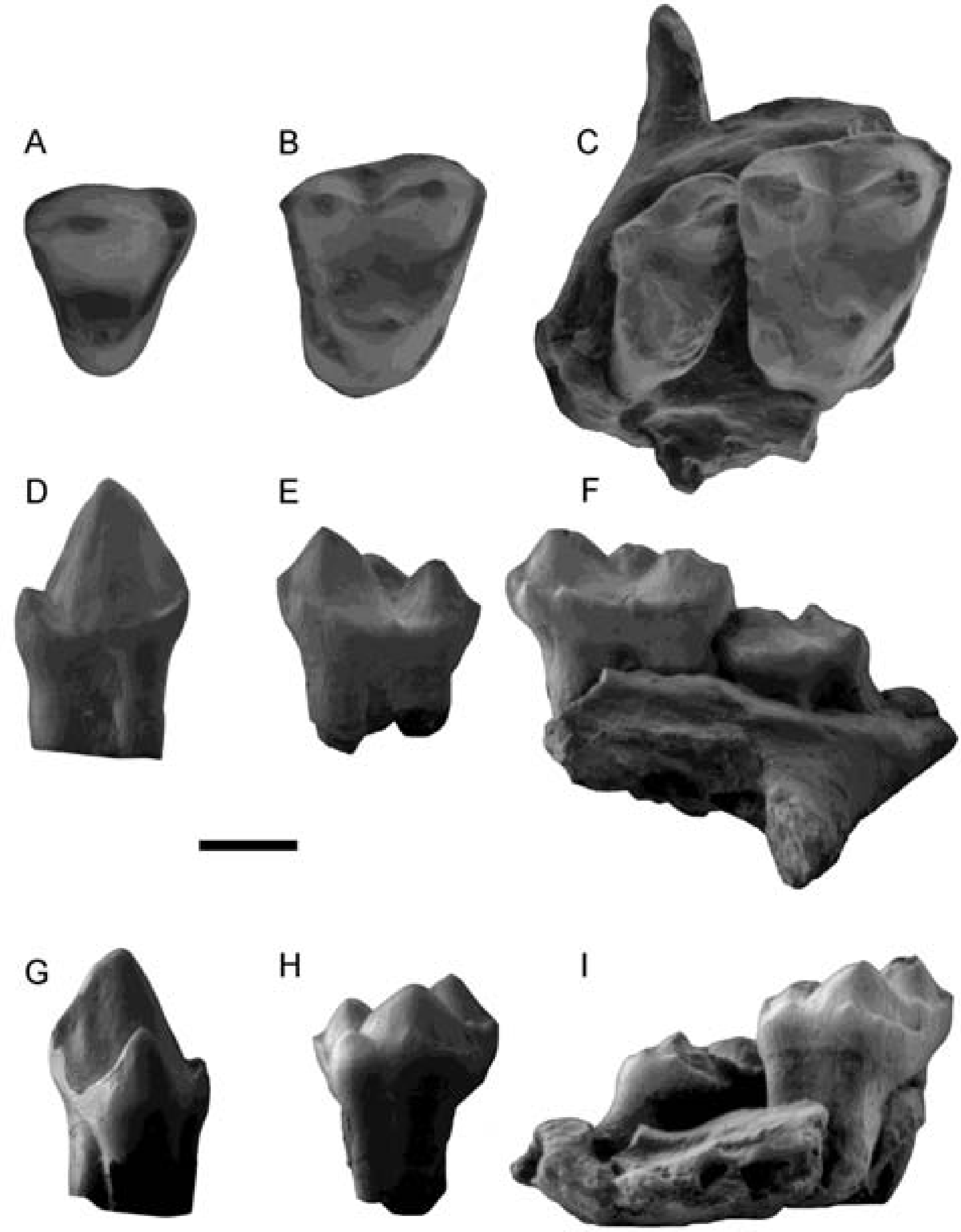

Figure 2. Micrographs of the upper dentition of *Nievesia sossisensis*. (A) Right P^4 (IPS-57269) in occlusal view; (B) Right M^1 or M^2 (IPS-57270) in occlusal view; (C) Right maxilla fragment with M^1 or M^2 and M^3 (IPS-57271, holotype) in occlusal view; (D) Right P^4 (IPS-57269) in buccal view; (E) Right M^1 or M^2 (IPS-57270) in buccal view; (F) Right maxilla fragment with M^2 and M^3 (IPS-57271, holotype) in buccal view; (G) Right P^4 (IPS-57269) in lingual view; (H) Right M^1 or M^2 (IPS-57270) in lingual view; (I) Right maxilla fragment with M^2 and M^3 (IPS-57271, holotype) in lingual view. Scale bar represents 1 mm.

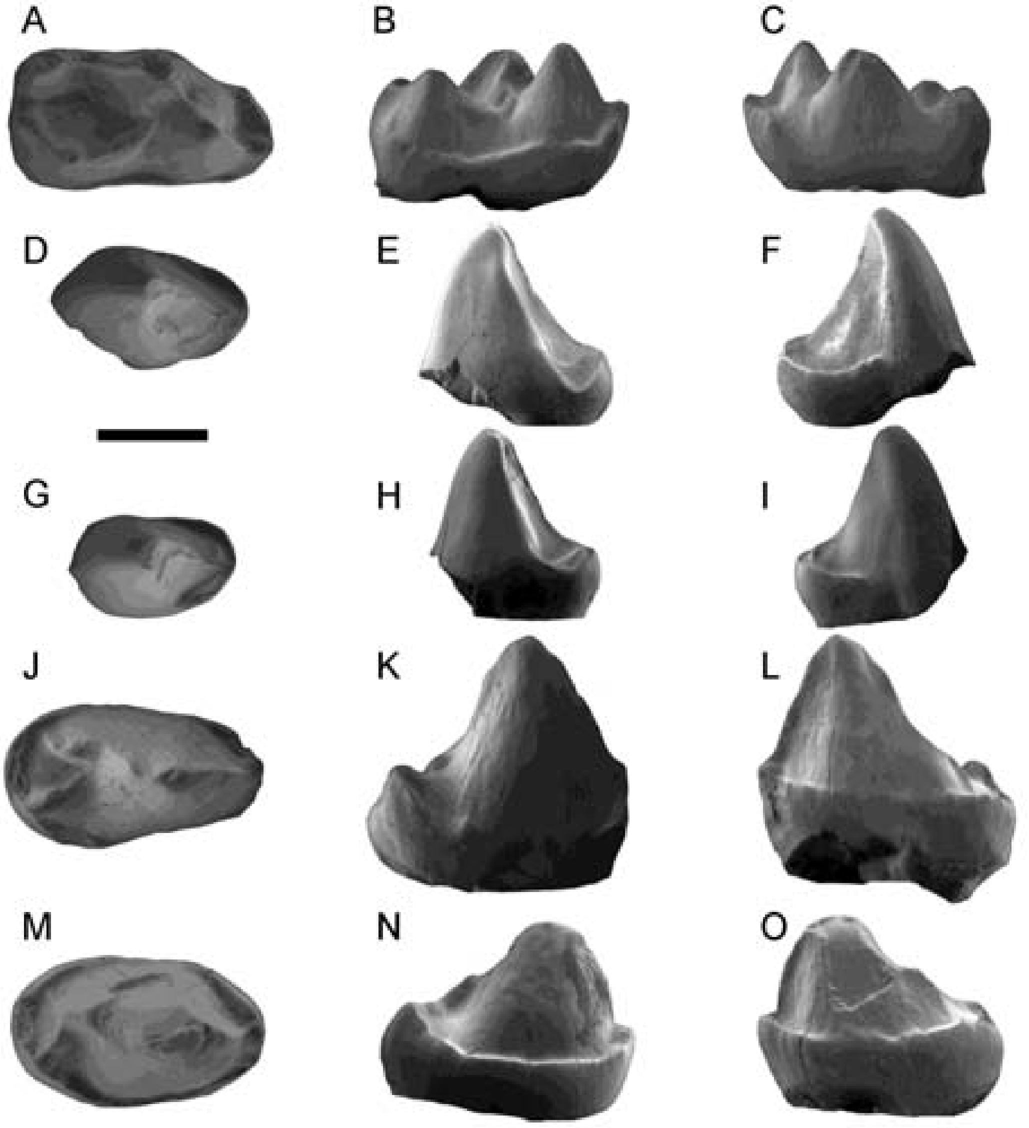

Figure 3. Micrographs of the lower premolars of *Nievesia sossisensis.* (A) Right dP_4 (IPS-57274) in occlusal view; (B) in buccal view; (C) in lingual view; (D) Left P_3 (IPS-57277) in occlusal view; (E) in buccal view; (F) in lingual view; (G) Left P_3 (IPS-57278) in occlusal view; (H) in buccal view); (I) in lingual view; (J) Right P_4 (IPS-57279) in occlusal view; (K) in buccal view; (L) in lingual view; (M) Right P_4 (IPS-57280) in occlusal view; (N) in buccal view; (O) in lingual view. Scale bar represents 1 mm.

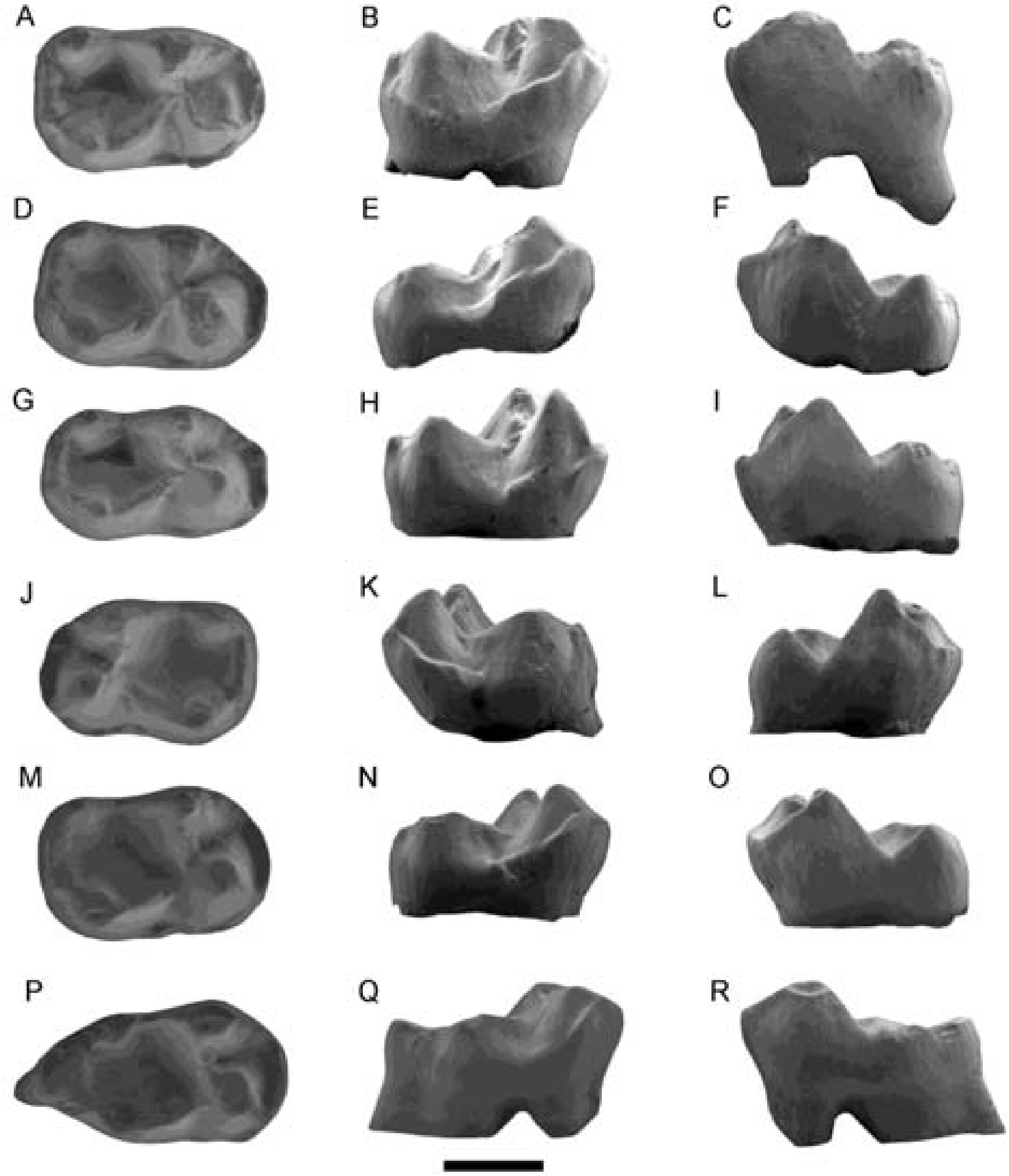

Figure 4. Micrographs of the lower molars of *Nievesia sossisensis.* (A) Right M_1 or M_2 (IPS-57281) in occlusal view; (B) in buccal view; (C) in lingual view; (D) Right M_1 or M_2 (IPS-57282) in occlusal view; (E) in buccal view; (F) in lingual view; (G) Right M_1 or M_2 (IPS-57284) in occlusal view; (H) in buccal view; (I) in lingual view; (J) Left M_1 or M_2 (IPS-57285) in occlusal view; (K) in buccal view; (L) in lingual view; (M) Right M_1 or M_2 (IPS-57287) in occlusal view; (N) in buccal view; (O) in lingual view; (P) Right M_3 (IPS-57289) in occlusal view; (Q) in buccal view; (R) in lingual view. Scale bar represents 1 mm.

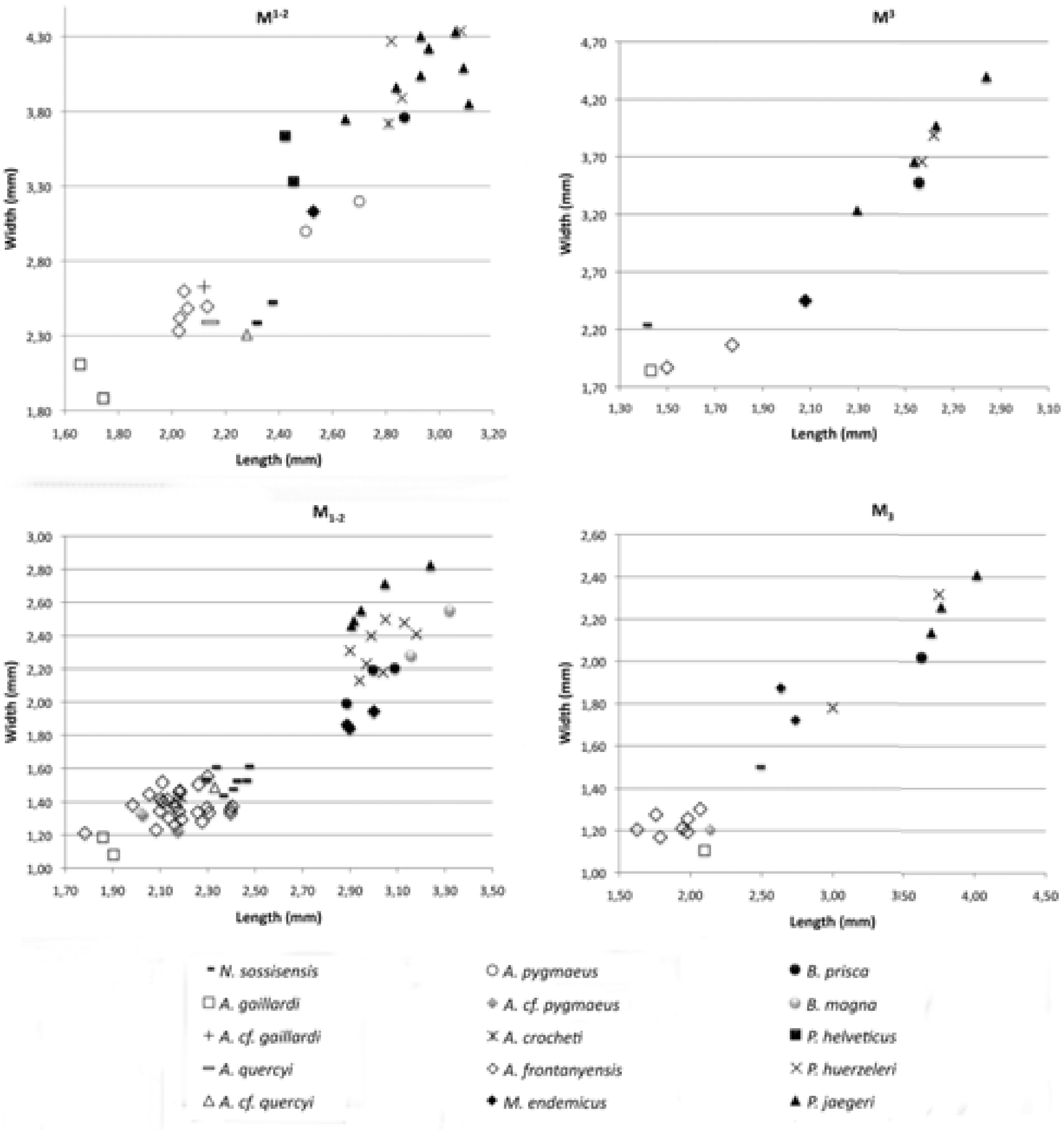

Figure 5. Size graphs of all known anchomomyin species. Measurements were taken from original specimens, high-quality casts, or the literature. Measurement of *Nievesia sossisensis*'s M^3 was included for comparison, even though its width couldn't be measured completely (see Table 2).

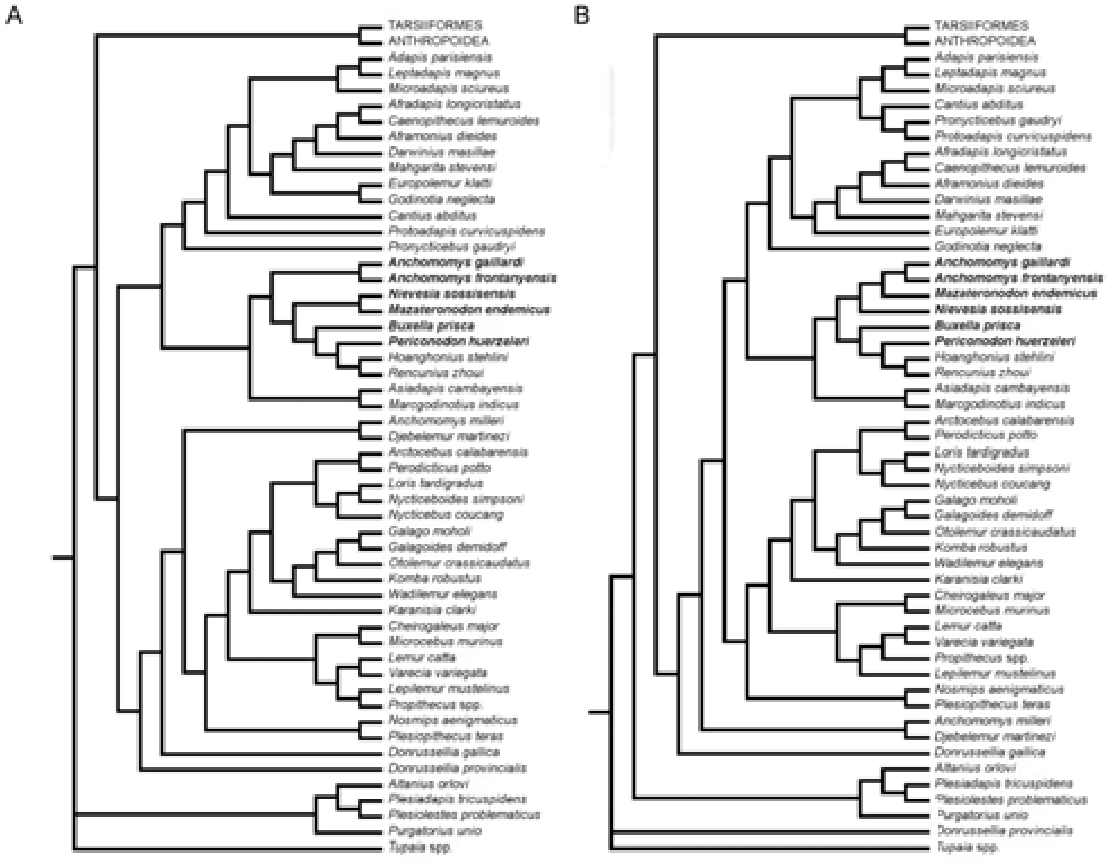

Figure 6. Phylogenetic analyses results. (A) Hypothesis 1: 1 most parsimonious tree was recovered (premolar reacquisition not allowed), tree length: 2232.944, consistency index: 0.195, retention index: 0.577. (B) Hypothesis 2: 1 most parsimonious tree was recovered (premolar reacquisition allowed), tree length: 2216.590, consistency index: 0.199, retention index: 0.563. All anchomomyins are in bold type.

MARSUPIALIA

Peratherium lavergnense

Peratherium perriense

CIMOLESTA

Apatemyidae indet.

RODENTIA

Treposciurus mutabilis

Estellomys ibericus

Paradelomys crusafonti

Theridomys euzetensis

Pseudoltinomys cf. *phosphoricus*

Elfomys parvulus

Gliravus robiaciensis

ARTIODACTYLA

Cebochoerus helveticus

Acotherulum sp.

Dacrytherium ovinum

Leptotheridium lugeoni

Haplomeryx euzetensis

Xiphodon intermedium

LIPOTYPHLA

Leptictis sp.

Saturninia pirenaica

CREODONTA

Hyaenodon minor

CARNIVORA

Miacis exilis

PERISSODACTYLA

Palaeotherium magnum stehlini

Palaeotherium medium euzetense

Palaeotherium crassum sossisenses

Plagiolophus annectens

Anchilophus dumasi

PRIMATES

Adapis cf. *parisiensis*

Pseudoloris parvulus

Microchoerus erinaceus

Nievesia sossisensis gen. et sp. nov.

Table 1. Faunal list of Sossís, modified from Casanovas Cladellas (1998) and Cuesta et al. (2006).

SPECIMEN	DENTAL ELEMENT	L	W
IPS-57269	P^4	1.91	2.11
IPS-57273	M^1	2.39	-
IPS-57270	M^2	2.30	2.39
IPS-57271	M^2	2.36	2.52
	M^3	2.24	>1.40
IPS-57274	dP_4	2.47	1.33
IPS-57275	P_3	>1.89	0.95
IPS-57278	P_3	-	1.01
IPS-57279	P_4	2.47	1.40
IPS-57280	P_4	2.38	1.40
IPS-57281	M_{1-2}	2.41	1.52
IPS-57282	M_{1-2}	2.45	1.53
IPS-57283	M_{1-2}	2.39	1.48
IPS-57284	M_{1-2}	2.35	1.44
IPS-57285	M_{1-2}	2.28	1.53
IPS-57286	M_{1-2}	2.46	1.61
IPS-57287	M_{1-2}	2.32	1.61
IPS-57289	M_3	2.47	1.50

Table 2. Measurements (mm) of dental elements of *Nievesia sossisensis*. L: length), W: width, H: height, >: specimens with a hidden small part (in the case of the M^3) or lacking it. Only those specimens where at least one measurement could be taken have been included. Specimen IPS-57274 was measured as an M_1 or M_2.

	Nievesia sossisensis	*Anchomomys gaillardi*	*A. quercyi* and *A.* cf. *quercyi*	*A. frontanyensis*	*A. pygmaeus* and *A.* cf. *pygmaeus*	*A. crocheti*	*Buxella prisca*	*B. magna*	*Periconodon helveticus*	*P. huerzeleri*	*P. jaegeri*	*Mazateronodon endemicus*
Overall size compared to *Nievesia*	-	smaller	smaller	smaller	larger	larger	larger	larger	larger	larger	larger	larger
Buccolingually compressed P^4	yes	no	no	no	?	?	?	?	?	?	no	no
Pericone in the upper molars	no	no	no	no	yes	no	yes	no	yes	yes	yes	no
Size of the hypocone in the M^{1-2} compared with *Nievesia*	-	smaller	similar	smaller	larger	larger	larger	larger	larger	larger	larger	similar
Straight postcingulum in the M^{1-2}	yes	no	no	no	yes	yes	yes	yes	yes	yes	yes	yes
Anterocingulum in the M^{1-2} compared with *Nievesia*	-	long	long except for *A.* cf. *quercyi*	long	long	long	long	short	short	longer	longer	shorter
M^3 metacone	very reduced	not reduced	?	not reduced	?	?	not reduced	?	?	reduced	not reduced	reduced
P_4 paraconid	no	yes	no	yes	yes	?	?	?	?	no	?	no
Paraconid in lower molars	no	present in M_1	no	present in M_1	present in M_1	present in M_1	present in M_1 and M_2	present in M_1	?	present in some M_1	no	no
Premetacristid in lower molars	yes, closing trigonid	no	no	no	no	no	not complete	present in M_2	?	no	present, but it may close trigonid or not	yes
M_3 hypoconulid lobe	centered and elongated	centered but more developed	?	centered but reduced	?	?	centered but more developed	?	?	more lingual	similar or more lingual	more lingual

Table 3. Comparison table showing the key characters that distinguish *Nievesia* from other anchomomyins.

Supplementary Online Material 1

The data matrix used in this paper matrix is modified from the one in Seiffert et al. (2010). No modifications to the original constraint tree were made. Original data matrix and constraint tree can be downloaded from the following website: http://www.anat.stonybrook.edu/eseiffert/nosmips.html.

All modifications made to the original matrix are explained in the Materials and Methods section, and the whole data matrix used will be available online when this article is published in Journal of Human Evolution. For allowing premolar reacquisition, erase the following text from the matrix:

```
USERTYPE p1_presence_a (Stepmatrix) =3
0	1	2
0	1	2
i	0	1
i	i	0
;
USERTYPE 'p2 roots/presence' (Stepmatrix) =5
0	1	2	3	4
0	1	2	3	4
i	0	1	2	3
i	i	0	1	2
i	i	i	0	1
i	i	i	i	0
;
USERTYPE P1_presence_b (Stepmatrix) =2
0	1
0	1
i	0
;
USERTYPE 'P2 root number/presence' (Stepmatrix) =5
0	1	2	3	4
0	1	2	3	4
i	0	1	2	3
i	i	0	1	2
i	i	i	0	1
i	i	i	i	0
;
```

And also delete this other text, which occurs twice:

```
p1_presence_a:  21, 'p2 roots/presence':  22, P1_presence_b:  120, 'P2 root number/presence':  121;
```

Supplementary Online Material 2

Anchomomyin material used for comparisons with *Nievesia sossissensis*:

SPECIES	CATALOG NUMBERS	INSTITUTION	FOSSIL SITE
Anchomomys gaillardi (type species)	UL NºL46 bis (holotype)	Faculté des Sciences, Université de Lyon (Lyon, France)	Lissieu
Anchomomys quercyi	QH 470 (holotype)	Naturhistorisches Museum Basel (Basel, Switzerland)	Quercy (level indet.)
Anchomomys cf. *quercyi*	Ma-PhQ 342 and 343 (VI-BrB 2957 and 2958)	Musée d'Histoire Naturelle de Montauban (Montauban, France)	Le Bretou
Anchomomys pygmaeus	Ef 367 (holotype) and Ef 372	Naturhistorisches Museum Basel (Basel, Switzerland)	Egerkingen Huppersand
Anchomomys cf. *pygmaeus*	En.1 (holotype), Eh.748 and Eh.749 (only roots remain)	Naturhistorisches Museum Basel (Basel, Switzerland)	Egerkingen Y
Anchomomys crocheti	SMF 152 (holotype), SMF 151, SMF 25, SMF 26 and SMF 27	Institut des Sciences de l'Évolution, Faculté des Sciences, Université de Montpellier (Montpellier, France)	St-Martin-de-Londres
Anchomomys frontanyensis	IPS8429 (holotype), IPS8423-8428, IPS8430-8456, IPS8458-8492, IPS8494-8516, IPS8518-8535, IPS8537-8543, IPS8545-8602, IPS8604-8611, IPS8613-8624, IPS8626-8637, IPS47868-47877, IPS47941-47947, IPS47949-47951, IPS47955, IPS55133-55146	Institut Català de Paleontologia Miquel Crusafont (Sabadell, Spain)	Sant Jaume de Frontanyà 3
Buxella prisca (type species)	BUX 80.69 (holotype), BUX 6.10-6.12, BUX 80.66-80.68, BUX 66.133 and CHMV 25	Institut des Sciences de l'Évolution, Faculté des Sciences, Université de Montpellier (Montpellier, France)	Bouxwiller

Buxella magna	BUX 66.122 (holotype), BUX 66.123, BUX 66.134 and BUX 80.70	Institut des Sciences de l'Évolution, Faculté des Sciences, Université de Montpellier (Montpellier, France)	Bouxwiller
Periconodon helveticus (type species)	Ef 366 (holotype)	Naturhistorisches Museum Basel (Basel, Switzerland)	Egerkingen Huppersand
Periconodon huerzeleri	Bchs 495 (holotype), Bchs 494, Bchs 640, Bchs 222 and Bchs 312	Naturhistorisches Museum Basel (Basel, Switzerland)	Bouxwiller
Periconodon jaegeri	CHMV 18 (holotype), CHMV 24, BUX 6.3, BUX 6.5, BUX 6.6, BUX 6.8, BUX 6.9, BUX 80.50-80.52, BUX 80.55 BUX 80.57 and BUX 66.120	Institut des Sciences de l'Évolution, Faculté des Sciences, Université de Montpellier (Montpellier, France)	Bouxwiller
Mazateronodon endemicus	IPS46238 (holotype), IPS46207-46237, IPS46239-46272	Institut Català de Paleontologia Miquel Crusafont (Sabadell, Spain)	Mazaterón

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RESULTATS I DISCUSSIÓ GENERALS

En aquesta tesi doctoral s'ha fet una revisió bibliogràfica de tot el registre de primats a la Península Ibèrica durant el Cenozoic. Aquesta informació detallada del grup a la Península, que es pot trobar a l'annex I, representa una gran aportació a l'estudi dels primats fòssils d'aquesta zona, ja que no se n'havia fet una revisió exhaustiva des que la feren Crusafont-Pairó i Golpe-Posse (1974). De totes maneres, degut a que aquesta tesi es basa en l'estudi de nous primats de l'Eocè, aquesta discussió es centrarà només en el registre de primats d'aquesta època. Des d'aquella última revisió, el coneixement dels primats de l'Eocè, tant de plesiadapiformes, d'adapoïdeus com d'omomioïdeus, ha incrementat notablement, tant pels estudis realitzats durant la dècada de 1990 (Moyà-Solà i Köhler, 1992, 1993; Köhler i Moyà-Solà, 1999) com per les publicacions que formen part d'aquesta tesi doctoral, entre altres.

A l'annex I s'enumeren els tàxons trobats a la Penísula i es donen detalls de la seva sistemàtica, de la distribució geogràfica i cronològica, de la seva paleobiologia i de les seves relacions filogenètiques. Pel que fa als plesiadapiformes, el seu registre a la Península queda restringit al gènere *Arcius*, trobat als jaciments de Silveirinha (Portugal) i Masia de l'Hereuet (Lleida) durant el Neustrià (Eocè inferior, MP7 i MP8+9 respectivament; veure taula 3).

El registre d'adapoïdeus a la Península comença també durant l'Eocè inferior amb la presència del gènere *Donrussellia* al jaciment de Silveirinha a Portugal. Durant el Grauvià (MP10), els gèneres *Cantius* i *Agerinia* es troben representats en jaciments de les conques pirinenques i de l'Ebre. El gènere *Agerinia* el trobem fins el Geiseltalià, on apareix per última vegada al jaciment de Casa Ramón (MP11/12, Osca). Els primers representants de la tribu Anchomomyini (Família Notharctidae), el grup d'adapoïdeus que s'estudia més a fons en aquesta tesi doctoral, els comencem a trobar durant l'Eocè Inferior-Mitjà (MP10-11) en diferents jaciments de la Conca de l'Ebre. Durant tot l'Eocè Mitjà els trobem en diferents jaciments de les conques pirinenques i a la Conca del Duero, i el seu registre arriba fins l'Eocè Superior (MP17a), al jaciment clàssic de Sossís. Aquesta tribu es troba representada a la Península pels gèneres *Anchomomys, Mazateronodon* i *Nievesia*, sent els dos últims gèneres nous que es presenten en aquesta tesi doctoral (Capítols 8 i 10).

MP	Jaciment/Locality	Tàxons/Taxa
22	Fonollosa 13 ▯	*Pseudoloris godinoti*
21	Aguatón ◆	*Microchoerus* sp.
	Santpedor 2 ▯	*Pseudoloris godinoti*
19	Sant Cugat de Gavadons (=Collsuspina) ▯	*Pseudoloris reguanti* *Necrolemur* sp. *Microchoerus ornatus*
18	Zambrana ○	Microchoerinae indet.
17a	Roc de Santa ❖	*Leptadapis magnus* *Necrolemur antiquus*
	Sossís ❖	*Adapis* cf. *parisiensis* *Pseudoloris parvulus* *Microchoerus erinaceus* *Nievesia sossissensis*
15-16	Caenes ▯	*Microadapis* sp. *Anchomomys* sp.
	Mazaterón ▯	*Mazateronodon endemicus* *Pseudoloris cuestai* cf. *Adapis* sp.
15	Pontils 38 ▯	Omomyidae indet.
	Sant Jaume de Frontanyà 1 ❖	*Anchomomys* sp. *Necrolemur* sp.
14-15	Sant Jaume de Frontanyà 2 ❖	*Necrolemur* sp.
	Sant Jaume de Frontanyà 3 ❖	*Anchomomys frontanyensis* *Pseudoloris pyrenaicus* *Adapis* sp.
14	Capella ❖	*Leptadapis priscus* *Leptadapis capellae* *Pseudoloris isabenae*
13-14	Santa Clara ▯	*Anchomomys* cf. *pygmaeus*
11/12	Casa Ramón ❖	*Pseudoloris* sp. *Agerinia* sp.
10-11	Ulldemolins I ▯ Montblanc ▯ Coll de l'Illa ▯	cf. Anchomomyini indet.
10	La Coma (=La Morera del Montsant) ▯	*Agerinia* sp. *Cantius* sp.
	Les Saleres ❖ Escarlà ❖ Les Badies ❖ Güell I ❖ Castigaleu ❖ Can Picantón ❖	*Agerinia roselli*
	Güell III ❖	*Cantius* sp.
	Mont de Roda ❖	Prosimii indet.
8+9	Masia de l'Hereuet ❖	*Arcius* sp.
7	Silveirinha ■	*Arcius zbyszewskii* *Donrussellia lusitanica* Notharctidae indet.

Taula 3. Llista dels tàxons de primats de l'Eocè i l'Oligocè trobats en diferents jaciments de la Península Ibèrica (veure Annex I). Conca de Mondego (■); Conca de Calatayud-Teruel (◆); Conca de Miranda-Trebiño (○); Conca de l'Ebre (▯); Conca del Duero (▯); conques sudpirinenques (❖).

Pel que fa als adàpids (Família Adapidae), el gènere *Leptadapis* el trobem al jaciment de Capella (MP14, Eocè Mitjà, Osca) i al de Roc de Santa (MP17a, Eocè Superior, Lleida); el gènere *Microadapis* apareix al jaciment de Caenes (MP15-16, Eocè Mitjà, Salamanca); i el gènere *Adapis* el trobem als jaciments de Sant Jaume de Frontanyà-3 (MP14-15, Eocè Mitjà, Barcelona) i Sossís (MP17a, Eocè Superior, Lleida). Per tant, els gèneres *Adapis* i *Leptadapis* representen el darrer registre dels adapoïdeus a la Península.

Els omomyoïdeus de la Península Ibèrica pertanyen tots a la subfamília Microchoerinae, i es troben representats per només tres gèneres: *Pseudoloris*, *Microchoerus* i *Necrolemur*. El gènere *Pseudoloris* té el seu registre més antic al jaciment de Casa Ramón (MP11/12, Osca), i es troba també en altres jaciments de l'Eocè Mitjà, a vegades juntament amb *Necrolemur*, gènere que apareix per primera vegada al jaciment de Sant Jaume de Frontanyà 2 (MP14-15, Barcelona). El gènere *Necrolemur* el trobem per última vegada durant l'Eocè Superior, al jaciment de Sant Cugat de Gavadons (MP19, Barcelona). En canvi, els gèneres *Pseudoloris* i *Microchoerus* aconsegueixen sobreviure el límit Eocè-Oligocè, el primer representat als jaciments de Fonollosa 13 (MP22, Barcelona) i Santpedor 2 (MP21, Barcelona), i el segon a la localitat d'Aguatón (MP21, Teruel). Ambdós respresenten l'únic registre d'aquest grup de primats durant l'Oligocè (Köhler i Moyà-Solà, 1999; Peláez-Campomanes, 2000).

A més a més de revisar el registre de primats a la Península, durant el transcurs d'aquesta tesi doctoral, s'han estudiat al detall les restes fòssils de primats de l'Eocè de quatre jaciments diferents: Masia de l'Hereuet (Capítol 5), Sant Jaume de Frontanyà (Capítols 6 i 7), Mazaterón (Capítols 8 i 9) i Sossís (Capítol 10). A continuació es detallen els resultats obtinguts després de la descripció, comparació i determinació taxonòmica de les restes dentàries de plesiadapiformes, adapoïdeus i omomioïdeus estudiats, i es fa una discussió dels resultats explicant també les implicacions filogenètiques i paleobiogeogràfiques d'aquests.

Pel que fa a la localitat de Masia de l'Hereuet (Eocè Inferior), les dents que s'hi han recuperat i que han estat estudiades en el context d'aquesta tesi doctoral presenten una morfologia que ha permès la seva atribució al gènere *Arcius* (Familia Paromomyidae, Semiordre Plesidapiformes). *Arcius* és l'únic paromòmyid que es coneix actualment a Europa, i en aquest jaciment se n'han trobat quatre dents, dues M^{1-2}, una M_{1-2} i una M_3.

La mida de les dents estudiades és més gran que el rang de mida conegut per a les espècies *Arcius rougieri* i *A. zbyszewskii*, més gran o similar als valors màxims de l'espècie *A. fuscus*, i més petita o semblant als valors mínims d'*A. lapparenti*. Morfològicament, les principals diferències del material de Masia de l'Hereuet amb *A. lapparenti* són el cíngol labial més desenvolupat a les M^{1-2} i l'absència de paracònid a l'M_{1-2} de l'*Arcius* sp. de Masia de l'Hereuet. Respecte a *A. fuscus*, les primeres i segones molars superiors d'aquesta espècie són diferents de les molars superiors de Masia de l'Hereuet en el seu contorn oclusal rectangular i en l'absència d'un parastil diferenciat, i les primeres i segones molars inferiors *d'A. fuscus* es poden distingir de l'exemplar de Masia de l'Hereuet per la presència de cingúlids i, en alguns casos, d'un paracònid ben diferenciat.

Tot i que el material recuperat ha permès assignar-lo al gènere *Arcius*, degut a l'escassetat de material, s'ha cregut preferible no fer una atribució a nivell d'espècie. Estudis futurs, recolzats amb troballes de nou material en aquest jaciment permetran clarificar la determinació específica d'aquest plesiadapiforme, que representa la primera cita d'aquest grup a Espanya.

L'estudi de les restes recuperades al jaciment de Sant Jaume de Frontanyà (nivells 3C i 3D) ha permès la definició de dues noves espècies. D'una banda, l'adapoïdeu *Anchomomys frontanyensis* (Família Notharctidae, Subfamília Cercamoniinae, Tribu Anchomomyini) i de l'altra l'omomioïdeu *Pseudoloris pyrenaicus* (Família Omomyidae, Subfamília Microchoerinae).

De l'*A. frontanyensis* se n'han recuperat, entre els dos nivells, més de 200 peces dentàries, des de les canines a les terceres molars, tant superiors com inferiors. Per tant, aquesta espècie ha estat definida tenint gairebé tota la dentició completa, mancant només la dentició anterior (incisives) tant superiors com inferiors. La resta d'espècies conegudes d'*Anchomomys* havien estat descrites només en base a escasses restes, i per tant la troballa d'aquesta espècie als Pirineus representa la col·lecció més important d'aquest gènere europeu.

Anchomomys frontanyensis es diferencia de la resta d'espècies d'aquest gènere pel seu petit hipocon i els seus paracònul i anterocíngol reduïts a les molars superiors, pel fet de tenir l'M_3 més petit que l'M_2, un metacònid molt alt i punxegut a les molars inferiors, i cúspules accessòries al talònid de molts espècimens d'M_3.

L'erecció d'aquesta nova espècie, diferent de totes les atribuïdes a *Anchomomys* conegudes fins ara ha permès la identificació d'un nou llinatge d'aquest gènere a la Península Ibèrica diferent del de la resta d'Europa. L'evolució del gènere *Anchomomys* a Europa es creia que corresponia a un únic llinatge que comprenia les espècies des d'*A. crocheti* a *A. quercyi*, amb una primera fase en la que es redueïen l'hipocon i la mida de les molars entre *A. crocheti* i *A. gaillardi,* i una segona fase, entre *A. gaillardi* i *A. quercyi*, definida per un lleuger increment en la mida de les molars i una tendència cap a cúspides més bunodontes (Godinot, 1988). En qualsevol cas, el fet que els nivells 3C i 3D de Sant Jaume de Frontanyà als Pirineus Orientals, on s'ha trobat l'espècie *A. frontanyensis,* tinguin una edat similar al jaciment francès de Lissieu (MP14), on es va recuperar l'espècie tipus *A. gaillardi*, implica l'existència d'un llinatge independent a la Península Ibèrica i un escenari filogenètic més complex del que es suposava prèviament (Godinot, 1988).

D'altra banda, l'omòmid *Pseudoloris pyrenaicus* recuperat també dels mateixos nivells del jaciment de Sant Jaume de Frontanyà representa la mostra més completa d'aquest gènere trobada a la Península Ibèrica, amb més de 90 espècimens, incloent peces dentàries aïllades i fragments de mandíbula amb diverses dents. Aquesta nova espècie, de mida intermitja, es diferencia de la resta d'espècies d'aquest gènere per unes molars inferiors sense un paracònid diferenciat però amb una paracrístida gruixuda, un hipoconúlid gran i arrodonit a les M_3, un cingúlid bucal ben desenvolupat a les molars inferiors, unes P^3 amb un protocon extremadament reduït, i un hipocon i un paracònul també reduïts a les M^1 i les M^2, i absents a les M^3.

Fins l'estudi exhaustiu de les restes dentàries de *P. pyrenaicus,* els canvis morfològics i biomètrics en poblacions successives del gènere *Pseudoloris* eren molt difícils d'observar degut al seu registre discontinu i a l'escassetat del material recuperat. La troballa de *P. pyrenaicus* resulta particularment interessant degut a l'abundància del material, amb pràcticament tots els elements dentaris representats, i degut també a la seva posició intermitja entre les espècies més antigues del gènere (*P. saalae* i *P. isabenae*) i l'espècie més ben coneguda, *P. parvulus*.

Tot això ha permès reconèixer diferents canvis direccionals en l'evolució inicial d'aquest gènere, com ara que a les molars inferiors el paracònid esdevé menys desenvolupat amb el temps, canviant des de ser un tubercle diferenciat a les espècies *P. saalae* i *P. isabenae* fins a ser una crístida afilada a l'espècie *P. parvulus*. *Pseudoloris pyrenaicus* representa un pas intermig entre aquestes dues formes. D'altra banda, tot i que la dentició superior de *P. saalae* i *P. isabenae* és encara desconeguda, quan es comparen les molars superiors de *P. pyrenaicus* i *P. parvulus*, es pot observar també un increment en la mida de l'hipocon, tret que continua en les espècies més modernes del gènere, juntament amb l'engrandiment del metacònul i el paracònul.

Tot i que les tendències que s'observen en les espècies més antigues del gènere són difícils d'avaluar en les espècies més modernes (*P. crusafonti*, *P. godinoti*, *Pseudoloris* sp. de Weissenburg 8), les relacions filogenètiques de les quals són encara confoses, els canvis observats des de les espècies més antigues fins a *P. pyrenaicus*, i finalment *P. parvulus*, sugereixen que aquests tàxons formen part d'un llinatge constituït per les espècies *P. saalae*, *P. isabenae*, *P. pyrenaicus*, i *P. parvulus*, amb modificacions morfològiques graduals. Per tant, d'acord amb les dades disponibles, almenys dos llinatges diferents existien a finals de l'Eocè Mitjà a Europa, respresentats per *P. parvulus*, de mida petita, i *P. crusafonti*, de mida gran. Més material seria necessari per determinar clarament les relacions i les tendències evolutives de les espècies més modernes del gènere.

L'anàlisi dels primats fòssils recuperats al jaciment de Mazaterón (Eocè Mitjà) ha portat a la definicó del nou gènere i espècie *Mazateronodon endemicus* (Subfamília Cercamoniinae, Tribu Anchomomyini), i la nova espècie *Pseudoloris cuestai* (Família Omomyidae, Subfamília Microchoerinae). El descobriment d'aquests dos tàxons, clarament diferents dels representants dels seus grups trobats a les conques pirinenques i la resta d'Europa, reforça el caràcter endèmic de les faunes de la Bioprovíncia Occidental Ibèrica (Badiola i Cuesta, 2007, 2008; Badiola et al., 2009).

El nou gènere i espècie *Mazateronodon endemicus* pertany a la mateixa tribu d'adapoïdeus que el gènere *Anchomomys*, trobat al jaciment de Sant Jaume de Frontanyà, que inclou també els gèneres *Buxella* i *Periconodon* i el nou gènere *Nievesia* recuperat del jaciment de Sossís. El material de *Mazateronodon* descrit representa la col·lecció més rica de primats de la Bioprovíncia Occidental Ibèrica recuperada fins ara, i presenta trets característics que el diferencien dels altres membres de la seva tribu, com ara l'absència de P_1, la P_2 uniradiculada, les premolars inferiors P_3 i P_4

extremadament comprimides bucolingualment, sent la P_3 més gran que la P_4, i unes premolars molt imbricades amb corones que es solapen i cíngols tant bucals com linguals. A banda d’això, presenta un trigònid completament tancat a les molars inferiors, amb una premetacrístida que s’uneix amb la paracrístida.

La nova espècie d’omomioïdeu *Pseudoloris cuestai*, recuperada del mateix jaciment, s’ha descrit en base a més de 20 espècimens amb gairebé totes les dents representades. *Pseudoloris cuestai* s’ha trobat en una edat intermitja entre *P. pyrenaicus* i *P. parvulus*, i presenta també característiques dentàries entre aquestes dues espècies, com ara que el cingúlid bucal de les molars inferiors és menys desenvolupat que a *P. pyrenaicus*, però més que a *P. parvulus*; que l’hipoconúlid de la tercera molar inferior és més estret que a *P. pyrenaicus*, però més ample que a *P. parvulus*, i que l’hipocon de les $M^{1\text{-}2}$ és més gran que a *P. pyrenaicus* i més petit que a *P. parvulus*. En canvi, la paracrístida de les molars inferiors és similar a la de *P. pyrenaicus*, però més gruixuda i alta que a *P. parvulus*.

Tot i així, les diferències més importants entre *P. cuestai* i les espècies *P. parvulus* i *P. pyrenaicus* es troben a la dentició anterior, ja que les incisives inferiors de *P. cuestai* són molt més grans i robustes que les de *P. parvulus* i *P. pyrenaicus*. Contràriament, les canines i les terceres premolars inferiors de *P. cuestai* són més petites que les de *P. pyrenaicus*, i només una mica més grans que les de *P. parvulus* de Sossís. Les incisives superiors també són més grans que les de *P. parvulus* de Perrière, i més llargues que les de *P. pyrenaicus*, tot i que s’hi assemblen pel que fa a l’amplada i l’alçada.

La forma i la mida de les arrels de les incisives inferiors de *P. cuestai* és especialment interessant, degut a que són gruixudes, engrandides lateralment i comprimides anteroposteriorment. Això implica que la mandíbula també hauria d’haver estat més ampla que en les altres espècies per les que es coneixen les incisives inferiors (*P. parvulus* i *P. pyrenaicus*, les dues espècies més properes geogràficament i temporal). D’altra banda, les arrels de les canines inferiors i de les P_3 són més curtes a *P. cuestai* que a *P. pyrenaicus* i *P. parvulus*, cosa que podria estar relacionada amb l’existència d’unes arrels més grans a les incisives inferiors.

Les característiques especials que presenten el gènere *Mazateronodon* i l’espècie *P. cuestai* i que fan diferents aquests primats dels representants dels seus grups a les conques pirinenques i a la resta d’Europa, podrien tenir implicacions paleobiogeogràfiques importants que podrien ser explicades per l'aïllament geogràfic que van patir algunes conques ibèriques fins el Lutecià superior (Meulenkamp et al., 2000), tot i alguns intercanvis faunístics intermitents. Casanovas-Cladellas i Santafé-Llopis (1989, 1991) ja van sugerir l'existència d'una regió occidental de la Península que presentava un gran endemisme en les seves faunes de l'Eocè, i van proposar que aquesta zona podria haver quedat aïllada durant la transgressió marina que va tenir lloc durant part de l'Eocè i que va connectar els mars Cantàbric i Mediterrani. La Bioprovíncia Occidental Ibèrica, definida per Cuesta Ruiz-Colmenares (1991), inclou les conques del Duero, d'Oviedo i de Miranda-Trebiño, que es caracteritzen per unes faunes de mamífers diferents a les trobades als Pirineus i a Europa, especialment pel que fa a artiodàctils, perissodàctils i rosegadors (Peláez-Campomanes et al., 1989; Cuesta Ruiz-Colmenares, 1991, 1993; Peláez-Campomanes, 1992, 1993; Cuesta Ruiz-Colmenares et al., 2006; Badiola et al., 2009). L'existència de condicions ecològiques especials, amb ambients més oberts i un clima més àrid que el de la resta d'Europa almenys fins l'Eocè Mitjà podria haver contribuït a diferenciar les faunes de mamífers d'aquesta bioprovíncia.

L'anàlisi paleoecològic del conjunt de mamífers fòssils de l'Eocè Mitjà i Superior de Mazaterón (Sector oriental de la Conca del Duero o Conca d'Almazán) i Zambrana (Conca de Miranda-Trebiño) sugereix que el canvi d'un hàbitat de bosc complex a un ambient més obert observat durant l'Eocè Superior en diferents regions europees podria haver començat abans a la Bioprovíncia Occidental Ibèrica, influenciant la seva composició faunística (Badiola, 2004; Badiola et al., 2009). Per tant, la peculiar morfologia de la dentició anterior de *P. cuestai* podria sugerir adaptacions tròfiques diferents, tal vegada relacionades amb canvis ambientals. Els únics estudis que s'han fet sobre la dieta de *Pseudoloris* s'han realitzat analitzant molars de *P. parvulus*, i han determinat que aquest taxó era principalment faunívor (Strait, 2001). Tot i així, com que només s'han tingut en compte les molars d'aquesta espècie i no la dentició anterior, que és la que presenta trets característics més peculiars en *P. cuestai*, no podem saber la relació de la morfologia de les seves incisives i canines amb un tipus concret de nutrició.

Badiola (2004) i Badiola et al. (2009) van concretar que alguns trets dentaris observats en perissodàctils i rosegadors de la Bioprovíncia Occidental Ibèrica podrien ser interpretats com adaptacions per mastegar plantes dures, associades a les condicions més àrides d'aquesta regió. Així mateix, la baixa diversitat de rosegadors al jaciment de Mazaterón i a altres localitats d'aquesta bioprovíncia (Miñana, Zambrana) també sugereix l'existència d'àrees boscoses menys denses que a la resta del continent (Peláez-Campomanes, 1993, 1996; Badiola, 2004). Per tant, podria ser que la dieta de *P. cuestai* hagués estat diferent que la de les altres espècies d'aquest gènere, i que fós per tant una adaptació als insectes d'ambients més àrids que haurien estat les seves preses. Tot i així, es necessita recuperar més material per interpretar més concretament els requisits nutricionals d'aquesta espècie.

En resum, tot i que el registre de primats a la Bioprovíncia Occidental Ibèrica és limitat, l'estudi detallat de dues de les tres formes presents al jaciment de Mazaterón revela que corresponen a nous tàxons, l'adapoïdeu *Mazateronodon endemicus* i l'omomioïdeu *P. cuestai*, que presenten diferències amb els membres dels seus grups presents a les conques pirinenques i la resta d'Europa. Per tant, aquestes troballes reforcen la idea de que les faunes de mamífers d'aquesta bioprovíncia presentaven un elevat grau d'endemisme.

Pel que fa al jaciment de Sossís, un nou gènere i espècie ha estat també erigit, l'adapoïdeu *Nievesia sossissensis*, l'únic Anchomomyini trobat a l'Eocè Superior d'Europa, juntament amb l'espècie *Anchomomys quercyi*. La resta d'anchomomyins no es troben després de l'Eocè Mitjà.

Aquest nou gènere presenta característiques que el diferencien d'*Anchomomys, Periconodon, Buxella* i *Mazateronodon,* com ara la seva P^4 molt comprimida bucolingualment, les seves molars superiors, amb un postcíngol recte, un mesostil minúscul, i l'extrema reducció del metacon a l'M^3, així com unes premolars inferiors sense paracònid i amb cingúlids bucal i lingual discontinus i la presència d'hipocònid a les P_4, amb un engruiximent de l'esmalt a la zona del metacònid. Les seves molars inferiors no tenen paracònid i presenten una premetacrístida que uneix la paracrístida i el metacònid, tancant completament la vall del trigònid, i les M_3 tenen un lòbul de l'hipoconúlid centrat i allargat distalment, amb el trigònid més ample que el talònid. Aquestes característiques, sobretot de les molars inferiors, el fan més semblant al *Mazateronodon* que a cap altre membre de la tribu Anchomomyini.

De cara a determinar les relacions filogenètiques entre els diferents membres d'aquesta tribu, a la que pertanyen tots els adapoïdeus estudiats en detall en aquesta tesi, es va decidir fer un anàlisi filogenètic quan es va definir l'espècie *Anchomomys frontanyensis* de Sant Jaume de Frontanyà, un cop ja erigit el gènere *Mazateronodon*, que va ser el primer primat estudiat. Més endavant, al estudiar les restes de Sossís i comprovar que corresponien a un nou gènere d'Anchomomyini, es va tornar a fer el mateix anàlisi, incorporant la informació de *Nievesia sossissensis* a la matriu de dades. Ambdós anàlisis es van dur a terme fent servir la matriu de Seiffert et al. (2010), tenint en compte dues hipòtesis filogenètiques diferents, amb el programa PAUP* 4.0b10 (Swofford, 1998).

Per afegir informació sobre la tribu Anchomomyini a l'anàlisi, es van introduir a la matriu original les codificacions de les espècies *Anchomomys frontanyensis*, *Mazateronodon endemicus*, *Periconodon huerzeleri* i *Buxella prisca* per al primer anàlisi que es va fer (veure capítol 6), a part de recodificar l'espècie *Anchomomys gaillardi*, present a la matriu original, degut a que es van observar errors en la codificació d'alguns trets. Per al segon anàlisi es va afegir també la codificació del nou tàxon *Nievesia sossissensis* (veure capítol 10), a més a més dels tàxons de djebelemurins "*Anchomomys" milleri* i *Djebelemur martinezii* trobats en jaciments africans i considerats estretament relacionats amb els estrepsirins corona (Seiffert et al., 2003, 2005a; Godinot, 2006).

En el primer anàlisi, seguint la hipòtesi 1, que consistia en no permetre la readquisició de premolars prèviament perdudes, els anchomomyins apareixen més estretament relacionats amb els lèmurs i loris actuals que amb altres adapoïdeus (veure figura 4A del capítol 6). Quan es va fer el mateix anàlisi seguint la hipòtesi 2, és a dir, permetent la readcquisió de premolars perdudes prèviament, els anchomomyins apareixien com el clade germà dels tàxons asiàtics *Asiadapis* i *Marcgodinotius*, pertanyents a la subfamília d'adapoïdeus Asiadapinae (veure figura 4B del capítol 6).

D'altra banda, un cop es va fer el segon anàlisi amb la inclusió a la matriu de la codificació de *Nievesia*, tots els anchomomyins apareixien com el grup germà de tota la resta d'adapoïdeus, excepte el tàxon *Donrussellia*, seguint qualsevol de les dues hipòtesis presentades (veure figures 6A i 6B del capítol 10), i sempre més estretament relacionats amb els asiadapins (*Asiadapis* i *Marcgodinotius*) i els sivaladàpids (*Hoanghonius* i *Rencunius*) que no pas amb els Lemuroidea i Lorisoidea actuals. Tenint en compte que aquest segon anàlisi inclou informació sobre més tàxons, considerem els seus resultats més provables.

Les relacions filogenètiques entre els membres de la tribu Anchomomyini en aquest segon anàlisi es mantenen igual tret de la relació entre *Nievesia* i *Mazateronodon*, que apareixen com a tàxons germans si seguim la hipòtesi 1, i que en canvi apareixen successivament a l'anàlisi, si seguim la hipòtesi 2, més propers a *Anchomomys gaillardi* i *Anchomomys frontanyensis* que als altres gèneres d'Anchomomyini (*Periconodon* i *Buxella*).

Tot i així, el clade format per asiadapins, anchomomyins i sivaladàpids, que en el nostre últim anàlisi queda exclòs del grup que comprèn la resta d'adapoïdeus, es veu suportat per alguns caràcters considerats apomorfies. D'aquests, només la meitat es consideren caràcters no ambigus, i de la resta, la majoria dels caràcters es consideren primitius pels adapoïdeus, com ara un metacònid reduït o absent a les P_4, la manca de metastílids a les molars inferiors, i la forma subtriangular de les molars superiors (Szalay i Delson, 1979). A més a més, l'altra meitat d'aquests caràcters es deuen a característiques postcranials que no s'han codificat pels anchomomyins inclosos a l'anàlisi. L'únic caràcter derivat que presenten és la reducció del paracònid a les molars inferiors, cosa que podria representar una convergència.

Tot i això, els anchomomyins aparexien estretament relacionats en els nostres anàlisis, i el gènere *Nievesia* sembla estar més proper filogenèticament a *Mazateronodon* almenys en un dels nostres anàlisis, cosa que ja s'observa en vàries similituds dentàries entre els dos tàxons.

En resum, el registre de primats de l'Eocè a la Península Ibèrica presenta una gran diversitat, i el seu coneixement es veu incrementat degut a l'estudi de nou material de localitats ja conegudes. Durant l'elaboració d'aquesta tesi doctoral s'han definit dos nous gèneres i espècies d'adapoïdeus (*Mazateronodon endemicus* i *Nievesia sossissensis*), tres noves espècies (l'adapoïdeu *Anchomomys frontanyensis* i els omomioïdeus *Pseudoloris pyrenaicus* i *Pseudoloris cuestai*), i s'ha descrit el material de plesiadapiforme atribuït al gènere *Arcius* que representa la primera cita d'aquest grup a Espanya.

Per tant, sembla altament probable que la diversitat coneguda de primats de l'Eocè a la Península Ibèrica es vegi incrementada en els propers anys, gràcies a l'estudi de noves restes i al mostreig de nous jaciments.

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CONCLUSIONS FINALS / FINAL CONCLUSIONS

CONCLUSIONS FINALS:

1. El coneixement del registre fòssil de primats de la Península Ibèrica queda actualitzat mitjançant una revisió bibliogràfica exhaustiva de tot el material recuperat de cada jaciment i, principalment, amb la descripció de material nou de localitats de l'Eocè ja conegudes que forma part d'aquesta tesi doctoral, incloent l'erecció de nous gèneres i espècies.

2. El material de plesiadapiforme del jaciment de Masia de l'Hereuet (Eocè Inferior, Lleida) s'assigna al gènere *Arcius*, l'únic gènere de paromòmyid descrit fins ara a Europa, i representa la primera cita d'un plesiadapiforme a Espanya. El material d'*Arcius* sp. presenta diferències amb la resta d'espècies del gènere, però no s'atribueix a cap espècie, ni permet la definició d'una de nova, degut a l'escassetat de material i a la manca d'elements diagnòstics. Nous mostrejos en aquest jaciment podrien proporcionar més restes que permetessin l'adscripció a una espècie concreta i ajudessin a desxifrar les distribucions geogràfica i temporal d'aquest grup de primats, poc comuns al registre fòssil europeu.

3. Es presenta la nova espècie d'adapoïdeu *Anchomomys frontanyensis* del jaciment de Sant Jaume de Frontanyà (Eocè Mitjà, Barcelona), que representa la col·lecció més gran d'aquest gènere, del que per primera vegada se'n donen a conèixer peces dentàries desconegudes fins ara. Tot i que presenta diferències amb la resta d'espècies d'*Anchomomys*, és més similar en morfologia a *Anchomomys pygmaeus* del jaciment d'Egerkingen γ (MP13), encara que se'n diferencia per tenir un hipocon i un paracònul més reduïts, un hipocon menys projectat cap a la part lingual, i unes molars superiors amb un anterocíngol menys desenvolupat que s'extén més cap a la part lingual. Aquesta nova espècie, existent a la Península simultàniament a *A. gaillardi* a França, revela l'existència d'un nou llinatge d'aquest gènere.

4. Procedent del mateix jaciment de Sant Jaume de Frontanyà (i també dels mateixos nivells 3C i 3D), s'erigeix la nova espècie d'omomioïdeu *Pseudoloris pyrenaicus*, que representa la mostra més completa del gènere a la Península Ibèrica, i que permet la descripció de gairebé totes les peces dentàries, incloent les incisives superiors i inferiors, no recuperades per a la majoria d'espècies atribuïdes al mateix gènere. Aquesta nova espècie representa una forma intermitja entre *P.*

isabenae i *P. parvulus*. El nou tàxon es pot distingir de la resta d'espècies del gènere per la seva mida mitjana i per altres característiques morfològiques com ara l'absència d'un paracònid diferenciat a les molars inferiors, el gran hipoconúlid a l'M_3, els petits hipocon i paracònul a les M^1 i M^2, i la manca d'aquestes dues cúspides a l'M^3. La progressiva reducció del paracònid a les molars inferiors i l'increment de mida de l'hipocon, el metacònul i el paracònul a les molars superiors sugereixen que les espècies *P. saalae*-*P. isabenae*-*P. pyrenaicus*-*P. parvulus* constitueixen un llinatge que va evolucionar durant l'Eocè Mitjà-Superior a Europa.

5. S'erigeix un nou gènere i espècie d'adapoïdeu del jaciment de Mazaterón (Eocè Mitjà, Sòria), pertanyent a la tribu Anchomomyini. Se'n descriu, per primera vegada en un representant d'aquesta tribu, la dentició anterior (incisives i canines superiors i inferiors). *Mazateronodon endemicus* es diferencia morfològicament i biomètrica de la resta d'anchomomyins, i es caracteritza, entre altres trets, per unes P_3 i P_4 molt comprimides bucolingualment, amb una P_3 més gran que la P_4. El material descrit de *Mazateronodon* representa la mostra més rica d'un primat de l'Eocè trobada a la Bioprovíncia Occidental Ibèrica. Les característiques que fan únic el nou gènere podrien ser causades per l'aïllament d'aquesta bioprovíncia de les conques pirinenques i de la resta d'Europa durant l'Eocè com a conseqüència de la transgressió marina que connectà els mars Cantàbric i Meditarrani, i que va fer que les faunes d'aquesta regió presentin un elevat grau d'endemisme, ja observat anteriorment en artiodàctils, perissodàctils i rosegadors.

6. També del jaciment de Mazaterón es descriu la nova espècie *Pseudoloris cuestai*. Tot i que presenta similituds amb les espècies més properes en edat i situació geogràfica (*P. pyrenaicus* i *P. parvulus*), també se'n diferencia clarament sobretot en la morfologia de la I_1, amb una corona engrandida bucolingualment i una arrel molt gruixuda, juntament amb una arrel curta a les canines inferiors i les P_3. Aquestes característiques podrien estar relacionades amb hàbits alimentaris diferents degut a les condicions ecològiques especials de la Bioprovíncia Occidental Ibèrica. Els trets que diferencien *P. cuestai* dels representants del seu grup a les conques pirinenques i a la resta d'Europa reforcen el caràcter endèmic de les faunes d'aquesta bioprovíncia observades també en el primat adapoïdeu *Mazateronodon*.

7. Es defineix un altre gènere nou d'adapoïdeu, *Nievesia*, recuperat del jaciment de Sossís (Eocè Superior, Lleida). *Nievesia sossissensis* es es caracteritza per una P^4 molt comprimida bucolingualment, unes molars superiors sense pericon, un hipocon de mida mitjana, un postcíngol recte, un mesostil minúscul, i un metacon extremadament reduït a l'M^3. Les seves premolars inferiors no tenen paracònid, presenten cingúlids bucals i linguals dicontinus, una P_4 amb hipocònid i un engruiximent a la zona del metacònid que sugereix la presència d'aquesta cúspide. Les seves molars inferiors no tenen paracònid i presenten una premetacrístida que s'uneix amb la paracrístida i el metacònid, tancant completament la vall del trigònid, i una M_3 amb un lòbul de l'hipoconúlid centrat i allargat, i un trigònid més ample que el talònid.

8. Les relacions filogenètiques dels adapoïdeus estudiats, pertanyents tots a la tribu Anchomomyini, s'han pogut clarificar, tot i que encara queden incògnites. Els nous gèneres *Nievesia* i *Mazateronodon* semblen estar més emparentats entre ells que no pas amb la resta d'anchomomyini, almenys en un dels anàlisis filogenètics desenvolupats. Si s'afegeix tota la informació disponible als anàlisis filogenètics incloent tots els nous gèneres i espècies d'Anchomomyini erigits, juntament amb la informació referent als djebelemurins ("*Anchomomys*" *milleri* i *Djebelemur martinezi*), tot sembla indicar que els anchomomyins no estarien més relacionats amb els estrepsirins corona que amb altres adapiformes, i que en canvi hi hauria una relació filogenètica més estreta entre els anchomomyins i els asiadapins i els sivaladàpids que amb altres adapiformes. Tot i això, aquests resultats s'han d'interpretar amb precaució, ja que futurs estudis podrien aportar nova informació que ajudés a desxifrar les relacions filogenètiques entre alguns tàxons.

FINAL CONCLUSIONS:

1. The available knowledge regarding the primate fossil record in the Iberian Peninsula is updated through an exhaustive bibliographic revision of all the material recovered from Iberian sites and, moreover, with the description of new material from several previously-known Eocene localities that is included in this thesis, including the erection of new genera and species.

2. The plesiadapiform material from the Masia de l'Hereuet fossil site (Early Eocene, Lleida) is assigned to the genus *Arcius*, the only paromomyid genus found until now in Europe, and represents the first citation of a plesiadapiform from Spain. This *Arcius* sp. material presents differences with the rest of the species of the genus, but neither it is attributed to any of them, nor it allows the definition of a new one, due to the scarcity of material and the lack of diagnostic elements. Future fieldwork campaigns in this site could lead to new findings that would allow its adscription to a certain species and help to decipher the geographic and temporal distribution of this group of primates, uncommon in the European record.

3. The new adapoid species *Anchomomys frontanyensis* from the fossil site of Sant Jaume de Frontanyà (Middle Eocene, Barcelona) is presented. It represents the largest *Anchomomys* collection ever found, and allows for the first time the description of teeth unknown until now for this genus. Even though *A. frontanyensis* is different from all the other *Anchomomys* species, it is more similar in morphology to *Anchomomys pygmaeus* from the site of Egerkingen γ (MP13). However, *A. frontanyensis* differs from the latter species in the reduced hypocone and paraconule, in having the hypocone less projected lingually, and in the upper molars with a less-developed anterocingulum that extends further lingually. This new species, that existed in the Iberian Peninsula simultaneously with *A. gaillardi* in France, reveals the existence of a new lineage of this genus.

4. From the same fossil site of Sant Jaume de Frontanyà (and also from the same levels 3C and 3D), the new omomyoid species *Pseudoloris pyrenaicus* is erected. It represents the most complete sample of this genus in the Iberian Peninsula, and allows the description of almost all the dental elements, including the upper and lower incisors, not recovered for most of the species attributed to this genus. This

new species represents an intermediate form between *P. isabenae* and *P. parvulus*. The new taxon can be distinguished from the rest of the species of this genus by its intermediate size and by several morphological features such as the absence of a differentiated paraconid in the lower molars, the large hypoconulid in the M_3, the small hypocone and paraconule in the M^1 and M^2, and the absence of these two cuspules in the M^3. The progressive reduction of the paraconid in the lower molars and the increase in size of the hypocone, the metaconule and the paraconule in the upper molars suggest that the species *P. saalae*-*P. isabenae*-*P. pyrenaicus*-*P. parvulus* constitute a lineage that evolved during the Middle-Late Eocene in Europe.

5. A new adapoid genus and species, attributed to the tribe Anchomomyini, from the Mazaterón fossil site (Middle Eocene, Soria) is erected. For the first time in a member of this tribe, the anterior dentition (upper and lower incisors and canines) is described. *Mazateronodon endemicus* differs morphologically and biometrically from the rest of the anchomomyins, and it is characterized, among other traits, by its buccolingually compressed P_3 and P_4, with the P_3 larger than the P_4. The material of the genus *Mazateronodon* represents the richest sample of an Eocene primate from the Western Iberian Bioprovince. The features that make this new genus unique could be explained by the isolation of this bioprovince from the Pyrenean basins and the rest of Europe during the Eocene, as a consequence of the marine transgression that connected the Cantabric and Mediterranean seas at that time, which is supposed to be the cause of the high degree of endemism presented by the faunas of this region, previously observed in artiodactyls, perissodactyls and rodents.

6. Also from Mazaterón, the new species *Pseudoloris cuestai* is described. Even though it presents similarities with the species closer to it in age and geographic situation (*P. pyrenaicus* and *P. parvulus*), it also shows clear differences mainly in the morphology of the I_1, with a buccolingually enlarged crown and a wide root, together with a short root in the lower canines and the P_3. These features could be related to differences in its dietary habits due to the special ecological conditions of the Western Iberian Bioprovince. The features of *P. cuestai* that make it different from the members of the same group present in the Pyrenean basins and

the rest of Europe reinforce the endemic character of the faunas of this bioprovince, also observed in the adapoid primate *Mazateronodon*.

7. Another new adapoid genus and species, *Nievesia sossissensis,* is defined. It was recovered from the fossil site of Sossís (Late Eocene, Lleida), and its main distinguishing features are the buccolingually compressed P^4, the upper molars with a medium-sized hypocone, a straight postcingulum, a minuscule mesostyle, and an extremelly reduced metacone in the M^3. Its lower premolars do not have paraconids, they present discontinuous buccal and lingual cingula, a P_4 with hypoconid and an enlargement of the enamel in the metaconid region, suggesting the presence of this cuspid. Its lower molars do not have paraconids and present a premetacristid that joins the paracristid and the metaconid, completely closing the trigonid basin, an M_3 with a centered and enlarged hypoconulid lobe, and a trigonid wider than the talonid.
8. The phylogenetic relationships of the adapoids studied in this thesis, all of them members of the tribe Anchomomyini, have been clarified, even though there are still some questions unanswered. The new genera *Nievesia* and *Mazateronodon* seem to be more closely related to each other than to the rest of the Anchomomyini, at least in one of the phylogenetic analyses performed. If all the information available is added to the analyses, including all the newly erected genera and species of Anchomomyini, together with the information regarding djebelemurines ("*Anchomomys*" *milleri* and *Djebelemur martinezi*), the results indicate that the anchomomyins would not be more related to crown strepsirhines than to other adapiforms, and that there would be a closer phylogenetic relationship between the anchomomyins and the asiadapines and sivaladapids than with other adapiformes. Nevertheless, these results need to be interpreted with caution, since future studies could provide new information that could help to decipher the phylogenetic relationships among some taxa.

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I

THE PRIMATE FOSSIL RECORD IN THE IBERIAN PENINSULA

The primate fossil record in the Iberian Peninsula
El registro fósil de los primates en la península Ibérica

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Palabras clave: Primates, Paleógeno, Neógeno, Cuaternario, Taxonomía, España.

Abstract

During the last decade, new discoveries in several Iberian basins, together with the description of previously unpublished finds, have significantly increased the recorded paleodiversity of fossil Primates (Mammalia: Euarchonta) in the Iberian Peninsula. Here we provide an updated compendium of the primate fossil record in Iberia during the Cenozoic and further summarize the changes in primate paleodiversity through time, which are then analyzed in the light of changing climatic conditions. Thanks to favorable climatic conditions, the highest diversity of Iberian primates was reached during the Eocene, thus reflecting the radiation of both adapoids and omomyoids; only a single plesiadapiform genus is in contrast recorded in the Iberian Peninsula. Near the Eocene-Oligocene boundary, paleoclimatic changes led to a primate diversity crisis and other faunal changes, although two Iberian omomyoids survived the Grande Coupure. From the Middle Miocene onwards, catarrhine primates are recorded in the Iberian Peninsula. During the Middle and Late Miocene, they are represented by pliopithecoids and hominoids, restricted to NE Iberia. The Miocene hominoids from Iberia are of utmost significance for understanding the Eurasian hominoid radiation and its role in the origins of the great-ape-and-human clade. Following the local extinction of these taxa during the early Late Miocene, due to progressively increased seasonality and concomitant changes in plant communities, cercopithecoids are also recorded in the Iberian Peninsula from the latest Miocene through the Plio-Pleistocene, although they finally became locally extinct, whereas hominoids are again represented by fossil humans during the Pleistocene.

Resumen

Durante la última década, nuevos descubrimientos en varias cuencas ibéricas, junto con la descripción de hallazgos previos inéditos, han incrementado significativamente la paleodiversidad de Primates fósiles (Mammalia: Euarchonta) registrada en la península Ibérica. Proporcionamos aquí un compendio actualizado del registro fósil de los primates en Iberia durante el Cenozoico, y resumimos además los cambios en paleodiversidad de los primates a lo largo del tiempo a la luz de las condiciones climáticas cambiantes. Gracias a condiciones climáticas favorables, la diversidad más alta de primates ibéricos se produjo durante el Eoceno, reflejando así la radiación tanto de los adapoideos como de los omomioideos; en cambio, sólo un único género de plesiadapiformes se registra en la península Ibérica. Hacia el límite Eoceno-Oligoceno, los cambios paleoclimáticos condujeron a una crisis de diversidad de los primates y otros cambios faunísticos, aunque dos omomioideos ibéricos sobrevivieron a la Grande Coupure. Del Mioceno Medio en adelante, los primates catarrinos se registran en la Península Ibérica. Durante el Mioceno Medio y Superior, están representados por pliopitecoideos y hominoideos, restringidos al NE de Iberia. Los hominoideos del Mioceno de Iberia son de gran importancia para comprender la radiación de los hominoideos eurasiáticos y su papel en los orígenes del clado de los grandes antropomorfos y los humanos. A continuación de la extinción local de estos taxones durante el Mioceno Superior inicial, debido al incremento progresivo de la estacionalidad así como a cambios en las comunidades vegetales, los cercopitecoideos también se registran en la Península Ibérica a partir del Mioceno más terminal en

adelante. Los cercopitecoideos se registran en la península Ibérica durante todo el Plio-Pleistoceno, aunque finalmente también se extinguieron localmente, mientras que los hominoideos vuelven a estar representados otra vez por los humanos fósiles durante el Pleistoceno.

Introduction

Primates

Primates (Mammalia: Euarchonta) are a eutherian order of moderate diversity, with about 300 extant species. They were traditionally divided into two major groups: prosimians and simians (or anthropoids) (e.g., Fleagle, 1999). Most authors, however, currently favor a distinction between strepsirrhines and haplorrhines. Unfortunately, many of the features that enable such division are related to soft anatomy, so that the classification of fossil ‘prosimians’ as either strepsirrhines or haplorrhines, albeit favored here, is not always straightforward. Crown primates (euprimates, or primates of modern aspect) constitute a monophyletic group including extant strepsirrhines and haplorrhines, together with the extinct taxa more closely related to either of them (see Fleagle, 1999, and Hartwig, 2002, for the most recent complete accounts on fossil primates). Morphologically, euprimates are characterized by the possession of a petrosal bulla (the auditory bulla is formed by an extension of the petrosal instead of by a separate entotympanic bone), which is a unique synapomorphy among mammals (Rasmussen, 2002). Other derived diagnostic traits of euprimates, uncommon in other mammals, are the following (e.g., Martin, 1990; Rasmussen, 2002): postorbital bar; orbital convergence, yielding stereoscopic binocular vision; grasping hands and feet, usually with opposable hallux and pollex; flat nails instead of claws on most digits; brains larger than expected on the basis of body size (high encephalization); and a slow life-history profile. The primate total group includes crown primates plus the primate stem lineage, the latter being those taxa preceding the haplorrhine-strepsirrhine divergence, but being more closely related to them than to other euarchontans, i.e. scandentians (tree shrews) and dermopterans (flying lemurs). It is generally thought that primates diverged from other mammals sometime during the Late Cretaceous. Undisputed fossil euprimates are not found until the earliest Eocene, ca. 56 Ma (Rasmussen, 2002), and although molecular estimates suggested in the past an ancient divergence data for crown subclades, recent studies suggest that haplorrhines and strepsirrhines diverged close to the Mesozoic/Cenozoic boundary (Steiper and Seiffert, 2012). The origin of euprimates has been related to plesiadapiforms, which show general dental similarities with primates but at the same time lack several euprimate derived features, such as the postorbital bone and the petrosal bulla. The phylogenetic relationships of plesiadapiforms with euprimates remain unresolved, but it seems currently likely that most of them constitute a paraphyletic assemblage of stem primates.

Aims of this study

Most primates are linked to tropical or subtropical forested environments, and currently, modern humans are the only primates naturally inhabiting the Iberian Peninsula. This, however, has not always been the case: during the Paleogene and Neogene, several major primate groups occupied the Iberian Peninsula. In Table 1, we have summarized the systematic scheme employed for primates in this paper down to the superfamily rank, indicating with bold bype those taxa recorded in the Iberian Peninsula. For many years, the study of fossil Iberian primates was led by Miquel Crusafont-Pairó, founder of the Institut Català de Paleontologia Miquel Crusafont (ICP), which currently bears his name. Beginning in the early 1940s, Crusafont and co-workers such as Josep F. de Villalta and Juana M. Golpe-Posse reported new material and described new taxa of "prosimians" and anthropoids alike. It is not surprising, therefore, that Crusafont-Pairó and Golpe-Posse (1974) finally published a synthetic review on the fossil primates from Spain. Since then, some summary syntheses devoted to particular primate groups at the Iberian level have been published (e.g., Moyà Solà et al., 1990; Marigó et al., 2011c), but no detailed and comprehensive synthesis of all Iberian primates has been undertaken since 1974. In the meantime, many new fossil discoveries, together with the restudy of previously available material, have led to a significant increase in the knowledge of their paleodiversity, chronology and paleobiology. Here, we provide an updated synthesis of the fossil primates from the Iberian Peninsula (Spain and Portugal) during the Cenozoic (Paleogene, Neogene and Quaternary), enumerating all the recorded taxa at the species level (when possible), and also providing details on their systematics, chronologic and geographic distribution, paleobiology, and phylogenetic relationships. We further discuss the Iberian primate record in the framework of the evolutionary history of this group as a whole, with particular emphasis on its relationship to paleogeographic and climatic changes through time.

Systematic paleontology

Order Primates Linnaeus, 1758
Semiorder Plesiadapiformes Simons and Tattersall, 1972
Superfamily Paromomyoidea Simpson, 1940
Family Paromomyidae Simpson, 1940
Genus *Arcius* Godinot, 1984
Arcius sp.
(Figure 1A-B)

Iberian localities: Masia de l'Hereuet (Lleida).

Remarks: The genus *Arcius* is mainly known from several Early Eocene (Neustrian, MP7–MP8+9) French sites (Godinot, 1984; Smith et al., 2011), and its Iberian record is comparatively scarce, including only *A. zbyszewskii* from Silveirinha (Portugal), and *Arcius* sp. from Masia de l'Hereuet (Spain). The scarce material (only four isolated molars) from the latter locality enable an attribution to the genus *Arcius*, to which all European paromomyids are currently attributed. This material is intermediate in size between *A. fuscus* and *A. lapparenti*, and shows several morphological differences compared to all the described species of this genus, but the scarcity of the material precludes erecting a new species.

Main references: Marigó et al. (2012a).

Arcius zbyszewskii Estravís, 2000

Geographic distribution: Exclusively known from the type locality.

Chronological range: 56–55.5 Ma (MP7, Neustrian, lowermost Eocene).

Iberian localities: Silveirinha [type locality] (Baixo Mondego).

Remarks: Previously attributed to *Phenacolemur* sp. by Antunes (1981) and *Phenacolemur* cf. *fuscus* by Antunes and Russell (1981), *A. zbyszewskii* is closely related to *Arcius rougieri* from Palette (France). The Portuguese species is however smaller and displays many other morphologic differences. The phylogenetic relationships between them are unclear.

Main references: Antunes et al. (1997); Estravís (2000).

Semiorder Euprimates Hoffstetter, 1977

Suborder Strepsirrhini É. Geoffroy Saint-Hilaire, 1812

Infraorder Adapiformes Hoffstetter, 1977

Superfamily Adapoidea Trouessart, 1879

Family Notharctidae Trouessart, 1879

Notharctidae indet.

Iberian localities: Silveirinha (Baixo Mondego).

Remarks: Besides *Dounrussellia lusitanica*, Estravís (2000) reported from Silveirinha some isolated teeth of another notharctid. Due to the scarce material available, this material has been left unassigned at the genus level, even though it resembles the Early Eocene genera *Cantius* and *Donrussellia*.

Main references: Antunes et al. (1997); Estravís (2000).

Subfamily Cercamoniinae Gingerich, 1975

Genus *Donrussellia* Szalay, 1976

Donrussellia lusitanica Estravís, 2000

Geographic distribution: Exclusively known from the type locality.

Chronological range: 56–55.5 Ma (MP7, Neustrian, lowermost Eocene).

Iberian localities: Silveirinha [type locality] (Baixo Mondego).

Remarks: *Donrussellia* is the most primitive known adapiform genus, and *D. lusitanica* is a very primitive species within this genus. It is much smaller than *D. magna*, somewhat larger than *D. gallica*, and of similar size or slightly larger than *D. provincialis*. The lower molars of *D. lusitanica* differ from those of the other species of the genus in the smaller paraconid and a shorter trigonid when compared to the talonid. The M^1 of *D. lusitanica* differ from those of *D. provincialis* and *D. gallica* in being larger and in having a more subquadrate outline among other features. Moreover, the nannopithex-fold present in the M^1 and M^2 of *D. lusitanica* is not present in those attributed to *D. gallica*, and the absence of a postparaconule crista in the upper molars of *D. lusitanica* makes them different from those of *D. provincialis*.

Main references: Estravís (2000).

Genus *Agerinia* Crusafont Pairó, 1973

Agerinia sp.

Iberian localities: La Coma (=La Morera del Monsant 2) (Tarragona); Casa Ramón (Huesca).

Remarks: This genus has been identified in several Spanish and French localities, ranging from the Neustrian (MP8+9) to the Geiseltalian (MP12). The scarce material from Casa Ramón (MP11 or MP12), which consists only of six isolated teeth, precludes erecting a new species, although it is smaller and displays some morphological differences compared to *A. roselli*. The material from La Coma (MP10), also very scarce, is still under study. Since these two localities are of different age, it is very plausible that two different species are represented.

Main references: Peláez-Campomanes (1995); Antunes et al. (1997); Marigó et al. (2011c).

Agerinia roselli (Crusafont-Pairó, 1967)

Geographic distribution: Spain and France.

Chronological range: 51–48.5 Ma (MP10, Grauvian, Early–Middle Eocene).

Iberian localities: Les Saleres [type locality] and Escarlà (Lleida); Can Picantón, Castigaleu, Les Badies and Güell I (Huesca).

Remarks: First attributed to the Necrolemuridae, it displays a very primitive upper dentition and a derived lower dentition without paraconid and with a very reduced trigonid (Crusafont-Pairó, 1967).

Main references: Crusafont-Pairó (1967, 1973); Szalay (1971); Crusafont-Pairó and Golpe-Posse (1968, 1973b, 1974, 1975); Antunes et al. (1997); Marigó et al. (2011c).

Genus *Cantius* Simons, 1962

Cantius sp.

Iberian localities: La Coma (=La Morera del Montsant 2) (Tarragona); Güell III (Huesca).

Remarks: The genus *Cantius* has a wide geographic distribution, including Europe (Spain and France) and North America. It has been identified in Neustrian (MP8+9) and Grauvian (MP10) sites. The material from the two Iberian localities is very scarce, so that an attribution to the species level is not possible until more material is recovered.

Main references: Antunes et al. (1997); Marigó et al. (2011c).

Tribe Anchomomyini Szalay and Delson, 1979 (sensu Godinot, 1988)

cf. Anchomomyini indet.

Iberian localities: Montblanc, Coll de l'Illa and Ulldemolins I (Tarragona).

Remarks: The attribution of material from Montblanc and Coll de l'Illa to Anchomomyini indet. by Antunes et al. (1997) cannot be confirmed based on the material currently housed at the Institut Català de Paleontologia Miquel Crusafont. Several isolated teeth from Ulldemolins I are also tentatively assigned to the tribe Anchomomyini, until a detailed study enables a more precise determination.

Main references: Antunes et al. (1997); Marigó et al. (2011c).

Anchomomyini nov.

Iberian localities: Sossís (Lleida).

Remarks: This taxon was previously thought to represent a new *Anchomomys* species (Marigó et al., 2011c), but further study of the available material has revealed that it displays several features distinguishing it from other anchomomyin genera (very buccolingually compressed P^4, extremely reduced metacone in the M^3, and the complete premetacristid closing the trigonid basin from the lingual side on the lower molars).

Main references: Marigó et al. (2011b,c).

Genus *Anchomomys* Stehlin, 1916

Anchomomys sp.

Iberian localities: Sant Jaume de Frontanyà 1 (Barcelona); Caenes (Salamanca).

Remarks: The genus *Anchomomys* is well known from several European sites (Switzerland, France, Spain), ranging in age from the Geiseltalian to the Headonian (MP13–17a, Middle–Late Eocene, 44–37 Ma). The material from Caenes, curently under study, consists of two complete and one fragmentary right upper molars, and two left mandible fragments, one showing a complete P_4 and the other presenting an almost complete P_4, a partial M_1 and a complete M_2, and both with the rest of the alveoli from the lower C to the M_3. In addition, a few isolated teeth from Sant Jaume de Frontanyà 1 can be assigned to the genus *Anchomomys*, although the scarcity of material precludes a determination to the species level.

Main references: Moyà-Solà and Köhler (1992); Antunes et al. (1997); Moyà-Solà et al. (2012); Marigó et al. (2011c, 2012b).

Anchomomys frontanyensis Marigó, Minwer-Barakat and Moyà-Solà, 2011a

(Figure 1E-F)

Geographic distribution: Exclusively known from the type locality.

Chronological range: 43–42 Ma (MP14, Robiacian, Middle Eocene).

Iberian localities: Sant Jaume de Frontanyà 3 [type locality] (Barcelona).

Remarks: The material from this locality represents the largest collection of *Anchomomys* material ever described, including all the permanent teeth except for the incisors. *A. frontanyensis* resembles *A. pygmaeus* from Egerkingen (Ef 372) although it has a more reduced hypocone and paraconule, its hypocone is less projected lingually, and its upper molars have a less developed anterocingulum extending further lingually. Despite sharing features with other anchomomyins, *A. frontanyensis* also shares certain characters with extinct asiadapines and extant lemurs and lorises. Moreover, the presence of *A. frontanyensis* in the Iberian Peninsula reveals a different lineage from that present at the same time in the rest of Europe. Phylogenetic analyses suggest that anchomomyins might be related to either asiadapines or crown strepsirhines.

Main references: Moyà-Solà and Köhler (1993b); Antunes et al. (1997); Marigó et al. (2011a, b, c); Minwer-Barakat et al. (2011a); Roig and Moyà-Solà (2011); Moyà-Solà et al. (2012).

Anchomomys cf. *pygmaeus* (Gingerich, 1977)

Geographic distribution: Switzerland and Spain.

Chronological range: 44–42 Ma (MP13–14, Geiseltalian-Robiacian, Middle Eocene).

Iberian localities: Santa Clara (Zamora).

Remarks: The only available material is an M_2 that resembles that of *A.* cf. *pygmaeus* En-1 specimen from Egerkingen, first attributed to *A. stehlini* by Gingerich (1977), but later assigned to *A.* cf. *pygmaeus* by Godinot (1988).

Main references: Gingerich (1977); Godinot (1988); Peláez-Campomanes et al. (1989); Antunes et al. (1997); Marigó et al. (2011c).

Genus *Mazateronodon* Marigó, Minwer-Barakat and Moyà-Solà, 2010

Mazateronodon endemicus Marigó, Minwer-Barakat and Moyà-Solà, 2010

(Figure 1C-D)

Geographic distribution: Exclusively known from the type locality.

Chronological range: 42–37 Ma, MP15–16, Robiacian, Middle Eocene.

Iberian localities: Mazaterón [type locality] (Soria).

Remarks: This taxon allowed the description, for the first time, of almost all the dental elements and the anterior dentition for a member of the Anchomomyini. The material attributed to *Mazateronodon endemicus* is the richest Eocene primate assemblage from the Western Iberian Bioprovince. *Mazateronodon* differs morphologically and biometrically from all the other anchomomyins, and it is characterized by its extremely buccolingually compressed P_3 and P_4, with the P_3 larger than the P_4, its highly imbricated premolars, with overlapping crowns and buccal and lingual cingulids. Some similarities with the material assigned to *Anchomomys* from Caenes (Duero Basin) and *Anchomomys frontanyensis* (Pyrenean Basin) strongly suggest an Iberian origin of this taxon. The unique features of *Mazateronodon* support the idea of endemism in the Eocene faunas of the Duero Basin, and the existente of a Western Iberian Bioprovince, isolated form the rest of Europe during the Eocene due to a marine transgression that connected the Cantabric and the Mediterranean Seas.

Main references: Antunes et al. (1997); Marigó et al. (2009, 2010, 2011b, c).

Family Adapidae Trouessart, 1879

Subfamily Adapinae Trouessart, 1879

Genus *Leptadapis* Gervais, 1876

Leptadapis priscus (Stehlin, 1916)

Geographic distribution: Switzerland and Spain.

Chronological range: 44–42 Ma (MP13–14, Geiseltalian-Robiacian, Middle Eocene).

Iberian localities: Capella (Huesca).

Remarks: The material from Capella was the first adapiform recovered from Spain. It consists of a single mandible fragment with I_2-M_3, which was attributed to *Adapis priscus* by Crusafont-Pairó (1965b). Later on, *Adapis priscus* was transfered to *Leptadapis* by Szalay and Delson (1979).

Main references: Crusafont-Pairó (1958a, 1965b, 1967); Crusafont-Pairó and Golpe-Posse (1974, 1975); Antunes et al. (1997); Marigó et al. (2011c).

Leptadapis capellae (Crusafont-Pairó, 1967)

Geographic distribution: Exclusively known from the type locality.

Chronological range: 43–42 Ma (MP14, Robiacian, Middle Eocene).

Iberian localities: Capella [type locality] (Huesca).

Remarks: This species, known exclusively from the holotype (a single M^3), was defined as *Arisella capellae* by Crusafont-Pairó (1965b), and then transfered to *Leptadapis* by Szalay (1971).

Main references: Crusafont-Pairó (1965b; 1967); Szalay (1971); Crusafont-Pairó and Golpe-Posse (1968, 1974); Antunes et al. (1997); Marigó et al. (2011c).

Leptadapis magnus (Filhol, 1874)

Geographic distribution: France, UK and Spain.

Chronological range: 40.5–34 Ma (MP16–MP18-19, Robiacian-Headonian, Middle–Late Eocene).

Iberian localities: Roc de Santa (Barcelona).

Remarks: Originally described within the genus *Adapis* by Filhol (1874), it was subsequently attributed to *Leptadapis* by Gervais (1876), which after more accurate studies was recently confirmed by Godinot and Couette (2008). The scarce material from Roc de Santa, a right maxilla with P^3-M^3 and a left mandible with a broken P_3 and the P_4-M_2 series, was assigned to *Adapis* cf. *magnus* by Crusafont-Pairó and Golpe-Posse (1974), given its somewhat smaller size compared to the type material. Nevertheless, subsequent studies have confirmed the ascription of the material from Roc de Santa to this species (Casanovas-Cladellas, 1975; Casanovas, 1998; Antunes et al., 1997).

Main references: Crusafont-Pairó and Golpe-Posse (1974, 1975); Agustí (1998); Antunes et al. (1997); Marigó et al. (2011c).

Genus *Adapis* Cuvier, 1821

Adapis cf. *parisiensis* Cuvier, 1821

Geographic distribution: France, UK and Spain.

Chronological range: 40.5–34 Ma (MP16–19, Robiacian–Headonian, Middle–Late Eocene).

Iberian localities: Sossís (Lleida).

Remarks: The published material from Sossís consists of an upper molar (probably an

M^1) and an upper premolar (Crusafont-Pairó and Golpe-Posse, 1974). They were attributed to *Adapis* cf. *parisiensis*, although Antunes et al. (1997) cited them as *Leptadapis* cf. *ruetimeyeri*. Later studies, however, attributed the material again to *A.* cf. *parisiensis* (Casanovas, 1998), so we think that the attribution by Antunes et al. (1997) to *L.* cf. *ruetimeyeri* was merely a mistake. The detailed study of additional material from this locality, recovered from subsequent field campaigns and still unpublished, may increase the number of specimens ascribed to this taxon.

Main references: Crusafont-Pairó (1967); Crusafont-Pairó and Golpe-Posse (1974; 1975); Antunes et al. (1997); Casanovas (1998); Marigó et al. (2011c).

Adapis sp.

Iberian localities: Sant Jaume de Frontanyà 3 (Barcelona).

Remarks: The genus *Adapis* has an exclusively European geographic distribution, including France, Switzerland, UK and Spain. It is known from the Robiacian (MP14, Middle Eocene) to the Headonian (MP19, Late Eocene). The material from Sant Jaume de Frontanyà 3 consists of several isolated teeth, currently under study, that may allow a specific determination.

Main references: Moyà-Solà and Köhler (1993b); Antunes et al. (1997); Marigó et al. (2011c); Miwer-Barakat et al. (2011a).

cf. *Adapis* sp.

Iberian localities: Mazaterón (Soria).

Remarks: A mandibular fragment with the complete molar series from this locality is currently under study. It has been tentatively assigned to *Adapis*, although the material may be too scarce to be determined to the species level.

Main references: Antunes et al. (1997); Marigó et al. (2009, 2010, 2011c); Minwer-Barakat et al. (2012).

Genus *Microadapis* Szalay, 1974

Microadapis sp.

Iberian localities: Caenes (Salamanca).

Remarks: The genus *Microadapis* is known from several Swiss and Spanish Middle Eocene localities ranging in age from the MP13 (Geiseltalian) to the MP16 (Robiacian). The material from Caenes consists only of a single upper molar. Until more material is recovered, it is not possible to reach a species determination.

Main references: Moyà-Solà and Köhler (1992); Antunes et al. (1997); Marigó et al. (2011c).

Suborder Haplorrhini Pocock, 1918

Infraorder Tarsiiformes Gregory, 1915

Superfamily Omomyoidea Trouessart, 1879

Family Omomyidae Trouessart, 1879

Omomyidae indet.

Iberian localities: Pontils 38 (Barcelona).

Remarks: The material consists of two isolated molars of a very small omomyid. The detailed study of these remains, as well as further fieldwork for obtaining more material, may allow the description of a new taxon.

Main references: Antunes et al. (1997); Marigó et al. (2011c).

Subfamily Microchoerinae Lydekker, 1887

Microchoerinae indet.

Iberian localities: Zambrana (Álava).

Remarks: The material from Zambrana consists of two well-preserved right mandibular fragments with relatively complete dental series, including P_3-M_3 and P_4-M_3. The overall dental morphology and the presence of enamel wrinkling are similar to those observed in the genera *Necrolemur* and *Microchoerus*. The detailed study of this material, now under way, will lead to a more precise determination. This discovery, together with that of *Pseudoloris cuestai* from Mazaterón (Minwer-Barakat et al., 2012), constitutes the first record of microchoerines in the Western Iberian Bioprovince.

Main references: Minwer-Barakat et al. (2011b).

Genus *Microchoerus* Wood, 1844

Microchoerus erinaceus Wood, 1844

Geographic distribution: UK, France, Switzerland and Spain.

Chronological range: 40.5–35 Ma (MP16–18, Robiacian–Headonian, Middle–Late Eocene).

Iberian localities: Sossís (Lleida).

Remarks: This large-sized microchoerine from Sossís was first reported by Crusafont-Pairó (1965b), and subsequently Crusafont-Pairó (1967) briefly described a quite complete sample of this species, including isolated teeth, some dental series and several fragments of mandibles and maxillae. This author further figured a lower dental series including P_3-M_3, and an upper dental series with M^1 and M^2. Crusafont-Pairó (1967) and Crusafont-Pairó and Golpe-Posse (1974) referred to this taxon as *Necrolemur erinaceus*, but later works (Antunes et al., 1997; Casanovas, 1998) employed the correct denomination, i.e. *Microchoerus erinaceus*. Subsequent field work led to the recovery of more abundant material, which is still unpublished. A preliminary observation of this material reveals some biometric and morphologic differences relative to the material from the type locality (Hordle Cliff Crocodile Bed, Hampshire, UK). However, until a detailed study of the population from Sossís is carried out, we prefer mantaining the attribution to *M. erinaceus*.

Main references: Crusafont-Pairó (1965b, 1967); Crusafont-Pairó and Golpe-Posse (1974); Antunes et al. (1997); Casanovas (1998); Marigó et al. (2011c).

Microchoerus ornatus Stehlin, 1916

Geographic distribution: Switzerland and Spain.

Chronological range: 35–34 Ma (MP19, Headonian, Late Eocene).

Iberian localities: Sant Cugat de Gavadons (=Collsuspina) (Barcelona).

Remarks: Only known from upper teeth, *Microchoerus ornatus* has been considered doubtfully distinct from *M. edwardsi* (Hooker, 1986; Gunnell and Rose, 2002). In the Iberian Peninsula, the only material assigned to this species is a fragment of maxilla with P^4-M^1 from Sant Cugat de Gavadons, which according to Crusafont-Pairó (1967) and Crusafont-Pairó and Golpe-Posse (1974), shares strong similarities with the material from the type locality of *M. ornatus* (Mormont-Entreroches, Switzerland).

Main references: Crusafont-Pairó (1967); Crusafont-Pairó and Golpe-Posse (1974); Golpe-Posse (1982c); Marigó et al. (2011c).

Microchoerus sp.

Iberian localities: Aguatón (Teruel).

Remarks: The genus *Microchoerus* is well represented in Central and Western Europe (Spain, France, UK, Switzerland and Germany), in localities that range in age from the Robiacian (MP16, Middle Eocene) to the Suevian (MP21, Early Oligocene). In the Iberian Peninsula, besides the above-metioned remains ascribed to *M. erinaceus* and *M. ornatus*, a single M_1 from the site of Aguatón was described by Peláez-Campomanes (2000). This tooth, similar in size to those of *M. erinaceus*, shows morphological and/or metrical differences with all the previously described species of *Microchoerus* (except for *M. ornatus*, only known from upper teeth). However, due to the scarcity of material, the author preferred not to describe a new species until more material is available.

Main references: Peláez-Campomanes (2000).

Genus *Pseudoloris* Stehlin, 1916

Pseudoloris isabenae (Crusafont-Pairó, 1967)

Geographic distribution: Spain and France.

Chronological range: 44–43 Ma (MP13–14, Geiseltalian-Robiacian, Middle Eocene).

Iberian localities: Capella [type locality] (Huesca).

Remarks: This species was originally ascribed to the genus *Pivetonia* by Crusafont-Pairó (1967); however, most authors have considered *Pivetonia* to be a junior subjective synonym of *Pseudoloris* (Szalay, 1971; Godinot, 1983; Gunnell and Rose, 2002; Minwer-Barakat et al., 2010, 2012). The only available material from Capella is a mandible fragment with P_3-M_2. It differs from other species of *Pseudoloris* found in the Iberian Peninsula in the smaller size and the presence of a well-individualized tubercular paraconid in the lower molars.

Main references: Crusafont-Pairó (1965b, 1967); Szalay (1971); Crusafont-Pairó and Golpe-Posse (1968, 1974); Antunes et al. (1997); Minwer-Barakat et al. (2010, 2012); Marigó et al. (2011c).

Pseudoloris pyrenaicus Minwer-Barakat, Marigó and Moyà-Solà, 2010

(Figure 1I-J)

Geographic distribution: Exclusively known from the type locality.

Chronological range: 43–42 Ma (MP14, Robiacian, Middle Eocene).

Iberian localities: Sant Jaume de Frontanyà 3 [type locality] (Barcelona).

Remarks: The material of this species represents the most complete sample of the genus *Pseudoloris* published from the Iberian Peninsula, having enabled the description of almost all the dental elements, including upper and lower incisors, undescribed for most species of this genus. *P. pyrenaicus* can be distinguished from the other *Pseudoloris* species by its medium size and by several morphological features, such as the absence of a distinct paraconid and the thickened paracristid in the lower molars, the large hypoconulid in the M_3, the small hypocone and paraconule in the M^1 and M^2, and the absence of these two cusps in the M^3. This species, an intermediate form between *P. isabenae* and *P. parvulus*, forms part of an anagenetic lineage that evolved in Europe during the Middle–Late Eocene.

Main references: Moyà-Solà and Köhler (1993b); Antunes et al. (1997); Minwer-Barakat et al. (2010, 2011a); Marigó et al. (2011b, c).

Pseudoloris cuestai Minwer-Barakat, Marigó and Moyà-Solà, 2012

(Figure 1G-H)

Geographic distribution: Exclusively known from the type locality.

Chronological range: 42–37 Ma (MP15–16, Robiacian, Middle Eocene).

Iberian localities: Mazaterón [type locality] (Soria).

Remarks: *P. cuestai* represents, together with the undetermined Microchoerinae from Zambrana, the only record of this subfamily in the Western Iberian Bioprovince. It can be distinguished from the other *Pseudoloris* species by its medium size, high and thick paracristid and absence of a distinct paraconid in the lower molars, large hypoconulid in the M_3, well-developed protocone in the P^3 and P^4, small hypocone in the upper molars, and especially for its particular lower incisors, with a large, buccolingually enlarged crown and a thick root. It shows several similarities with *P. pyrenaicus* and *P. parvulus*, the closest species in age and geographic situation. Nevertheless, there are also clear differences with those species, especially in the anterior dentition. The peculiar morphology of the I_1, together with the short roots of the lower canine and P_3, suggests an anterior dentition that differs from that of *P. pyrenaicus* and *P. parvulus*, perhaps in relation to dietary differences.

Main references: Antunes et al. (1997); Marigó et al. (2009, 2011b, c); Minwer-Barakat et al. (2010, 2012).

Pseudoloris parvulus (Filhol, 1890)

Geographic distribution: France and Spain.

Chronological range: 40.5–36.5 Ma (MP16–17, Robiacian-Headonian, Middle-Late Eocene).

Iberian localities: Sossís (Lleida).

Remarks: The material described by Crusafont-Pairó (1965b, 1967) and Crusafont-Pairó and Golpe-Posse (1974) consists of a single mandibular fragment with P_4-M_3. However, there is additional, still unpublished material of *P. parvulus* from Sossís housed at the Institut Català de Paleontologia Miquel Crusafont. Among other features, *P. parvulus* from Sossís shows a low and sharp paracristid in the lower molars, a compressed hypoconulid in the M_3, and the hypocone of the upper molars more developed than *P. pyrenaicus* and *P. cuestai*. This species has been identified in several Robiacian and Headonian French sites, but the only mention in the Iberian Peninsula corresponds to Sossís.

Main references: Crusafont-Pairó (1965b, 1967); Crusafont-Pairó and Golpe-Posse (1974); Antunes et al. (1997); Minwer-Barakat et al. (2010); Marigó et al. (2011c).

Pseudoloris reguanti Crusafont-Pairó, 1967 (nomen dubium)

Geographic distribution: Exclusively known from the type locality.

Chronological range: 35–34 Ma (MP19, Headonian, Late Eocene).

Iberian localities: Sant Cugat de Gavadons (=Collsuspina) [type locality] (Barcelona).

Remarks: This species was described by Crusafont-Pairó (1967) on the basis of a single isolated lower molar from Sant Cugat de Gavadons, larger than those of *P. parvulus,* and with a paracristid instead of a tubercular paraconid. Schmidt-Kittler (1977) considered this species as a *nomen nudum* because of the lack of illustrations of the holotype; however, according to the International Code of Zoological Nomenclature, this reason does not invalidate the species name from a nomenclatural viewpoint. Unfortunately, as pointed out by Köhler and Moyà-Solà (1999), this specimen was lost in the 1970s. Therefore, until more material is available, the taxonomic validity of this nominal taxon cannot be further evaluated, so we consider it a *nomen dubium*.

Main references: Crusafont-Pairó (1967); Crusafont-Pairó and Golpe-Posse (1974); Schmidt-Kittler (1977); Golpe-Posse (1982c); Köhler and Moyà-Solà (1999); Minwer-Barakat et al. (2010, 2012); Marigó et al. (2011c).

Pseudoloris godinoti Köhler and Moyà-Solà, 1999

Geographic distribution: Exclusively known from Spain.

Chronological range: 34–31 Ma (MP21–22, Suevian, Early Oligocene).

Iberian localities: Fonollosa 13 [type locality] and Santpedor 2 (Barcelona).

Remarks: *P. godinoti* is known only by six complete teeth (including an upper series of P^2-M^1 designated as the holotype) and two fragments, recovered from the Oligocene localities of Santpedor-2 and Fonollosa-13. The M^1 has a reduced trigon basin, a large and well-individualized hypocone and a prominent metastyle, and the M_1 shows a distinct paraconid. This is the only record of the genus *Pseudoloris* after the Eocene-Oligocene boundary.

Main references: Köhler and Moyà-Solà (1999); Minwer-Barakat et al. (2010, 2012); Marigó et al. (2011c).

Pseudoloris sp.

Iberian localities: Casa Ramón (Huesca).

Remarks: The genus *Pseudoloris* is known from several sites in France, UK, Germany and Spain, ranging in age from the Geiseltalian (Middle Eocene, MP11–12) to the Suevian (Early Oligocene, MP22). The Geiseltalian Spanish site of Casa Ramón (Peláez-Campomanes, 1995) has yielded two fragments of M^1 and M^3 and a complete M^2 ascribed to *Pseudoloris* sp., being similar in size but morphologically different compared to those of *P. parvulus*. The M^2 from Casa Ramón shows poorly-developed metaconule crests, and small paraconule and metaconule. The scarce material from this Spanish site, assigned to the MP11 or MP12, represents the earliest record of the genus *Pseudoloris*.

Main references: Peláez-Campomanes (1995); Antunes et al. (1997); Minwer-Barakat et al. (2010, 2012); Marigó et al. (2011c).

Genus *Necrolemur* Filhol, 1873

Necrolemur antiquus Filhol, 1873

Geographic distribution: France and Spain.

Chronological range: 37–36.5 Ma (MP17–20, Headonian, Late Eocene).

Iberian localities: Roc de Santa (Barcelona).

Remarks: Known from several Late Eocene sites from France, *N. antiquus* has only been mentioned in the Iberian Peninsula from the locality of Roc de Santa. The material consists of a single, heavily worn M_3 described by Casanovas-Cladellas (1975). The scarcity and poor preservation of the material makes such specific assignation doubtful, but until a more detailed study is carried out, we prefer mantaining the above-mentioned determination.

Main references: Casanovas-Cladellas (1975); Antunes et al. (1997); Casanovas (1998); Marigó et al. (2011c).

Necrolemur sp.

Iberian localities: Sant Jaume de Frontanyà 1 and 2, and Sant Cugat de Gavadons (=Collsuspina) (Barcelona).

Remarks: The genus *Necrolemur* is known from several French, Swiss and Spanish sites ranging in age from the Geiseltalian (MP13, Middle Eocene) to the Headonian (MP20, Late Eocene). There are two citations of the genus *Necrolemur* without specific determination in the Iberian Peninsula. On the one hand, Crusafont-Pairó (1967) and Crusafont-Pairó and Golpe-Posse (1974) assigned to this genus a single, large and very worn M^2 from Sant Cugat de Gavadons. There is no available illustration of this specimen, whose attribution cannot be confirmed based on the material from the Institut Català de Paleontologia Miquel Crusafont. The generic ascription of this tooth is therefore doubtful, since another large-sized microchoerine, ascribed by the same authors to *Microchoerus ornatus*, was identified in this locality; it seems probable that these remains belong to the same taxon. On the other hand, *Necrolemur* sp. has also been cited from the Robiacian levels of Sant Jaume de Frontanyà 1 and 2 (Busquets et al., 1992; Antunes et al., 1997). The material consists of several isolated teeth and a mandible with P_4-M_3 of a small microchoerine. A detailed study, currently under way, will allow a more precise determination of this material.

Main references: Crusafont-Pairó (1967); Crusafont-Pairó and Golpe-Posse (1974); Golpe-Posse (1982c); Busquets et al. (1992); Antunes et al. (1997); Marigó et al. (2011c).

Infraorder Simiiformes Hoffstetter, 1974 (=**Anthropoidea** Mivart, 1864)

Remarks: Hoffstetter (1974) proposed Simiiformes as a replacement name for Anthropoidea, apparently on the basis of insufficient grounds (Delson, 1977), although it has several advantages such as avoiding the standard superfamily ending in –oidea for a taxon above the family-group level (see Delson, 1977, and Hoffstetter, 1982, for further details). Both Simiiformes and Anthropoidea have been recently used by several authors with the same meaning (e.g., Groves, 2001 and Fleagle, 1999, respectively; but see Rosenberger, 2006, for a different option), and hence there are considered synonyms here. The International Code of Zoological Nomenclature does not regulate these taxonomic ranks, and hence the use of one or the other remains arbitrary.

Parvorder Catarrhini É. Geoffroy Saint-Hilaire, 1812

Superfamily Pliopithecoidea Zapfe, 1960

Family Pliopithecidae Zapfe, 1960

Subfamily incertae sedis

Pliopithecidae indet.

Iberian localities: Abocador de Can Mata/C3-B2.

Remarks: The oldest record of Iberian pliopithecids corresponds to an isolated M^3 from ACM/C3-B2 (Alba et al., 2012a), which has an estimated age of 12.0 Ma (MN7, late Aragonian, Middle Miocene). This tooth displays a very peculiar occlusal morphology, which enables it to be distinguished from all other pliopithecids for which this dental position is known (including *Barberapithecus*, see below, but not *Pliopithecus canmatensis*). It is also possible that this primate tooth does not belong to the Pliopithecidae but to some other group of stem catarrhines previously not recorded in Eurasia. However, on paleobiogeographic grounds, an attribution to the Pliopithecidae was favored by Alba et al. (2012a).

Main references: Alba et al. (2012a).

Subfamily Pliopithecinae Zapfe, 1960

Genus *Pliopithecus* Gervais, 1849

Pliopithecus canmatensis Alba et al., 2010

(Figure 2A)

Geographic distribution: Restricted to the Vallès-Penedès Basin (Barcelona).

Chronological range: 11.8–11.7 Ma (MN8, late Aragonian, Middle Miocene).

Iberian localities: Abocador de Can Mata localities ACM/C5-C3, ACM/C4-Cb, ACM/C5-C2, ACM/C5-A8 and ACM/C4-A1.

Remarks: This species is knwon from several mandibles, dentognathic fragments and isolated teeth that overall record most of the permanent dentition as well as the dP_4. These remains correspond to at least 8 individuals from 5 different localities of the Abocador de Can Mata series; although an age range of 11.7–11.6 was originally reported for this species (Alba et al., 2010d), subsequent analyses have redated it to

11.8–11.7 Ma (Alba et al., 2012a). The pliopithecine morphology and the small size of the dental remains from these several localities from Abocador de Can Mata is most similar to that of *Pliopithecus antiquus* from the French localities of Sansan (MN6) and La Grive (MN7+8), but dental proportions as well as several occlusal details (less peripheral position of the protoconid and more median position of the hypoconulid, more mesial position of the buccal cuspids compared to the lingual ones, narrower but distinct mesial fovea, higher trigonid, and more extensive buccal cingulid) justify a taxonomic distinction at the species level for the ACM material (Alba et al., 2010d).

Main references: Alba et al. (2010c, d, 2012a).

Pliopithecus sp.

Iberian localities: Sant Quirze (Barcelona).

Remarks: Pliopithecids are recorded in the late Aragonian (MN8, ca. 11.8–11.2 Ma) locality of Sant Quirze by an isolated M^2 described by Harrison et al. (2002). Both in size and morphology, this tooth is consistent with an attribution to *Pliopithecus platyodon*, otherwise unknown from the Iberian Peninsula. However, the scarcity of the available material precludes evaluating whether it might represent a different species. In any case, an attribution to *P. canmantensis* can be easily discarded on the larger size of the Sant Quirze molar.

Main references: Harrison et al. (2002).

Subfamily Crouzeliinae Ginsburg and Mein, 1980
Tribe Anapithecini Alba and Moyà-Solà, 2012
Genus *Barberapithecus* Alba and Moyà-Solà, 2012
Barberapithecus huerzeleri Alba and Moyà-Solà, 2012

(Figure 2B)

Geographic distribution: Exclusively known from the type locality.

Chronological range: 11.2–10.5 Ma (MN8 or MN9, late Aragonian or early Vallesian, Middle or Late Miocene).

Iberian localities: Castell de Barberà [type locality] (Barcelona).

Remarks: This taxon is only known from isolated dental remains recovered at the locality of Castell de Barberà, initially attributed to the Aragonian, but currently attributable to the latest Aragonian or, most likely, the earliest Vallesian. The find was initially reported more than three decades ago (Crusafont-Pairó, 1975, 1978). Most of the remains, including upper and lower teeth, correspond to a single, female adult individual. They were partly described and initially attributed to *Pliopithecus* sp. by Crusafont-Pairó and Golpe-Posse (1981), who nevertheless noted dental similarities with *Plesiopliopithecus lockeri*, currently attributed to the Crouzeliini. These authors noted that this material was likely to represent a new pliopithecid taxon, but refrained from formally erecting it. Later, Ginsburg (1986) attributed the Castell de Barberà remains to Crouzeliinae nov., but subsequently the taxon was considered a pliopithecin similar or attributable to *Pliopithecus antiquus* by several authors (Moyà Solà et al., 1990; Andrews et al., 1996; Harrison et al., 2002). Both Begun (2002a) and Alba et al. (2010d) considered it to be a new pliopithecid taxon, and most recently Alba and Moyà-Solà (2012) erected a new genus and species for it within the Crouzeliinae. Besides the holotype individual, an isolated P_3 and male C^1 from the type locality are also attributed to this taxon (Alba and Moyà-Solà et al., 2012). The latter was formerly considered a female upper canine of the hominoid *Hispanopithecus laietanus* (Harrison, 1991; Golpe Posse, 1993), but on morphological grounds it is best attributable to the Pliopithecidae (Begun, 2002a; Alba et al., 2010d; Alba and Moyà-Solà, 2012). Like crouzeliins, *Barberapithecus* is characterized by buccolingually-compressed cusps, well-developed and sharp crests, and large and well-defined occlusal fovea. Its dental morphology, however, might have evolved from a pliopithecine ancestor similar to *Pliopithecus canmatensis*, which leaves open the possibility that, as currently conceived, the crouzeliines are polyphyletic (Alba and Moyà-Solà, 2012).

Main references: Crusafont-Pairó (1978); Crusafont-Pairó and Golpe-Posse (1981, 1982); Moyà Solà et al. (1990); Andrews et al. (1996); Begun (2002a); Alba and Moyà-Solà (2012); Alba et al. (2012a).

Genus *Egarapithecus* Moyà-Solà, Köhler and Alba, 2001

Egarapithecus narcisoi Moyà-Solà, Köhler and Alba, 2001

Geographic distribution: Exclusively known from the type locality.

Chronological range: 9.0–8.9 Ma (MN10, Vallesian, Late Miocene).

Iberian localities: Torrent de Febulines [type locality] (Barcelona).

Remarks: This taxon is known on the basis of a fragmentary mandible with right P_3-M_3 and left P_3-M_2 (holotype), as well as an isolated P^3 probably from the same individual. This material was initially published by Golpe-Posse (1982b), who attributed it to *Pliopithecus* sp. in spite of noting several differential features that, according to her, might justify the erection of a new taxon. This was confirmed by Moyà Solà et al. (1990) and Andrews et al. (1996), although the new genus and species were not erected until Moyà-Solà et al. (2001) described it and attributed it to the Crouzeliinae. Subsequently, Begun (2002a) considered it to be a Pliopithecinae, but this has been subsequently dismissed by other authors (Harrison et al., 2002; Alba et al., 2010d; Alba and Moyà-Solà, 2012).

Main references: Golpe Posse (1982b); Moyà-Solà et al. (1990, 2001); Andrews et al. (1996); Begun (2002a); Alba et al. (2010c).

cf. Anapithecini indet.

(Figure 2C)

Iberian localities: Can Sant Feliu (=Can Feliu, Barcelona).

Remarks: Crouzeliine affinities were noted by several authors (Moyà Solà et al., 1990; Andrews et al., 1996) for the isolated dP_4 from the late Aragonian (MN8, ca. 11.8–11.2 Ma) locality of Can Sant Feliu, initially mistaken for an M_3 (Crusafont-Pairó and Golpe-Posse, 1981). Begun (2002a) suggested that it might correspond to a larger individual of the same taxon represented at Castell de Barberà (currently, *Barberapithecus huerzeleri*), but given the presence of other pliopithecids (*Pliopithecus canmatensis*) during the late Aragonian in the same basin, most recently Alba and Moyà-Solà (2012) refrained from providing a formal taxonomic attribution.

Main references: Crusafont-Pairó and Golpe-Posse (1981, 1982); Moyà Solà et al. (1990); Begun (2002a); Harrison et al. (2002); Alba and Moyà-Solà (2012).

Superfamily Cercopithecoidea Gray, 1821

Family Cercopithecidae Gray, 1821

Subfamily Cercopithecinae Gray, 1821

Tribe Papionini Burnett, 1828

Subtribe Macacina Owen, 1843

Genus *Macaca* Lacépède, 1799

Macaca sp.

Iberian localities: Almenara-Casablanca M (Castellon); Orrios 7 (Teruel); Sima del Elefante TE9 (Burgos); Ambrona (Soria).

Remarks: The genus *Macaca* is first recorded in Europe in the latest Miocene locality of Almenara-Casablanca M (Köhler et al., 2000), after which it is known across the continent throughout the Pliocene and Pleistocene. Although there is consensus that fossil European macaques belong to the *Macaca sylvanus* lineage (Szalay and Delson, 1979; Alba et al., 2011c), of African origin, the scarce material from Almenara-Casablanca M does not enable an attribution to the species level. All other Iberian citations of *Macaca* sp. are most likely attributable to *M. sylvanus*, since this is the only fossil European macaque species recognized besides the endemic *M. majori* from Sardinia.

Main references: Aguirre and Fuentes (1969); Delson, 1974; Szalay and Delson, 1979; Delson, 1980; Ardito and Mottura (1987); Mein et al. (1990); Moyà Solà et al. (1990); Köhler et al. (2000); Carbonell et al. (2008).

Macaca sylvanus (Linnaeus, 1758)

Geographic distribution: Western Eurasia and Northern Africa.

Chronological range: Pliocene and Pleistocene.

Remarks: This species, the Barbary macaque, currently presents a disjunct distribution in Algeria and Morocco, and is also represented by the Gibraltar population, which has an anthropocorous origin (Fooden, 2007). This species was also widely distributed throughout the Plio-Pleistocene in Western Eurasia, where three distinct subspecies are customarily recognized (Szalay and Delson, 1979; Delson, 1980): *M. s. prisca*, from the earlier Pliocene; *M. s. florentina*, from the late Pliocene to the early Pleistocene; and *M. s. pliocena*, from the Middle and perhaps Late Pleistocene.

Macaca sylvanus ssp.

Iberian localities: Cova Negra (Valencia); Cueva Negra del Estrecho del Quípar (Murcia); Solana del Zamborino (Granada); Galeria Pesada - Gruta da Aroeira (Ribatejo); Canal Negre I (Barcelona).

Remarks: With the exception of Solana del Zamborino (Martín Penela, 1983, 1988), the material from the above-mentioned localities has not been described in detail, and the published citations did not include an attribution to the species level except for Guillén-Castejón (2010; see below). On chronological grounds, the macaque remains from the Middle Pleistocene localities of Cueva Negra, Solana del Zamborino and Gruta da Aroeira probably belong to *M. s. pliocena*. The remains from Canal Negre I, of uncertain age, have been attributed to both *M. s. florentina* and *Macaca* cf. *sylvanus prisca* by Guillén-Castejón (2010), mainly on the basis of size. However, size does not seem to be a reliable criterion for distinguishing among the several extinct subspecies of *M. sylvanus* (Rook et al., 2001), and given that no detailed description or measurements are provided by Guillén-Castejón (2010), the remains from Canal Negre are best left unassigned at the subspecies level.

Main references: Pérez Ripoll (1977); Martín Penela (1983, 1988); Ardito and Mottura (1987); Trinkaus et al. (2003); Walker et al. (2010).

Macaca sylvanus florentina (Cocchi, 1872)

(Figure 2E)

Geographic distribution: Southern and Central Europe.

Chronological range: Late Pliocene to Early Pleistocene.

Iberian localities: Quibas (Murcia).

Remarks: The sample from the late Early Pleistocene site of Quibas (ca. 1.3–1.0 Ma) includes dentognathic remains, isolated teeth and some postcranial bone fragments (Alba et al., 2010c). Dental morphometric comparisons indicate that this sample is morphologically similar to *M. s. florentina* from the type locality (Upper Valdarno, Italy), further reinforcing the view that this subspecies is morphologically distinct from the extant nominotypical subspecies, by displaying on average absolutely longer upper molars, relatively wider upper molars, longer M^3 compared to the M^2, absolutely longer M_1 and M_3, and relatively narrower M_3 (Alba et al., 2011c).

Main references: Montoya et al. (1999, 2001); Alba et al. (2011c).

Macaca sylvanus cf. *florentina* (Cocchi, 1872)

(Figure 2D)

Iberian localities: Cal Guardiola D7, Vallparadís Estació EVT7 and EVT10, and Canal Negre I (Barcelona), and maybe La Puebla de Valverde (Teruel).

Remarks: Although the macaque dentognathic remains from the Vallparadís Section (Cal Guardiola and Vallparadís Estació, ca. 1.0–0.78 Ma) differ metrically from the extant, nominotypical subspecies, its taxonomic attribution will remain tentative until the taxonomic distinction between *M. s. florentina* and the Middle Pleistocene *M. s.*

pliocena is further clarified (Alba et al., 2008). The specimens from Canal Negre, previously attributed to *M. s. florentina* by Guillén-Castejón (2010), have an uncertain age, and a more detailed morphometric study would be required in order to more conclusively ascertain its taxonomic attribution to this subspecies. A dP_4 from the Early Pleistocene locality (Middle Villafranchian, MN17) of La Puebla de Valverde, initially attributed to *Macaca* sp. (Heintz et al., 1971), might belong to this taxon, although subsequently Moyà Solà et al. (1990) attributed it to *Paradolichopithecus* sp.
Main references: Heintz et al. (1971); Alba et al. (2008, 2010c); Madurell-Malapeira et al. (2010); Guillén-Castejón (2010).

Macaca sylvanus cf. *pliocena* Owen, 1846

Geographic distribution: Europe, Caucasus and Israel.
Chronological range: Late Pleistocene.
Iberian localities: Lezetxiki II (Guipuzkoa).
Remarks: The mandible from Lezetxiki was tentatively attributed to *M. s. pliocena* by Castaños et al. (2011) merely on chronological grounds.
Main references: Castaños et al. (2011).

Genus *Paradolicopithecus* Necrasov, Samson and Radulesco, 1961

cf. *Paradolichopithecus* sp.

Iberian localities: Almenara-Casablanca 1 (Castellón).
Remarks: A fragmentary incisor from this Early Pleistocene locality (ca. 1.8 Ma) was tentatively assigned to the genus *Paradolichopithecus* by Moyà Solà et al. (1990). Additional dental material would be required to discount an alternative attribution to the genus *Macaca*.
Main references: Moyà Solà et al. (1990).

Paradolichopithecus sp.

(Figure 2F)

Iberian localities: Moreda 1a (Granada) and Cova Bonica (Barcelona).
Remarks: The Late Pliocene remains from Moreda 1a (3.5–3.2 Ma) and Cova Bonica (3.2–2.6 Ma) represent de oldest records of this genus in the Iberian Peninsula. According to Moyà Solà et al. (1990), they may correspond to a different species than *P. arvernensis*. Additional studies, however, are required in order to clarify the

taxonomic status of these remains. In the past, several authors also cited the presence of *Macaca* at Cova Bonica (e.g., Delson, 1971; Crusafont-Pairó and Golpe-Posse, 1974, 1984), whereas, according to Moyà Solà et al. (1990), only *Paradolichopithecus* is recorded there. The detailed study of the material from Moreda and Cova Bonica, currently in progress, will enable a decision as to whether *Macaca* is present in either of these localities and hopefully also provide a determination of the *Paradolichopithecus* remains to the species level.

Main references: Delson (1971); Crusafont-Pairó and Golpe-Posse (1984); Moyà Solà et al. (1990); Alba et al. (2010c).

Paradolichopithecus cf. *arvernensis* Depéret, 1929

Geographic distribution: Europe and Central Asia.

Chronological range: Late Pliocene to Early Pleistocene (Middle Villafranchian, MN17).

Iberian localities: La Puebla de Valverde (Teruel); Canal Negre I (Barcelona).

Remarks: The *Paradolichopithecus* material from La Puebla de Valverde was attributed to *P.* cf. *arvernensis* by Aguirre and Soto (1978). We provisionally maintain such an attribution here, although noting that the species attribution might be further refined after the study of the *Paradolichopithecus* remains from Moreda 1a and Cova Bonica, currently unders study (see comments above). Several isolated dental remains from Canal Negre, of uncertain age, have been also attributed to *P. arvernensis* by Guillén-Castejón (2010), but given the lack of a detailed description and uncertainties in the attribution of other Iberian *Paradolichopithecus* remains, the teeth from this locality are only tentatively attributed here to that species.

Main references: Heinz et al. (1971); Aguirre and Soto (1974, 1978); Ardito and Mottura (1987); Moyà Solà et al. (1990); Guillén-Castejón (2010).

Subtribe Papionina Burnett, 1828

Genus *Theropithecus* I. Geoffroy Saint-Hilaire, 1843

Subgenus *Theropithecus* I. Geoffroy Saint-Hilaire, 1843

Theropithecus (Theropithecus) oswaldi Andrews, 1916

Theropithecus (Theropithecus) oswaldi ssp. indet.

(Figure 2G)

Geographic distribution: Africa, India, Spain and perhaps Israel.

Chronological range: Late Pliocene to Late Pleistocene.

Iberian localities: Cueva Victoria (Murcia).

Remarks: Here we follow the distinction in *T. oswaldi* of three distinct subspecies (Jablonski, 2002): late Early to Late Pleistocene remains of *T. oswaldi* are attributed to *T. oswaldi leakeyi,* whereas the remains from the late Early or Middle Pleistocene of India are attributed to *T. oswaldi delsoni*, morphologically more similar to the latter, and remains from the Late Pliocene to the Early Pleistocene of Africa are attributed to the nominotypical subspecies (Delson, 1993; Jablonski, 2002). The Iberian remains of *Theropithecus*, unambiguously recorded at Cueva Victoria by dental remains (Gibert et al., 1995), were attributed to *T. o. oswaldi*, although it is uncertain that it belongs to the same subspecies recorded in Africa (E. Delson, pers. com.). A phalanx from the same locality, originally attributed to humans (Gibert Clols and Pons Moyà, 1985; Gibert et al., 1985; Gibert and Pérez-Pérez, 1989), was later reassigned to *Theropithecus* (Martínez-Navarro et al., 2005); although no consensus has been reached in this regard (see discussion in Gibert et al., 2008; Martínez-Navarro et al., 2008), we tentatively favor the former interpretation.

Main references: Gibert et al. (1995); Martínez-Navarro et al. (2005).

Subfamily Colobinae Blyth, 1863

Tribe incertae sedis

Genus *Mesopithecus* Wagner, 1839

Mesopithecus sp.

Geographic distribution: Eurasia.

Chronological range: Late Miocene to Pliocene.

Iberian localities: Venta del Moro (Valencia); Canal Negre I (Barcelona).

Remarks: The presence of the genus *Mesopithecus* in the Iberian Peninsula was first reported by Montoya et al. (2006) as *Mesopithecus* sp., on the basis of the Turolian remains from Venta del Moro (5.8–5.5 Ma). An ongoing study of the available dental remains from this locality will hopefully determine whether these remains correspond to the type species *M. pentelicus* (undoubtedly known from MN11–MN13 of Europe, Iran and Afghanistan) or to *M. monspessulanus* (from MN14–MN17 and perhaps also MN13 of Europe) (Andrews et al., 1996; Koufos, 2009). The presence of *Mesopithecus* in the Iberian Peninsula is further confirmed by the remains of uncertain age from Canal Negre reported by Guillén-Castejón (2010). The latter author attributed these remains to both *M. pentelicus* and *Mesopithecus* sp., but given age uncertainties and the lack of detailed metrical comparisons, here these remains are provisionally left unassigned to the species level.

Main references: Montoya et al. (2006); Guillén-Castejón (2010); Alba et al. (2010c).

Genus *Dolichopithecus* Depéret, 1889

Dolichopithecus ruscinensis Depéret, 1889

Geographic distribution: Europe and Russia.

Chronological range: Pliocene (4.0–3.2 Ma).

Iberian localities: Layna (Soria); Canal Negre I (Barcelona).

Remarks: A juvenile mandible from the Late Pliocene locality of Layna (4.2–3.6 Ma; Minwer-Barakat et al., in press, their Fig. 6), even though not described in detail, was attributed to this colobine species by Delson (1973, 1974; also Szalay and Delson, 1979; Pérez and Soria, 1990; Moyà Solà et al., 1990). A single molar from Canal Negre, of uncertain age, was also assigned to this taxon (albeit with some doubts) by Guillén-Castejón (2010).

Main references: Delson (1973, 1974); Moyà Solà et al. (1990); Guillén-Castejón (2010).

Superfamily Hominoidea Gray, 1825

Family Hominidae Gray, 1825

Subfamily incertae sedis

Hominidae indet.

Iberian localities: Abocador de Can Mata localitiy ACM/C1-E* (Barcelona).

Remarks: With an estimated age of 12.3–12.2 Ma (MN7, late Aragonian), the two partial upper postcanine series of a single individual from ACM/C1-E* constitute the oldest hominoid record from the Vallès-Penedès Basin (Casanovas-Vilar et al., 2011; Alba et al., 2012a). The description and study of these remains, currently under way, will hopefully enable to ascertain whether they correspond to any of the other dryopithecin taxa recorded at Abocador de Can Mata (*Pierolapithecus*, *Anoiapithecus*, *Dryopithecus*) or to another, otherwise unrecorded hominid taxon.

Main references: Casanovas-Vilar et al. (2011); Alba et al. (2012a).

Subfamily Dryopithecinae Gregory and Hellman, 1939

Tribe incertae sedis

Dryopithecinae indet.

Iberian localities: Hostalets de Pierola indeterminate, Can Mata 1, Sant Quirze, and Abocador de Can Mata localites ACM/C4-Cp and ACM/BCV4 (Barcelona).

Remarks: Several upper teeth of a single individual from ACM/C4-Cp and a mandibular fragment from ACM/BCV4, with similar estimated ages of 11.9 Ma (late Aragonian), are currently under study; attributed to Hominidae indet. by Casanovas-Vilar et al. (2011), their dental morphology indicates that they can be attributed to the Dryopithecinae, and most likely, any of the three dryopithecine genera recorded at Abocador de Can Mata (*Pierolapithecus*, *Anoiapithecus*, *Dryopithecus*). An isolated upper molar from the area of els Hostalets de Pierola, initially mistaken for a suid, was attributed by van der Made and Ribot (1999) to *Dryopithecus*. Given the greater diversity of hominoids evidence in the area of Hostalets during the last decade, Casanovas-Vilar et al. (2011) merely attributed it to the Hominidae, although on the basis of its occlusal morphology, an attribution to the Dryopithecinae is warranted. A female lower canine from the same area, in particular from the locality of Can Mata 1 (ca. 11.2 Ma, MN8, late Aragonian), was tentatively attributed to *Hispanopithecus laietanus* by Crusafont-Pairó and Golpe-Posse (1973a), and subsequently Golpe Posse (1993) reafirmed such attribution. Again, given the unexpected diversity of dryopithecines in this area, and the lack of homologous material for the three above-mentioned genera, Casanovas-Vilar et al. (2011) attributed this canine to Hominidae indet., although an assignment to the Dryopithecinae is most likely. Finally, a fragment of molar crown attests the presence of dryopithecines in the locality of Sant Quirze (11.8–11.2 Ma, MN8, late Aragonian); attributed to *H. laietanus* in the past (Golpe Posse, 1993), and most recently to Hominidae indet. (Casanovas-Vilar et al., 2011), the preserved morphology precludes an attribution to the genus level.

Main references: Crusafont-Pairó and Hürzeler (1969); Crusafont-Pairó and Golpe-Posse (1973a, 1974); Moyà Solà et al. (1990); Golpe Posse (1993); van der Made and Ribot (1999); Casanovas-Vilar et al. (2011); Alba et al. (2012a).

"Sivapithecus" occidentalis Villalta Comella and Crusafont Pairó, 1944 (nomen dubium)

(Figure 2K)

Geographic distribution: Exclusively known from the type locality.

Chronological range: 12.5–11.5 Ma.

Iberian localities: Can Vila [type locality] (Barcelona).

Remarks: This nominal taxon is based on two lower molars of a single individual (Villalta Comella and Crusafont Pairó, 1941, 1944; Pickford, 2012) from the locality of Can Vila, of uncertain stratigraphic provenance (Moyà-Solà et al., 2004; Casanovas-Vilar et al., 2011). Initially attributed to *Dryopithecus fontani* by Villalta Comella and Crusafont Pairó (1941), the same authors subsequently used them to erect a new taxon (Villalta Comella and Crusafont Pairó, 1944), which was subsequently synonymized with *Hispanopithecus laietanus*. According to the description of the site location provided by Villalta Comella and Crusafont Pairó (1941), the type locality must have been situated within or very near the area of Abocador de Can Mata, with an estimated age of 12.5–11.5 Ma (Casanovas-Vilar et al., 2011). However, according to the recollections of Jordi Martinell (pers. comm. to DMA), the classical locality of Can Vila would have been situated in the Barranc de Can Vila, in a lower stratigraphic position than BCV1 (the type locality of *Pierolapithecus catalaunicus*), in which case an estimated age of 12.1–11.9 Ma would be attributable to the former. Even though an attribution to the genus *Sivapithecus* can be readily dismissed, *"Sivapithecus" occidentalis* remains a nomenclaturally valid taxon, whose taxonomic affinities remain to be ascertained. This is complicated by the presence of several dryopithecine genera at Abocador de Can Mata around 11.9–11.8 Ma, and especially by the lack of lower teeth attributable to *Pierolapithecus catalaunicus*. At the species level, *"S." occidentalis* is potentially a senior synonym of *P. catalaunicus*, in which case, the former would take precedence. However, this potential synonymy cannot be resolved on the basis of currently available material, so we concur with other authors (Moyà-Solà et al., 2004; Casanovas-Vilar et al., 2011) that this nominal taxon is best considered a *nomen dubium*. Most recently, Pickford (2012) synonymized *"S." occidentalis* with *Neopithecus brancoi* (Schlosser, 1901); the latter, however, has been also considered a *nomen dubium* by Casanovas-Vilar et al. (2011). Additional material is required to solve this taxonomic and nomenclatural conundrum.

Main references: Villalta Comella and Crusafont Pairó (1941, 1944); Golpe Posse (1993); Moyà-Solà et al. (2004); Pickford (2012); Alba (in press).

Tribe Dryopithecini Gregory and Hellman, 1939

Genus *Dryopithecus* Lartet, 1856

Dryopithecus fontani Lartet, 1856

(Figure 2H)

Geographic distribution: Spain, France and Austria.

Chronological range: MN7 and MN8, late Aragonian (Middle Miocene).

Iberian localities: Abocador de Can Mata localities ACM/C3-Ae and ACM/C4-Ap.

Remarks: A partial face of an adult male individual from ACM/C3-Ae (11.9 Ma, MN7 or MN8, late Aragonian) was attributed to *Dryopithecus fontani* by Moyà-Solà et al. (2009a) on the basis of several craniodental features that do not fit with other Vallès-Penedès hominoids. If this attribution is correct, this is the only specimen representing the facial morphology of the type species of *Dryopithecus*, otherwise known from several mandibles and a few isolated upper teeth. On the basis of the Abocador de Can Mata specimen, *D. fontani* displays a mosaic of derived great-ape features, coupled with several primitive hominoid retentions and several gorilla-like features of uncertain phylogenetic interpretation (Moyà-Solà et al., 2009a). An upper male canine from ACM/C4-Ap (11.9 Ma, MN7 or MN8, late Aragonian), figured but incorrectly attributed by Pickford (2012) to *Hispanopithecus laietanus*, is in fact attributable to *Dryopithecus fontani* (Alba and Moyà-Solà, 2012).

Main references: Moyà-Solà et al. (2009a); Begun (2009); Alba et al. (2010b, c); Casanovas-Vilar et al. (2011); Pickford (2012); Begun et al. (2012); Alba and Moyà-Solà (2012).

cf. *Dryopithecus fontani* Lartet, 1856

Iberian localities: Abocador de Can Mata locality ACM/C3-Az and Castell de Barberà (Barcelona).

Remarks: A partial (proximal) femur from ACM/C3-Az, with an estimated age of 11.9 Ma (MN7 or MN8, late Aragonian), and an estimated body mass around 44 kg, has been tentatively attributed to *D. fontani* mainly on the basis of its large size (Moyà-Solà et al., 2009a). This specimen displays several modern hominoid-like characteristics, coupled with pronograde-related features, suggesting a greater emphasis on quadrupedalism than in *Hispanopithecus laietanus* (Moyà-Solà et al., 2009a). With regard to Castell de Barberà (ca. 11.2–10.5 Ma), the presence of hominoids at this locality was originally reported on the basis of a purported female upper canine (e.g., Golpe Posse, 1993), which in fact belongs to a male specimen of *Barberapithecus* (Begun, 2002a; Alba and Moyà-Solà, 2012). However, the undoubted presence of hominoids at Castell de Barberà is documented by two (proximal and distal) pollical phalanges as well as a partial humeral diaphysis (Moyà Solà et al., 1990; Alba et al., 2011a; Almécija et al., 2011, 2012). The humeral diaphysis displays several modern hominoid-like features, most closely resembling the more complete and slender (presumably female) humerus of *D. fontani* from Saint Gaudens in France (Alba et al., 2011a). The phalanges more closely resemble those of other Miocene apes than those of extant great apes, indicating a significant degree of thumb-assisted, powerful grasping during above-branch quadrupedalism and cautious climbing (Almécija et al., 2012).

Main references: Moyà-Solà et al. (1990, 2009a); Casanovas-Vilar et al. (2011); Alba et al. (2011a, 2012a); Almécija et al. (2011, 2012).

Genus *Pierolapithecus* Moyà-Solà et al., 2004

Pierolapithecus catalaunicus Moyà-Solà et al., 2004

(Figure 2I)

Geographic distribution: Exclusively known from the type locality.

Chronological range: 11.9 Ma (MN7, late Aragonian, Middle Miocene).

Iberian localities: Abocador de Can Mata – Barranc de Can Vila 1 (ACM/BCV1) [type locality] (Barcelona).

Remarks: The holotype and currently only known individual of this taxon includes a partial face and skeleton with more than 80 bones or bone fragments from an adult male individual (Moyà-Solà et al., 2004), with an estimated body mass of 34 kg. Although an age of ca. 12.5–13.0 Ma was initially proposed (Moyà-Solà et al., 2004), based on magnetostratigraphic data, ACM/BCV1 has been subsequently dated to 11.9 Ma (Moyà-Solà et al., 2009a; Casanovas-Vilar et al., 2011; Alba et al., 2012a). *Pierolapithecus* displays a low face with a posteriorly-situated glabella and a prognathous profile, coupled with a modern, great-ape-like facial configuration (Moyà-Solà et al., 2004). In turn, the postcranial remains indicate that *Pierolapithecus* possessed a modern-hominoid-like, orthograde bodyplan (Moyà-Solà et al., 2004; Ward, 2007; Susanna et al., 2010), so that this taxon represents the oldest evidence of orthogrady combined with a cranial morphology more derived than that of hylobatids. On this basis, *Pierolapithecus* was originally interpreted as a stem hominid, i.e. as a basal member of the great-ape-and-human clade (Moyà-Solà et al., 2004, 2009b), although the possession of several pongine-like cranial features (such as the lack of frontal sinus; Pérez de los Ríos et al., 2010, in press) suggest that it might be alternatively interpreted, probably together with other dryopithecins, as a sister-taxon of the Asian Pongini (see discussion in Casanovas-Vilar et al., 2011; Alba, in press; Pérez de los Ríos et al., in press). Interestingly, despite its orthograde body plan, *Pierolapithecus*, however, still retains manual adaptations for powerful-grasping and above-branch palmigrady (Moyà-Solà et al., 2004, 2005; Almécija et al., 2009) further suggesting that unlike *Hispanopithecus* (see below) this taxon lacked adaptations to below-branch suspensory behaviors (Moyà-Solà et al., 2005; Almécija et al., 2009; Alba et al., 2010a; for an alternative interpretation, see Begun and Ward, 2005; Deane and Begun, 2008, 2010). Some authors (Begun, 2009; Begun et al., 2012) remain skeptical on the taxonomic distinctiveness of *Pierolapithecus* from *Dryopithecus*, but this is contradicted by several differences in craniodental morphology (Moyà-Solà et al., 2004, 2009a), including the possession of much thicker-enameled molars in *Pierolapithecus* (Alba et al., 2010b; contra Begun, 2009).

Main references: Moyà-Solà et al. (2004, 2005, 2009b); Begun and Ward (2005); Deane and Begun (2008, 2010); Almécija et al. (2009); Begun (2009); Alba et al. (2010a, b, c, 2011d); Pérez de los Ríos et al. (2010); Susanna et al. (2010); Begun et al. (2012); Alba (in press); Pérez de los Ríos et al., in press.

Genus *Anoiapithecus* Moyà-Solà et al., 2009b

Anoiapithecus brevirostris Moyà-Solà et al., 2009b

(Figure 2J)

Geographic distribution: Exclusively known from the type locality.

Chronological range: 11.9 Ma (MN7, late Aragonian, Middle Miocene).

Iberian localities: Abocador de Can Mata locality ACM/C3-Aj [type locality] (Barcelona).

Remarks: *A. brevirostris* has been described on the basis of a partial face and associated mandible from ACM/C3-Aj (Moyà-Solà et al., 2009b), although unpublished dental remains from a second individual have been recovered from the same locality. As for *Pierolapithecus*, doubts have been raised regarding the distinct taxonomic status of *Anoiapithecus* relative to *Dryopithecus* (Begun, 2009; Begun et al., 2012). In fact, however, *Anoiapithecus* can be distinguished from both

Pierolapithecus and *Dryopithecus* by the strikingly orthognathous facial profile of the former (Moyà-Solà et al., 2009b), which cannot be merely discounted on the basis of purported distortion (contra Begun et al., 2012). Moreover, *Anoiapithecus* further differs from the other dryopithecins by several other craniodental features, most notably, in the case of *Pierolapithecus*, by the presence of a frontal sinus (Moyà-Solà et al., 2009b; Pérez de los Ríos et al., 2010, in press). Nevertheless, the three dryopithecin genera display several hominid facial synapomorphies, suggesting that they are more closely related to crown hominids than to kenyapithecines from the earlier Middle Miocene (Moyà-Solà et al., 2009b; Casanovas-Vilar et al., 2011).

Main references: Moyà-Solà et al. (2009b); Begun (2009); Alba et al. (2010b, c, 2011d); Pérez de los Ríos et al. (2010); Begun et al. (2012); Alba (in press).

Tribe Hispanopithecini Cameron, 1997
Genus *Hispanopithecus* Villalta Comella and Crusafont Pairó, 1944
Subgenus *Hispanopithecus* Villalta Comella and Crusafont Pairó, 1944
Hispanopithecus (Hispanopithecus) laietanus Villalta Comella and Crusafont Pairó, 1944

(Figure 2N-O)

Geographic distribution: Only known from several localities of the Vallès-Penedès Basin (NE Spain).

Chronological range: 10.0–9.5 Ma (MN9–MN10, early to late Vallesian, Late Miocene).

Iberian localities: La Tarumba 1 [type locality], Can Llobateres 1 and 2, Polinyà 2, Can Feu, EDAR6 and EDAR7 (Barcelona).

Remarks: *H. laietanus* (the type species of the genus *Hispanopithecus*) was originally defined on the basis of lower jaw and dental remains from La Tarumba 1 (Villalta Comella and Crusafont Pairó, 1944). Subsequently, *Hispanopithecus* was treated as a junior subjective synonym of *Dryopithecus* by many authors (Szalay and Delson, 1979; Moyà Solà et al., 1990; Begun et al., 1990; Harrison, 1991; Andrews et al., 1996; Begun, 1992, 2002b), albeit with some exceptions (Golpe Posse, 1993; Cameron, 1997, 1999). Recently, *Hispanopithecus* was resurrected (Moyà-Solà et al., 2009a), including not only the type species, but also *H. crusafonti* (see below)—a proposal that has been subsequently followed by most researchers (e.g., Begun, 2009; Alba et al., 2010a, 2011a, b, 2012b; Begun et al., 2012). Dental remains of *H.*

laietanus are known from several localities, although the largest sample comes from the early Vallesian site of Can Llobateres 1 (Begun et al., 1990; Harrison, 1991; Golpe Posse 1993; Alba et al. 2012b), with an estimated age of 9.7 Ma. The intial hominoid dental finds from Can Llobateres 1 were attributed to *H. laietanus*, but subsequent finds resulted in the naming of two additional taxa (*Dryopithecus piveteaui* and *Rahonapithecus sabadellensis*), which are currently considered *nomina nuda* (e.g., Golpe Posse, 1993; but see Pickford, 2012). During the last decades, the dental sample from this locality has been generally attributed to a single species (e.g., Begun et al., 1990; Harrison, 1991; Alba et al., 2012c), with some authors setting apart an upper canine (Crusafont-Pairó and Golpe-Posse, 1973a; Golpe Posse, 1993) that nevertheless can be also attributed to the same taxon. With regard to the cranial anatomy of *H. laietanus*, it is known by a partial cranium from Can Llobateres 2 (Moyà-Solà and Köhler, 1993a, 1995; Köhler et al., 2001a, b), with an estimated age of 9.6 Ma. This taxon displays several cranial features indicative of hominid status, being in some regards more derived towards the modern great-ape condition than the Middle Miocene dryopithecins. Finally, besides some isolated bones from Can Llobateres 1 and the unpublished remains from EDAR (Checa Soler and Rius Font, 2003), the postcranial anatomy of *H. laietanus* is best known from the partial skeleton (comprising about 60 elements) from Can Llobateres 2 (Moyà-Solà and Köhler, 1996; Köhler et al., 2001a; Almécija et al., 2007) and the more incomplete partial skeleton from Can Feu (Alba et al., 2011b, 2012d). Several features of these skeletons indicate the possession of an orthograde body plan with suspensory adaptations (Moyà-Solà and Köhler, 1996; Köhler et al., 2002; Almécija et al., 2007; Alba et al., 2010a; Susanna et al., 2011; Pina et al., 2012a,b), although some manual features and other anatomical characteristics indicate the simultaneous retention of features functionally-related to above-branch quadrupedalism (Almécija et al., 2007; Alba et al., 2010a, 2012d).

Main references: Villalta Comella and Crusafont Pairó (1944); Crusafont Pairó (1958b, 1965a); Crusafont-Pairó and Hürzeler (1961, 1969); Crusafont-Pairó and Golpe-Posse (1973a); Golpe Posse (1982a, 1993); Moyà Solà et al. (1990); Begun et al. (1990); Harrison (1991); Moyà-Solà and Köhler (1993a, 1995, 1996); Andrews et al. (1996); Cameron (1997, 1999); Köhler et al. (1999, 2001a, b, 2002); Ribot et al. (1996); Begun (2002b, 2009); Checa Soler and Rius Font (2003); Almécija et al. (2007); Deane and Begun (2008); Alba et al. (2010a, c, 2011b, 2012b,c,d);

Casanovas-Vilar et al. (2011); Susanna et al. (2011); Pickford (2012); Pina et al. (2012b); Alba (in press).

Hispanopithecus (Hispanopithecus) crusafonti (Begun, 1992)

(Figure 2L-M)

Geographic distribution: NE Spain.
Chronologic range: 10.4–10.0 (MN9, early Vallesian, Late Miocene).
Iberian localities: Can Poncic 1 [type locality] (Barcelona); Teuleria del Firal (Lleida).
Remarks: Most of the dentognathic remains attributed to *H. crusafonti* come from Can Poncic 1. Although initial finds were assigned to *Hispanopithecus laietanus*, after the recovery of more abundant material, *Dryopithecus crusafonti* was distinguished (Begun, 1992); it was recently transferred to the genus *Hispanopithecus* by Moyà-Solà et al. (2009a). After its description, this taxon has been accepted (Begun, 2002b; Casanovas-Vilar et al., 2011; Pickford, 2012), questioned (Andrews et al., 1996), or formally synonymized with *H. laietanus* (Ribot et al., 1996). On the basis of dental differences between the Can Poncic 1 sample and those of *H. laietanus* from later Vallesian localities (Begun, 1992), a distinct species status is favored here, following Alba et al. (2012c). At the same time, several shared-derived dental features suggest that they belong to a single genus, even though the lack of cranial material from Can Poncic makes the generic attribution to *Hispanopithecus* somewhat provisional, and some authors maintain its original assignment to *Dryopithecus* (Pickford, 2012). The partial mandible from Teuleria del Firal (Vidal, 1913a, b; Woodward, 1914), traditionally attributed to *Dryopithecus fontani* (Harrison, 1991; Andrews et al., 1996; Ribot et al., 1996), is also included here in the hypodigm of *H. crusafonti* (Begun, 1992; Casanovas-Vilar et al., 2011; Alba et al., 2012c), given some dental differences relative to *D. fontani* from France and several resemblances to the few lower teeth available from Can Poncic 1.
Main references: Vidal (1913a, b); Woodward (1914); Golpe Posse (1982a, 1993); Moyà Solà et al. (1990); Harrison (1991); Begun (1992, 2002b, 2009); Andrews et al. (1996); Ribot et al. (1996); Alba et al. (2010c); Casanovas-Vilar et al. (2011); Pickford (2012); Alba (in press); Alba et al. (2012c).

Subfamily Homininae Gray, 1825

Tribe Hominini Gray, 1825

Genus *Homo* Linnaeus, 1758

Homo sp.

Iberian localities: Sima del Elefante TE9 (Burgos).

Remarks: The partial mandible recovered from the Early Pleistocene site (ca. 1.2 Ma) of Sima del Elefante (Atapuerca) was initially assigned to *H. antecessor* by Carbonell et al. (2008), but most recently it has been argued that it might correspond to a different taxon (Bermúdez de Castro et al., 2011). On this basis, we prefer to leave unassigned to the species level the remains from this locality, which represent the oldest osteological record of the genus *Homo* in the Iberian Pensinsula. Slightly older stone tool assemblages from Fuente Nueva-3 and Barranco León-5 in Orce (Guadix-Baza Basin) further record the early presence of humans in southern Iberia (Martínez-Navarro et al., 1997; Oms et al., 2000), although the even older (1.4 Ma; Duval et al., 2011), purported human remains from Venta Micena (e.g., Gibert et al., 2002), in the same region, are not currently accepted as such (Moyà-Solà & Köhler, 1997; Martínez-Navarro, 2002; Martínez-Navarro et al., 1997).

Main references: Carbonell et al. (2008), Bermúdez de Castro et al. (2011); Martinón-Torres et al. (2011).

Homo heidelbergensis Schoetensack, 1908 s.l.

Geographic distribution: Eurasia and Africa.

Chronological range: Latest Early Pleistocene to Middle Pleistocene.

Iberian localities: Gran Dolina TD6 and Sima de los Huesos in Atapuerca (Burgos); Cueva Negra del Estrecho del Quípar (Murcia); Galeria Pesada - Gruta da Aroeira (Ribatejo); Cova de Mollet I (Girona).

Remarks: The classification of latest Early and Middle Pleistocene humans is still one of the most hotly debated topics in paleoanthropology and remains largely unresolved (e.g., Rightmire, 2007; 2008; Hublin, 2009; Harvati et al., 2010). Traditionally, they were lumped, together with Neandertals, into a single informal category termed 'archaic' *H. sapiens*. In this way, the phylogenetic affinities of such taxa with later *Homo* and their mosaic morphology, showing a combination of plesiomorphic (*Homo erectus*-like) traits with some more derived features, were recognized. However, such grade classification failed to address the alpha taxonomy of these specimens (Harvati et al., 2010). Currently, there are two main views on the phylogeny and taxonomy of these forms (Rightmire, 2007; Hublin, 2009). One considers that there is a single species *H. heidelbergensis* s.l., which would be ancestral to both *Homo neanderthalensis* and modern *H. sapiens*, being distributed in Europe, Africa and probably Asia (e.g., Rightmire, 1998, 2007, 2008; Mounier et al., 2009). Alternatively, several authors (e.g., Arsuaga et al., 1997) have argued that European Middle Pleistocene humans display several Neandertal derived features, thereby indicating that these forms should be classified into *H. neanderthalensis*, or alternatively that *H. heidelbergensis* should be restricted to European forms (a chronospecies ancestral to Neandertals, i.e. *H. heidelbergensis* s.s.), their African counterparts being attributed to a different species, *H. rhodesiensis* (see also Stringer, 2012).

The hominin remains from Sima de los Huesos (0.53 Ma; but see Stringer, 2012, regarding dating uncertainties) were initially attributed to *Homo heidelbergensis* by Arsuaga et al. (1993), although most recently Martinón-Torres et al. (2012) argued that the dental remains from this locality display more derived Neandertal traits than the typical *H. heidelbergensis* from Mauer or Aragó. We however think that an attribution to *H. heidelbergensis* is still warranted, especially when it is taken into account that this taxon is here considered in a broad sense. Similarly, the older hominin remains from Gran Dolina TD6 (ca. 0.88–0.78 Ma) were also initially assigned to an archaic form of *H. heidelbergensis* by Carbonell et al. (1995), but later Bermúdez de Castro et al. (1997) erected a new species, *Homo antecessor*, arguing that it would be the common ancestor of both modern humans and Neandertals. Such a phylogenetic hypothesis is currently uncertain, although the validity of the species, definitely identified only from Atapuerca, is accepted by some researchers (Stringer, 2012). Its distinctive taxonomic status, either at the species or subspecies level, might ultimately be vindicated in the future by the find of additional remains. Currently, however, the available remains from TD6 are relatively scarce, fragmentary and/or subadult, and one of its purported most diagnostic features (the development of the canine fossa) is much more obvious in the juvenile than in the adult specimen, this feature further being variable in other populations attributed to *H. heidelbergensis* (Rightmire, 2008). Resolving the taxonomy of fossil European hominins is of course outside the scope of this paper. However, given recent taxonomic analyses favoring the distinction of a single, Afro-European species *H. heidelbergensis* s.l. (Mounier et al., 2009; see Stringer, 2012, for a recent review on this species), we provisionally prefer to attribute the Gran Dolina hominins to the latter taxon. The somewhat younger population from Sima de los Huesos, on the other hand, display a mosaic of morphologic features indicating that they are already derived towards Neandertals (Martinón-Torres et al., 2012), so that their removal from *H. heidelbergensis* and their inclusion into *H. neanderthalensis* might be justified (Stringer, 2012). Following the same criterion of *H. heidelbergensis* understood in a broad sense, the Middle Pleistocene remains from Cueva Negra del Estrecho de Quípar (Walker et al., 2010), Galeria Pesada (Trinkaus et al., 2003) and Cova de Mollet (Maroto et al., 1987) are here also attributed to *H. heidelbergensis* s.l.

Main references: Arsuaga et al. (1993, 1997, 1999); Carbonell et al. (1995, 2005); Bermúdez de Castro et al. (1997, 2008, 2012a); Carretero et al. (1999); Lorenzo et al. (1999); Trinkaus et al. (2003); Maroto et al. (1987); Walker et al. (2010); Martinón-Torres et al. (2012); Maroto et al. (2012).

Homo neanderthalensis King, 1864

Geographic distribution: Europe and Middle East.

Chronological range: Latest Middle to Late Pleistocene.

Iberian localities: Banyoles (Girona); Cova del Gegant (Barcelona); Cova del Tossal de la Font (Castellón); Cova Negra, Cova del Bolomor and Cova Foradà (Valencia); El Salt (Alicante); Sima de las Palomas del Cabezo Gordo (Murcia); Cueva de los Moros de Gabasa (Huesca); Pinilla del Valle (Madrid); Valdegoba (Burgos); Cueva del Castillo, Cueva del Esquilleu, Cueva de Covalejos and Cueva del Castillo (Cantabria); Cueva del Sidrón (Oviedo); Arrillor (Álava); Axlor (Vizcaya); Lezetxiki VII, IV (Guipuzkoa); Cueva de los Casares and Cueva de los Torrejones (Guadalajara); Cueva del Boquete de Zafarraya (Málaga); Cueva de La Carihuela (Granada); Forbe's Quarry (=Gibraltar I), Devil's Tower (=Gibraltar II) and Cueva Genista (Gibraltar, UK); Gruta da Figueira Brava (Setúbal); Gruta de Salemas (Lisboa); Gruta da Oliveira (Santarém); Gruta Nova da Columbeira (Leiria); Lapa da Rainha (Lisboa).

Remarks: There are more than 30 Iberian localities where osteological remains of *H. neanderthalensis* have been found, although no partial or complete skeletons have been unearthed up to date. Several of these localities, situated in southwestern Iberia, record the latest Neandertals from Europe (Hublin et al., 1995), with a chronology of 35 ka (Trinkaus, 2007).

Main references: Alférez et al. (1982, 1985); Dean et al. (1986); Arsuaga et al. (1984, 1989, 2007); Antunes and Santinho Cunha (1992); Hublin et al. (1995); Vega-Toscano et al., (1997); Sanchez (1999); Quam et al. (2001); Barroso (2003); Daura et al. (2005); Grün et al. (2006); Rosas et al. (2006); Aguirre Enríquez (2007); Trinkaus et al. (2007); Walker et al. (2008, 2010, 2011); Arsuaga et al. (2012).

Homo sapiens Linnaeus, 1758

Chronological range: Latest Middle Pleistocene to Holocene.

Geographic distribution: Worldwide.

Oldest Iberian localities: Gruta do Caldeirão (Santarém); Lagar Velho (Leiria); Malladetes (Valencia).

Remarks: There are numerous Iberian localities with fossil remains of *H. sapiens*, so that only the oldest citations are provided above. On the basis of osteological remains, *H. sapiens* is first recorded at the Iberian Peninsula in Lagar Velho (Duarte et al., 1999) and Malladetes (Arsuaga et al., 2002), and slightly later at Gruta do Caldeirão (Trinkaus et al., 2001). These remains of modern humans postdate the last Iberian Neandertals, but this is not the case of the archeological remains associated to the former. Thus, although the attribution of archeological remains to a particular human species is questionable when not accompanied by osteological remains, the recent dating of Paleolithic cave art from Spain—presumably made by *H. sapiens*—to 40.8 ka suggests that modern humans arrived to the Iberian Peninsula ca. 41.5 ka, like in other areas of Western Europe (Pike et al., 2012). The find of an almost complete skeleton of a child in the Lagar Velho cave caused a lot of controversy, because Duarte et al. (1999) initially concluded that it displayed modern human and Neandertal traits simultaneously. Subsequently, however, other authors have pointed out that the Lagar Velho child is clearly *H. sapiens* and does not display Neandertal characters (Tattersall and Schwartz, 1999).

Main references: Duarte et al. (1999); Arsuaga et al. (2002); Trinkaus et al. (2001).

Results

An updated summary of Iberian primate taxa and localities from the Cenozoic is provided here, based on the revision of more than 200 bibliographic references. A total of 25 primate genera, corresponding to 7 families (one of plesiadapiforms, 2 of strepsirhines and 4 of haplorhines), from up to 116 different localities, are reported (27 from the Eocene, 3 from the Oligocene, 32 from the Miocene, 4 from the Pliocene, 51 from the Pleistocene and one with an undetermined age). This information is summarized in Figures 3 and 4, which show the ranges of the different Iberian primate taxa in relation to climatic evolution during the Cenozoic. In the following section, we discuss primate diversity dynamics in the Iberian Peninsula through time, further emphasizing its interplay with global and regional paleogeographic and climatic events.

Discussion

Iberian primate diversity in the Paleogene

In Europe, the earliest occurrence of plesiadapiforms is dated to the Late Paleocene, as documented by the record of *Berruvius* and some members of the Saxonellidae and Plesiadapidae in France and Germany (Silcox, 2001; Bloch et al., 2007). In contrast, the record of primates (including plesiadapiforms) in the Iberian Peninsula does not go back beyond the Early Eocene. This lack of evidence for Paleocene primates in Iberia may be due to the scarcity of Paleocene continental sites: mammal remains from this epoch have been only identified in the localities of Claret, Tendruy, Palau, Fontllonga and Campo (Gheerbrant et al., 1997; López-Martínez and Peláez-Campomanes, 1999; Peláez-Campomanes et al., 2000). Anyway, the Eocene record of plesiadapiforms in this area is sparse, being restricted to the paromomyoid *Arcius*, known from the locality of Silveirinha (Mondego Basin, Portugal; Estravís, 2000) and recently identified also in Masia de l'Hereuet (Àger sub-basin, Spain; Marigó et al., 2012a). In the former locality, eight isolated teeth enabled description of the species *A. zbyszewskii*, whereas the four molars recovered from the latter site did not allow a specific determination.

The record of euprimates during the Iberian Eocene shows a much greater diversity, being represented by two distinct groups of Paleogene "prosimians": adapoids and omomyoids (8 and 3 genera, respectively, apart from several forms without generic ascription, which in some cases may lead to the description of new taxa after further studies). The record of adapoids begins, together with that of plesiadapiforms, in the Neustrian, with the presence of the genus *Donrussellia* in the Mondego Basin. In the Grauvian, the genera *Cantius* and *Agerinia* are well represented in several localities from the Pyrenean and Ebro basins, *Agerinia* persisting into the Geiseltalian. The Robiacian records a great diversity of adapoids, represented in the Pyrenean and Duero basins by the genera *Anchomomys, Mazateronodon, Microadapis, Adapis* and *Leptadapis*, the latter two being also identified in Headonian levels. With respect to omomyoids, the genus *Pseudoloris* has its oldest record in the Iberian locality of Casa Ramón (Geiseltalian). It is also well represented, together with *Necrolemur*, in the Robiacian and Headonian, while *Microchoerus* is recognized in several Headonian sites. Such abundance and diversity of both adapoids and omomyoids parallels the diversity peak that primates experienced during the Eocene in the Northern hemisphere (e.g., Fleagle, 1999). The Eocene represents the warmest epoch of the Tertiary, especially during the Paleocene/Eocene Thermal Maximum and the subsequent sustained period of global warmth known as the Early Eocene Climatic Optimum (Zachos et al., 2001). Warm temperatures and not-marked seasonality favored the development of tropical forests with a predominance of evergreen thermophilic elements in latitudes as far north as 50º (Collison and Hooker, 2003). Although variable in different regions and time intervals, these dense forests would have provided suitable habitats for the radiation of these groups of prosimians.

During the Middle and Late Eocene, the mammal faunas from the western and central Iberian basins were clearly different from those of the Pyrenean basins, the latter being similar to those from Central Europe (France and Switzerland). This faunal differentiation, mainly observed in perissodactyls, artiodactyls and rodents, led to the definition of the Western Iberian Bioprovince (Cuesta, 1991), which included several western and central Iberian basins (Duero, Almazán and Oviedo Basins) characterized by Eocene mammal faunas different from those of the Pyrenees and the rest of Europe. Subsequent studies of these mammalian groups have further reinforced this contention (see Badiola et al., 2009, and references therein). The recent description of the adapiform *Mazateronodon endemicus* and the microchoerine *Pseudoloris cuestai* (Marigó et al., 2010; Minwer-Barakat et al., 2012) from the site of Mazaterón demonstrates that primates from the Western Iberian Bioprovince were also clearly different from their counterparts in the Pyrenean basins, thus reinforcing the endemic nature of the mammal faunas from this bioprovince.

The Eocene–Oligocene boundary was marked by a major faunal turnover that dramatically affected the continental vertebrate faunas and involved the extinction of a large number of Eocene mammals. This global event, named the "*Grande Coupure*" by Stehlin (1910), was mainly related to the climatic deterioration that took place at the Eocene–Oligocene transition, which led to a marked loss of diversity in both the marine and continental realms (Prothero, 1994; Hooker et al., 2004). Primates were not an exception, and the number of species of both adapoids and omomyoids, which had been highly succesful during the Eocene, drastically decreased in the Early Oligocene. Adapiforms persisted until the Miocene, although their record is very scarce and geographically restricted to Southeastern Asia (Gebo, 2002), whereas in Europe there is no mention of this group after the Eocene–Oligocene boundary. Regarding omomyoids, there are some brief appearances in the Oligocene and the earliest Miocene of North America (Macdonald, 1963; Albright, 2005) and Egypt (Simons et al., 1986). In Europe, however, after the *Grande Coupure* the omomyoid record is restricted to two finds from the Early Oligocene of Spain. Thus, *Pseudoloris* was able to survive the Eocene–Oligocene faunal turnover, as evidenced by *Pseudoloris godinoti* from the Suevian sites of Fonollosa and Santpedor in the Ebro Basin (Köhler and Moyà-Solà, 1999). Also, a single lower molar from the Early Oligocene of Aguatón evidences the persistence of *Microchoerus* in the Calatayud-Teruel Basin (Peláez-Campomanes, 2000). Therefore, at least two (*Pseudoloris* and *Microchoerus*) of the three microchoerine genera that inhabited the Iberian Peninsula during the Eocene further persisted, although rarely at best, into the Early Oligocene, constituting the only record of this group in Europe—the German fissure fillings of Ehrenstein and Harrlingen, containing microchoerine remains and originally assigned to the Early Oligocene (Schmidt-Kittler, 1971, 1977), were later considered to be Late Eocene in age (BiochroM’97, 1997). This might be related to maintenance of warmer temperatures in the Iberian Peninsula, compared to more northern areas of Europe, which would have favored the persistence of tropical to subtropical forested areas allowing the survival of some omomyoids until the Early Oligocene.

In summary, the Paleogene primate record in the Iberian Peninsula shows a great diversity of both adapoids and omomyoids in the Eocene, followed by a marked drop in the number of species in the Oligocene, in agreement with other areas of the Northern hemisphere (e.g., Fleagle, 1999). However, it is remarkable that the diversity of Eocene primates from the Iberian Peninsula has notably increased in recent years. For instance, in the last three years four new primate taxa have been described from the Iberian Eocene: the adapoids *Mazateronodon endemicus* and

Anchomomys frontanyensis, and the omomyoids *Pseudoloris pyrenaicus* and *P. cuestai* (Marigó et al., 2010, 2011a; Minwer-Barakat et al., 2010, 2012). Moreover, the first citation of plesiadapiforms in Spain has been reported (Marigó et al., 2012a), raising to two the mentions of this group in the Iberian Peninsula. Therefore, it seems highly probable that the diversity of Paleogene (especially Eocene) primates in the Iberian Peninsula recorded by currently available remains is even higher than recognized, and that the knowledge of this group of mammals will grow in the next few years as more detailed studies are carried out.

Primate Iberian diversity in the Miocene and Plio-Pleistocene

In the Iberian Peninsula, simians (anthropoids) are not recorded until well within the Miocene (late Aragonian), being represented by pliopithecoids (a Eurasian clade of stem catarrhines) as well as hominoids (apes and humans), whereas cercopithecoids (Old World monkeys) are recorded from the latest Miocene onwards.

Pliopithecoids from the Miocene of Eurasia are currently considered to be stem catarrhines on the basis of the possession of only two premolars (e.g. Andrews et al., 1996; Begun, 2002a), although it is uncertain whether they are more derived than African propliopithecoids and other stem catarrhines (Begun, 2002a). Once considered to be phylogenetically related to hylobatids, in fact they retain several primitive features indicating that they precede the cercopithecoid-hominoid split. In any case, they were the first anthropoids that dispersed into Eurasia, where they experienced an evolutionary radiation, in a continent previously devoid of other anthropoids, from the Early Miocene onwards (Begun, 2002a; Harrison, 2005). Pliopithecoids are first recorded by dionysopithecins from the Early Miocene of Asia (Harrison and Gu, 1999), whereas pliopithecines and crouzeliines are recorded in the Middle and Late Miocene of both Europe and Asia (Begun, 2002a; Harrison, 2005). In the Iberian Peninsula, pliopithecoids are exclusively known from the Vallès-Penedès Basin (NE Spain), where they are recorded by both pliopithecines (the genus *Pliopithecus*) and crouzeliines (the genera *Barberapithecus* and *Egarapithecus*). This restricted geographic distribution is probably attributable to the peculiar physiographic and paleoecological conditions of the Vallès-Penedès Basin, which by the Middle and early Late Miocene was more similar to France and other Central European countries than to the inner Iberian Basins (Agustí et al., 1984; Agustí, 1990; Casanovas-Vilar and Agustí, 2007; Casanovas-Vilar et al., 2008). Their oldest record in Iberia (ca. 12.0 Ma; Alba et al., 2012a), however, is quite late compared to France and Central Europe (where finds occur from MN5), perhaps due to the lack of adequate outcrops from the early Middle Miocene in the Vallès-Penedès Basin. The best known pliopithecine from Iberia is *Pliopithecus canmatensis*, from the late Middle Miocene of several localities from the Abocador de Can Mata series (Alba et al., 2010d). Crouzeliines, in turn, are recorded by the anapithecins *Barberapithecus huerzeleri*, from the latest Middle or earliest Late Miocene of Castell de Barberà (Alba and Moyà-Solà, 2012), and *Egarapithecus narcisoi*, from the Late Miocene of Torrent de Febulines (Moyà-Solà et al., 2001). With an estimated age of ca. 9 Ma, *Egarapithecus* represents the last record of a Miocene primate in Iberia before the occurrence of cercopithecoids.

With regard to hominoids, like pliopithecoids and probably due to the same paleoecological reasons, in the Iberian Neogene they are restricted to the late Middle and early Late Miocene, further displaying a similar geographic distribution, restricted to the Vallès-Penedès Basin and to the small, intra-Pyrenean Seu d'Urgell Basin (Casanovas-Vilar et al., 2011). This group, including extant apes and humans, originated around the Oligocene/Miocene boundary in Africa, where they experienced a remarkable evolutionary radiation during the Early and Middle Miocene (Begun, 2007; Harrison, 2010). From the beginning of the Middle Miocene, hominoids are also recorded in Eurasia, where they diversified into a plethora of genera, most of which are considered members of the great-ape-and-human clade (Hominidae) (Begun, 2002b, 2007; Kelley, 2002; Casanovas-Vilar et al., 2011). Some authors have favored a Eurasian origin of hominids and their early divergence during the middle Miocene into pongines and hominines, followed by a later hominine dispersal event back into Africa by the late Miocene (Begun, 2002b, 2007, 2009; Begun et al., 2012). However, given the incomplete nature of the primate fossil record and the probable multidirectional nature of hominoid intercontinental dispersal and range extension events during the Middle Miocene, the place of origin of hominids cannot be currently resolved. The oldest record of Eurasian hominoids corresponds to the latest Early Miocene, just before the Langhian transgression (ca. 16.3 Ma), but undoubted kenyapithecines such as *Griphopithecus* (most likely being stem hominids) are not recorded until the early Middle Miocene (ca. 14 Ma) (Casanovas-Vilar et al., 2011; contra Andrews and Kelley, 2007, who favor an older dating). By this time, roughly coinciding with the following Mid-Miocene Climatic Optimum (Zachos et al., 2011), the kenyapithecines of African origin apparently expanded their range into eastern Europe and Turkey, and apparently gave rise to the Eurasian radiation of hominids (Moyà-Solà et al., 2009b; Casanovas-Vilar et al., 2011; Alba, in press).

Whereas Miocene hominoids from Asia are generally regarded as pongines (i.e., members of the orangutan clade) (Kelley, 2002; Begun, 2007), the Miocene hominoids from Europe, here included into the Dryopithecinae, have been variously considered to be stem hominids (e.g., Casanovas-Vilar et al., 2011), pongines (e.g., Agustí et al., 1996) or hominines (e.g., Begun, 2009; Begun et al., 2012). Despite these phylogenetic disagreements, the discoveries of Miocene hominoids from Spain that have taken place during the last two decades have provided a wealth of new information that provides several insights into hominoid evolution. The fact that the pongine *Sivapithecus* is first recorded at ca. 13.0–12.5 Ma in Asia (Kunimatsu et al., 2004), whereas almost simultaneously (ca. 12.3–12.2) a hominid of uncertain affinities is recorded at the other end of Eurasia in the Vallès-Penedès Basin, suggests that the initial diversification of Eurasian hominoids took place somewhat earlier, probably between 14–13 Ma (Casanovas-Vilar et al., 2011). At the same time, the cranial and dentognathic characteristics of the later, Middle Miocene Spanish dryopithecins, suggest they descended from a thick-enameled kenyapithecine ancestor (Moyà-Solà et al., 2009b; Alba et al., 2010b; Casanovas-Vilar et al., 2011). The global climatic trend towards progressive cooling and increased seasonality initiated during the middle Miocene (Zachos et al., 2001; Kovar-Eder, 2003; Mosbrugger et al., 2005) apparently favored the adaptive radiation of Eurasian hominoids (Casanovas-Vilar et al., 2011), as reflected by their widened geographic range and increased taxonomic diversity, probably as a result of the new selection pressures posed by changing ecological conditions towards more heterogeneous biotopes with increased seasonality (Begun et al., 2012). Soon after the early/late Vallesian transition (ca. 9.6 Ma), however, hominoids became extinct in Western and Central Europe, with the exception of the insular endemic *Oreopithecus*, which survived until ca. 7 Ma in Italy (Casanovas-Vilar et al., 2011).

In the Iberian Peninsula, dryopithecines are last recorded by *Hispanopithecus* at ca. 9.5 Ma, slightly predating the last occurrence of pliopithecoids ca. 9.0 Ma. The extinction of European hominoids has been linked to the vegetation changes that took place during the late Vallesian (Fortelius and Hokkanen, 2001; Agustí et al., 2003), which further resulted in the extinction of many other mammalian taxa (i.e., the

Vallesian Crisis; see Agustí and Moyà-Solà, 1991; Agustí et al., 1999; Casanovas-Vilar et al., 2010). The climatic trend towards cooling and increased seasonality initiated after the Mid-Miocene Climatic Optimum (Zachos et al., 2001) apparently led to the crossing of some paleoenvironmental threshold, to which hominoids and several other mammals did not adapt (Casanovas-Vilar et al., 2011). This is further supported by the paleoenvironmental reconstruction of Can Llobateres 1 (Marmi et al., 2012), which records one of the latest occurrences of the hispanopithecin *Hispanopithecus laietanus* (9.6 Ma) before its last apperance datum at ca. 9.5 Ma (Casanovas-Vilar et al., 2011). The vegetation from Can Llobateres 1 is consistent with a subtropical to warm-temperate climate, but evidence from other Vallès-Penedès sites indicates that such habitats would have been restricted to lowland humid areas, with warm-temperate mixed forests with a significant proportion of deciduous elements growing elsewhere (Marmi et al., 2012). Following global climatic changes (Zachos et al., 2001), the progressive disappearance of tropical and subtropical plants—providing a continuous supply of fruits all year long—, and the concomitant increasing dominance by deciduous trees, may have resulted in the lack of adequate trophic resources for both hominoids and pliopithecoids during the unfavorable season, ultimately leading to their extinction not only in Iberia but also in the rest of Europe and most of Asia.

The same global changes that, in most of Eurasia, drove the extinction of pliopithecoids and hominoids, probably favored the dispersal and diversification of monkeys. By the Early and Middle Miocene, cercopithecoids were already distinct but much less diverse than hominoids, but from the Late Miocene onwards, their disparity, geographic distribution and paleodiversity increased dramatically (Szalay and Delson, 1979; Jablonski, 2002; Eronen and Rook, 2004; Jablonski and Frost, 2010). This might be related to different dietary adaptations between both groups (Andrews, 1981) and/or to differences in life-history parameters between them (Jablonski and Kelley, 1997). Such factors likely conditioned differently the evolutionary responses of cercopithecoids and hominoids to the changing climatic conditions initiated by the Middle Miocene, but most strongly expressed during the latest Miocene and the Pliocene. Thus, both colobines and cercopithecines possess specific dietary adaptations for more efficient folivory and/or consumption of unripe fruits compared to hominoids (Andrews, 1981), thereby enabling the former to more easily thrive when the ripe fruits habitually consumed by most hominoids are scarce.

Moreover, hominoids display a low life-history profile, suitable for the tropical to subtropical forested conditions with low seasonality of the African Early Miocene, providing an abundant provision of high-quality food resources; in contrast, the faster life history of cercopithecoids is more suitable for the highly seasonal environments that prevailed in Europe by the latest Miocene, thus enabling them to thrive in a wider range of habitats compared to hominoids (Jablonski and Kelley, 1997; Eronen and Rook, 2004). Hence, many latest Miocene and Pliocene cercopithecoid lineages occupied less heavily forested and more seasonal habitats than the preceding hominoids. Two distinct families of cercopithecoids are usually distinguished: crown cercopithecoids are classified into a single family, Cercopithecidae, with two distinct subfamilies (Colobinae and Cercopithecinae), distinguished at the family level by some authors (e.g., Jablonski, 2002); whereas stem cercopithecoids are classified into another, extinct family (the Victoriapithecidae). In the Iberian Peninsula, both cercopithecines and colobines are recorded. Colobines are represented by *Mesopithecus* in the latest Miocene, and by its presumed descendant, *Dolichopithecus*, during the Pliocene. Cercopithecines, in turn, are recorded by *Macaca*, from the latest Miocene onwards, as well as by *Paradolichopithecus* from the Late Pliocene and Early Pleistocene, and *Theropithecus* from the Early Pleistocene.

Until recently, the colobine *Mesopithecus* had not been recorded in the Iberian Peninsula, but recent finds (Montoya et al., 2006; Guillén Castejón, 2010) have shown that this was merely an artifact of the record. At Venta del Moro, *Mesopithecus* is recorded ca. 5.8–5.5 Ma (Montoya et al., 2002, 2006), thus conclusively indicating that *Mesopithecus* dispersed into westernmost Europe by at least the latest Turolian (MN13). Similarly, *Macaca* is recorded by ca. 6.1–5.3 Ma at Almenara-Casablanca M (Köhler et al., 2000). The dispersal of these semi-terrestrial and oportunistic genera into the Iberian Peninsula must be understood within the framework of the significant faunal turnovers that took place in Europe by this time (van der Made, 2006; Agustí et al., 2006), apparently before the first evaporitic cycle of the Messinian Salinity Crisis. This event implied the clousure of the Gibraltar strait, ultimately leading to the total (or almost complete) desiccation of the Mediterranean between 5.5–5.3 Ma (Hsü et al., 1973). At the same time, this created an African-European connection that allowed the dispersal of certain mammal taxa including hippopotamids, gerbils, crested rats and likely cercopithecines as well (Agustí et al., 2006).

Subsequent dispersal and range extension events took place into the Iberian Peninsula during the Pleistocene, as reflected by the record of the gelada *Theropithecus* at ca. 1.0 Ma in Cueva Victoria (Gibert et al., 1995), and that of early *Homo* from ca. 1.2 Ma (Carbonell et al., 2008; Bermúdez de Castro et al., 2011, 2012b) onwards. Throughout the remaining Pleistocene, humans and macaques were apparently the only primates that managed to survive in the Iberian Peninsula and the rest of Europe, being (for different biological reasons) well suited to survive under the changing paleoenvironmental conditions (with marked glacial cycles) of the Pleistocene (Eronen and Rook, 2004). In the case of European macaques, they apparently extended their geographical range much farther northwards during the interglacials, and retreated into their Mediterranean refugia during glacials, although they ultimately became locality extinct due to their inability to tolerate the most severe stage of the last glaciation (Fooden, 2007), being last recorded in Iberia by ca. 80 ka (Castaños et al., 2011). With regard to humans, there is the possibility that different dispersal events of early humans into the Iberian Peninsula and Western Eurasia in general took place during the Pleistocene (Bermúdez de Castro and Martinón-Torres, 2012), thus being still uncertain (see discussion in Madurell-Malapeira et al., 2012) whether humans continuously occupied the Iberian Peninsula between their early record at ca. 1.2 Ma and their subsequent record at ca. 0.88–0.78 Ma (Carbonell et al., 1995; Bermúdez de Castro, 1997).

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Figures and tables

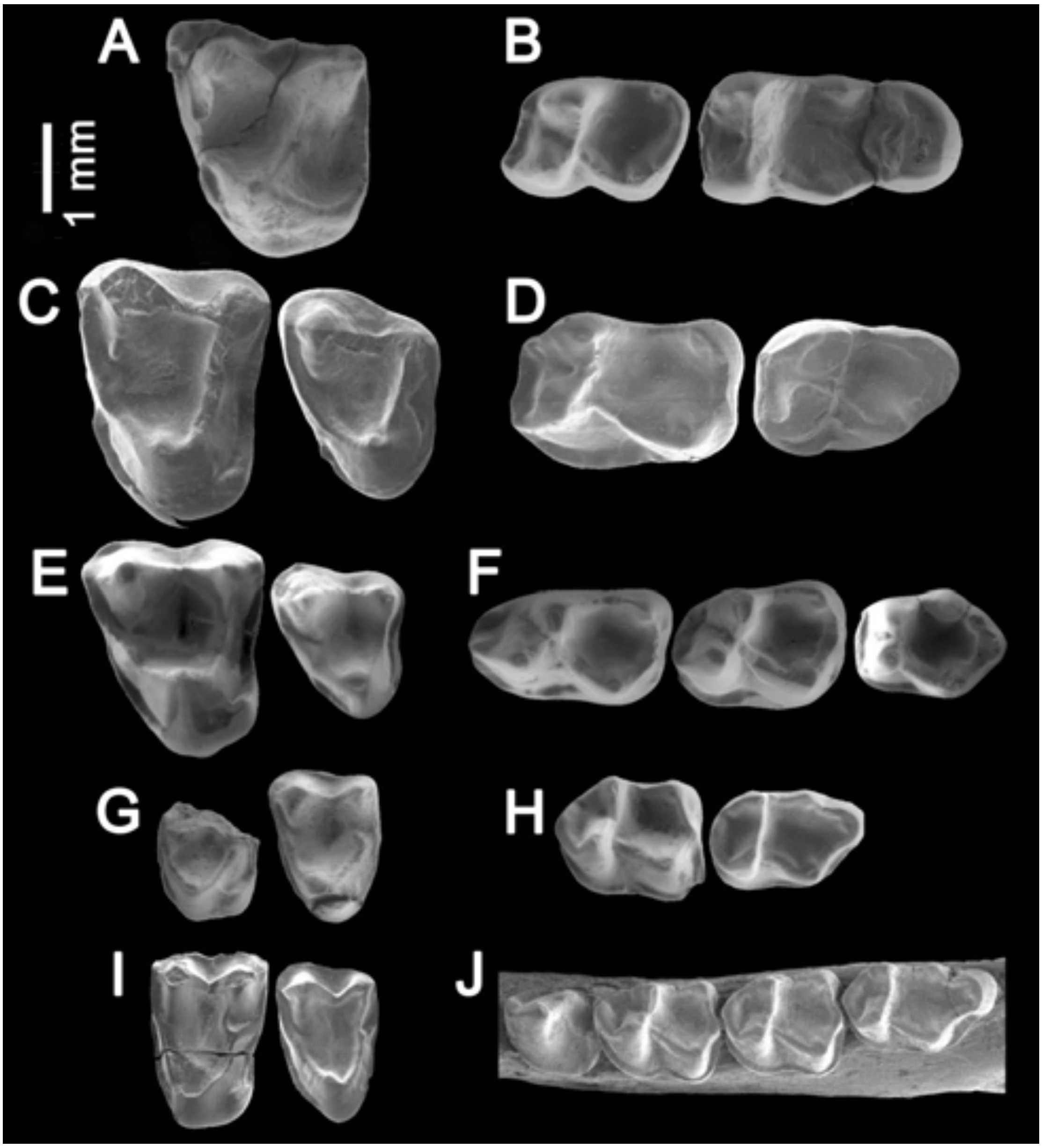

Figure 1. Selected dentognathic remains of fossil primates from the Iberian Paleogene. **A**, Left $M^{1\text{-}2}$ (IPS57508) of *Arcius* sp. from Masia de l'Hereuet; **B**, Right $M_{1\text{-}2}$ (IPS57510, reversed) and right M_3 (IPS57511, reversed) of *Arcius* sp. from Masia de l'Hereuet; **C**, Right $M^{1\text{-}2}$ (IPS46263, reversed) and right M^3 (IPS46266, reversed) of *Mazateronodon endemicus* from Mazaterón; **D**, Left M_2 (IPS46232) and left M_3 (IPS46234) of *Mazateronodon endemicus* from Mazaterón; **E**, Right $M^{1\text{-}2}$ (IPS8429, holotype, reversed) and right M^3 (IPS8423, reversed) of *Anchomomys frontanyensis* from Sant Jaume de Frontanyà 3; **F**, Left M_1 (IPS8543), left M_2 (IPS8487) and right M_3 (IPS8447, reversed) of *Anchomomys frontanyensis* from Sant Jaume de Frontanyà 3; **G**, Right $M^{1\text{-}2}$ (IPS46205, reversed) and right M^3 (IPS46206, reversed) of *Pseudoloris cuestai* from Mazaterón; **H**, Right M_2 (IPS46195, reversed) and left M_3 (IPS46196, holotype) of *Pseudoloris cuestai* from Mazaterón; **I**, Left $M^{1\text{-}2}$ (IPS46335) and right M^3 (IPS46342, reversed) of *Pseudoloris pyrenaicus* from Sant Jaume de Frontanyà 3; **J**, Fragment of a right mandible with P_4-M_3 (IPS46297, holotype, reversed) of *Pseudoloris pyrenaicus* from Sant Jaume de Frontanyà 3.

Figura 1. Restos dentognáticos seleccionados de primates fósiles del Paleógeno ibérico. **A**, $M^{1\text{-}2}$ izquierdo (IPS57508) de *Arcius* sp. de Masia de l'Hereuet; **B**, $M_{1\text{-}2}$ derecho (IPS57510, invertido) y M_3 derecho (IPS57511, invertido) de *Arcius* sp. de Masia de l'Hereuet; **C**, $M^{1\text{-}2}$ derecho (IPS46263, invertido) y M^3 derecho (IPS46266, invertido) de *Mazateronodon endemicus* de Mazaterón; **D**, M_2 izquierdo (IPS46232) y M_3 izquierdo (IPS46234) de *Mazateronodon endemicus* de Mazaterón; **E**, $M^{1\text{-}2}$ derecho (IPS8429, holotipo, invertido) y M^3 derecho (IPS8423, invertido) de *Anchomomys frontanyensis* de Sant Jaume de Frontanyà 3; **F**, M_1 izquierdo (IPS8543), M_2 izquierdo (IPS8487) y M_3 derecho (IPS8447, invertido) de *Anchomomys frontanyensis* de Sant Jaume de Frontanyà 3; **G**, $M^{1\text{-}2}$ derecho (IPS46205, invertido) y M^3 derecho (IPS46206, invertido) de *Pseudoloris cuestai* de Mazaterón; **H**, M_2 derecho (IPS46195, invertido) y M_3 izquierdo (IPS46196, holotipo) de *Pseudoloris cuestai* de Mazaterón; **I**, $M^{1\text{-}2}$ izquierdo (IPS46335) y M^3 derecho (IPS46342, invertido) de *Pseudoloris pyrenaicus* de Sant Jaume de Frontanyà 3; **J**, Fragmento de mandíbula derecha con P_4-M_3 (IPS46297, holotipo, invertido) de *Pseudoloris pyrenaicus* de Sant Jaume de Frontanyà 3.

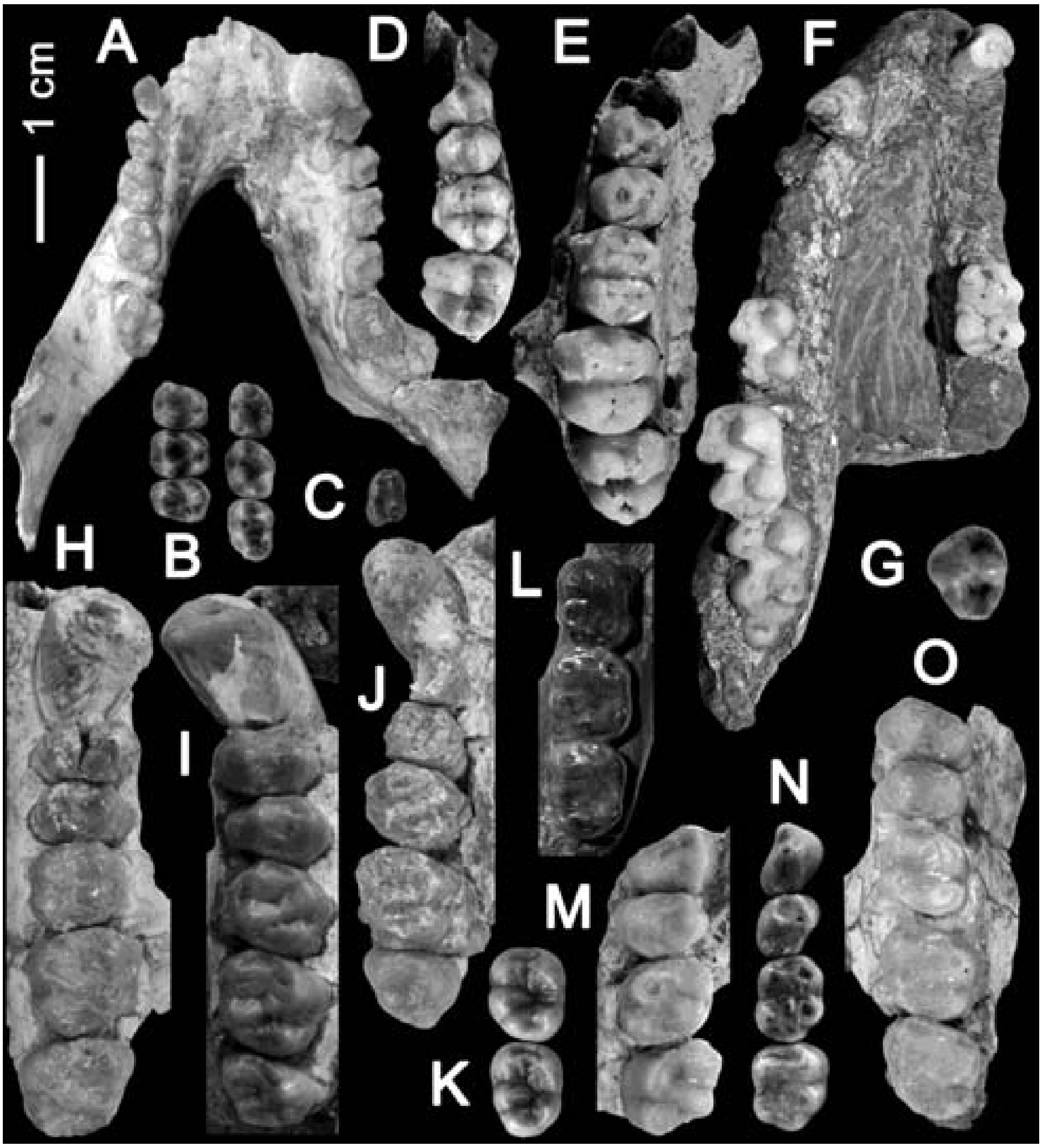
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Figure 2. Selected dentognathic remains of fossil primates from the Iberian Neogene and Quaternary. **A**, Mandible with left P_3-M_3 and right C_1-M_3 (IPS35036, holotype) of *Pliopithecus canmatensis* from ACM/C4-A1; **B**, Right M^1-M^3 and left M_1-M_3 (IPS1724, holotype; M_2 reversed) of *Barberapithecus canmatensis* from Castell de Barberà; **C**, Right dP_4 (IPS35565) of cf. Anapithecini indet. from Can Sant Feliu; **D**, Right P^3-M^2 (EVT24036) of *Macaca sylvanus* cf. *florentina* from Vallparadís Estació; **E**, Right P^3-M^3 (Q05-Ec-88) of *Macaca sylvanus florentina* from Quibas; **F**, Mandible with right M_1-M_3 and left M_1 (Museu del Seminari) of *Paradolichopithecus* sp. from Cova Bonica; **G**, Left P_4 (no catalogue number) of *Theropithecus oswaldi* from Cueva Victoria; **H**, Left C^1-M^3 (IPS35026) of *Dryopithecus fontani* from ACM/C3-Ae; **I**, Right C^1-M^3 (IPS21350, holotype) of *Pierolapithecus catalaunicus* from ACM/BCV1; **J**, Right C^1-M^3 (IPS43000, holotype) of *Anoiapithecus brevirostris* from ACM/C3-Aj; **K**, Left M_2-M_3 (IPS1826+IPS1827, holotype) of *"Sivapithecus" occidentalis* (nomen dubium) from Can Vila; **L**, Mandible with left M_1-M_3 (Museu del Seminari) of *Hispanopithecus crusafonti* from Teuleria del Firal; **M**, Left P^3-M^2 (IPS1798, holotype) of *Hispanopithecus crusafonti* from Can Poncic 1; **N**, Right P_3-M_2 (IPS1803, holotype) of *Hispanopithecus laietanus* from La Tarumba 1; **O**, Right P^3-M^3 (IPS18000.5) of *Hispanopithecus laietanus* from Can Llobateres 2.

Figura 2. Restos dentognáticos seleccionades de primates fósiles del Neógeno y Cuaternario ibéricos. **A**, Mandíbula com P_3-M_3 izquierdos y C_1-M_3 derechos (IPS35036, holotipo) de *Pliopithecus canmatensis* de ACM/C4-A1; **B**, M^1-M^3 derechos y M_1-M_3 izquierdos (IPS1724, holotipo; M_2 invertido) de *Barberapithecus canmatensis* de Castell de Barberà; **C**, dP_4 derecho (IPS35565) de cf. Anapithecini indet. de Can Sant Feliu; **D**, P^3-M^2 derechos (EVT24036) of *Macaca sylvanus* cf. *florentina* de Vallparadís Estació; **E**, P^3-M^3 derechos (Q05-Ec-88) de *Macaca sylvanus florentina* de Quibas; **F**, Mandíbula con M_1-M_3 derechos y M_1 izquierdo (Museu del Seminari) de *Paradolichopithecus* sp. de Cova Bonica; **G**, P_4 izquierdo (sin número de catálogo) de *Theropithecus oswaldi* de Cueva Victoria; **H**, C^1-M^3 izquierdo (IPS35026) de *Dryopithecus fontani* de ACM/C3-Ae; **I**, C^1-M^3 derecho (IPS21350, holotipo) de *Pierolapithecus catalaunicus* de ACM/BCV1; **J**, C^1-M^3 derecho (IPS43000, holotipo) de *Anoiapithecus brevirostris* de ACM/C3-Aj; **K**, M_2-M_3 izquierdo (IPS1826+IPS1827, holottipo) de *"Sivapithecus" occidentalis* (nomen dubium) de Can Vila; **L**, Mandíbula con M_1-M_3 izquierdo (Museu del Seminari) de *Hispanopithecus crusafonti* de Teuleria del Firal; **M**, P^3-M^2 izquierdos (IPS1798, holotipo) de *Hispanopithecus crusafonti* de Can Poncic 1; **N**, P_3-M_2 derechos (IPS1803, holotipo) de *Hispanopithecus laietanus* de La Tarumba 1; **O**, P^3-M^3 derechos (IPS18000.5) de *Hispanopithecus laietanus* de Can Llobateres 2.

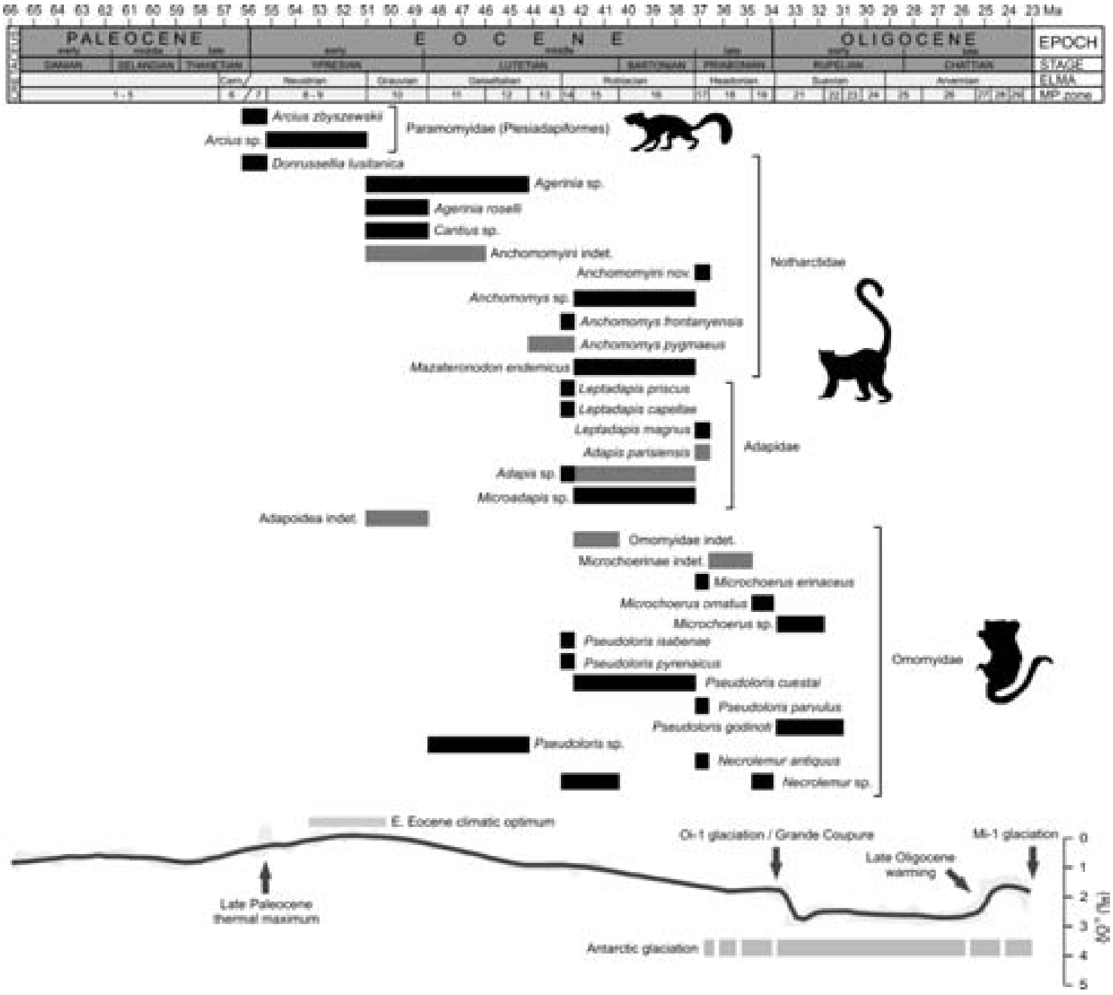

Figure 3. Range chart of Paleogene Iberian primate taxa. Uncertain attributions (cf., indet.) are shown in dark gray, whereas *nomina nuda* and *nomina dubia* are not considered. The global oxygen isotope record, together with the development of ice-sheets and major climatic/physiographic events, are also included. Age boundaries for epochs, stages, European Land Mammal Ages (ELMA) and Paleogene Mammal Zones (MP) are after Luterbacher et al. (2004). Climatic data are taken from Zachos et al. (2001).

Figura 3. Gráfico de rangos de los taxones de primates ibéricos del Paleógeno. Las atribuciones inciertas (cf., indet.) se muestran en gris oscuro, mientras que los *nomina nuda* y *nomina dubia* no se toman en consideración. También se incluyen el registro isotópico global del oxígeno, junto con el desarrollo de los casquetes de hielo y los principales cambios climáticos/fisiográficos. Los límites de edad para las épocas, pisos, Edades de Mamíferos Terrestres Europeos (ELMA) y Zonas de Mamíferos del Paleógeno (MP) se han tomado de Luterbacher et al. (2004). Los datos climáticos se han tomado de Zachos et al. (2001).

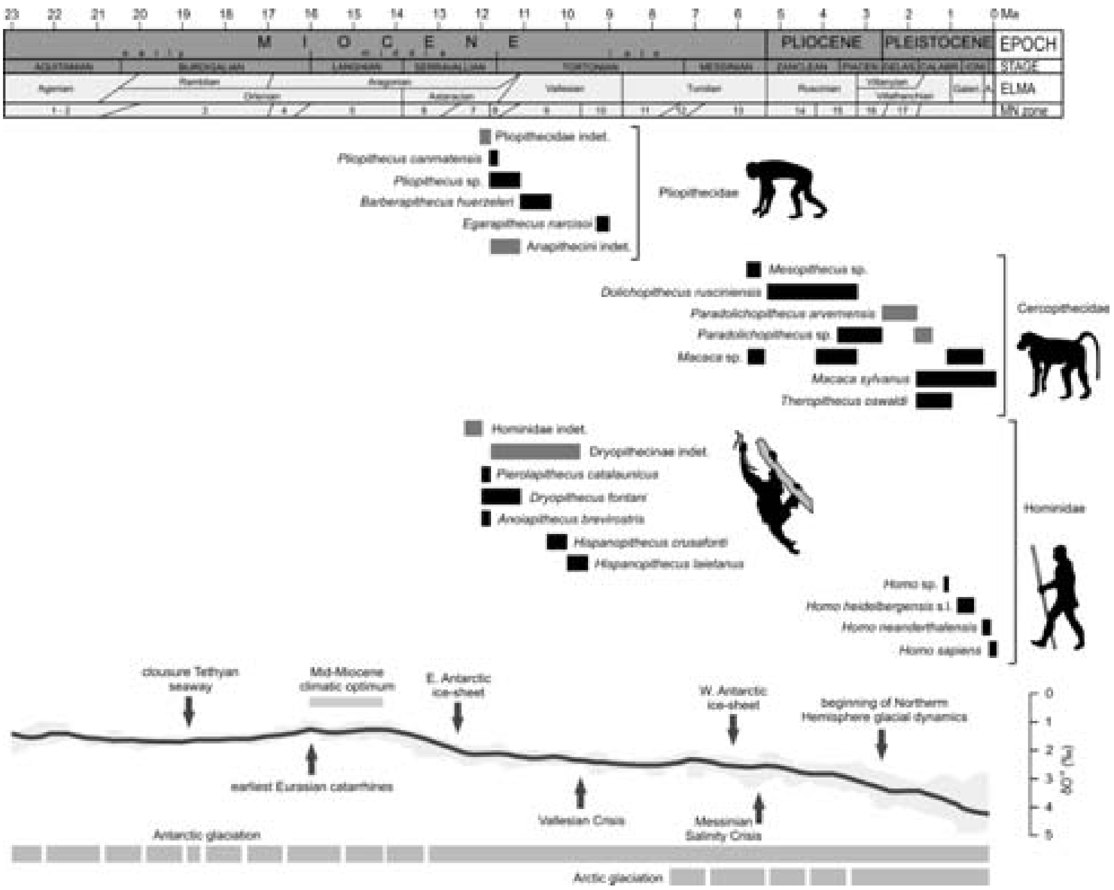

Figure 4. Range chart of Neogene and Quaternary Iberian primate taxa. Uncertain attributions (cf., indet.) are shown in dark gray, whereas *nomina nuda* and *nomina dubia* are not considered. The global oxygen isotope record, together with the development of ice-sheets and major climatic/physiographic events, are also included. Age boundaries for epochs and stages are after Lourens et al. (2004). European Land Mammal Ages (ELMA) and Neogene Mammal Zones (MN) after Steiniger (1999), Agustí et al. (2001), Rook and Martínez-Navarro (2010) and Van der Meulen et al. (2011). Climatic data are taken from Zachos et al. (2001).

Figura 4. Gráfico de rangos de los taxones de primates ibéricos del Neógeno y Cuaternario. Las atribuciones inciertas (cf., indet.) se muestran en gris oscuro, mientras que los *nomina nuda* y *nomina dubia* no se toman en consideración. También se incluyen el registro isotópico global del oxígeno, junto con el desarrollo de los casquetes de hielo y los principales cambios climáticos/fisiográficos. Los límites de edad para las épocas, pisos, Edades de Mamíferos Terrestres Europeos (ELMA) y Zonas de Mamíferos del Neógeno (MN) se han tomado de Steiniger (1999), Agustí et al. (2001), Rook y Martínez-Navarro (2010) y Van der Meulen et al. (2011). Los datos climáticos se han tomado de Zachos et al. (2001).

Tables

- Order **Primates** Linnaeus, 1758
  - Semiorder **Plesiadapiformes**† Simons and Tattersall, 1972
    - Superfamily **Paromomyoidea**† Simpson, 1940
    - Superfamily Plesiadapoidea† Trouessart, 1897
  - Semiorder **Euprimates** Hoffstetter, 1977
    - Suborder **Strepsirhini** Geoffroy Saint-Hilaire, 1812
      - Infraorder **Adapiformes**† Hoffstetter, 1977
        - Superfamily **Adapoidea**† Trouessart, 1879
      - Infraorder Lemuriformes Gregory, 1915
        - Superfamily Lemuroidea Gray, 1821
        - Superfamily Cheirogaleoidea Gray, 1872
        - Superfamily Indrioidea Burnett, 1828
        - Superfamily Daubentonioidea Gray, 1863
      - Infraorder Lorisiformes Gregory, 1915
        - Superfamily Lorisoidea Gray, 1821
    - Suborder **Haplorhini** Pocock, 1918
      - Infraorder **Tarsiiformes** Gregory, 1915
        - Superfamily **Omomyoidea**† Trouessart, 1879
        - Superfamily Tarsioidea Gray, 1825
      - Infraorder **Simiiformes** Hoffstetter, 1974 (=**Anthropoidea** Mivart, 1864)
        - Parvorder Platyrrhini Geoffroy Saint-Hilaire, 1812
          - Superfamily Ceboidea Bonaparte, 1831
        - Parvorder **Catarrhini** Geoffroy Saint-Hilaire, 1812
          - Superfamily Propliopithecoidea† Straus, 1961
          - Superfamily **Pliopithecoidea**† Zapfe, 1960
          - Superfamily **Cercopithecoidea** Gray, 1821
          - Superfamily **Hominoidea** Gray, 1825

Table 1. Primate systematics down to the superfamily rank. Taxa represented in Iberia are shown in bold type. A dagger (†) denotes extinct taxa.

Tabla 1. Sistemática de los primates hasta rango de superfamilia. Los taxones representados en iberia se muestran en negrita. Una daga (†) denota los taxones extintos.