

## New mammals from south-central Pyrenees (Trempe Formation, Spain) and their bearing on late Paleocene marine-continental correlations

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**Key words.** – Mammals, Late Paleocene, Global change, Pyrenees, Spain.

**Abstract.** – Ten mammalian taxa have been recovered from four localities in the upper part of the Trempe Formation (south-central Pyrenees). Its stratigraphic position allows the localities to be correlated with the *Sphaerochara edda* charophyte zone, the lower part of the NP9 nannoplankton zone and magnetochron C24r, below the marine Paleocene/Eocene boundary. Seven of these taxa are described, among them: *Afrodon ivani* PELÁEZ-CAMPOMANES nov. sp., related to other congeneric species from the MP 5-6 mammal units; *Nosella europaea* PELÁEZ-CAMPOMANES nov. gen. nov. sp. also found in the MP 6 Cernay locality, and *Microhyus cf. musculus* TEILHARD DE CHARDIN, similar to the MP 7 Dormaal sample. The mixed composition between Cernaysian and Neustrian faunas of the Trempe sites make/necessary the definition of a new reference level MP 6b with Claret 4 as a reference locality. The new reference level MP 6b is correlated with the lower Clarkforkian Cf 1-2 units, both showing a low species richness and low diversity index comparing with earlier and younger assemblages. This diversity change is related to the late Paleocene Thermal Maximum event, detected in a similar chronological situation (base of C24r chron) in the marine and continental realms. The beginning of the Neustrian reference level MP 7 with highly diversified faunas is correlated with upper Clarkforkian Zone Cf 3, based on faunal composition and the  $\delta^{13}\text{C}$  excursion.

## Nouveaux mammifères du Paléocène supérieur de la formation Trempe (Pyrénées sud-centrales, Lleida, Espagne)

**Mots clés.** – Mammifères, Paléocène supérieur, Événements globaux, Pyrénées.

**Résumé.** – Dix espèces de mammifères ont été trouvées dans quatre gisements situés sous le stratotype de l'étage Ilerdien, dans la partie supérieure de la formation Trempe (Pyrénées Sud-Centrales, Lleida, Espagne). Leur situation stratigraphique permet de les corréliser avec la partie inférieure du chron C24r, en-dessous de la limite Paléocène/Eocène marine. Sept de ces taxa sont décrits, parmi lesquels, *Afrodon ivani* PELÁEZ-CAMPOMANES nov. sp., apparenté à d'autres espèces congénériques du niveau repère MP 5-6; *Nosella europaea* PELÁEZ-CAMPOMANES nov. gen. nov. sp., identifié aussi à Cernay (niveau repère MP 6), et *Microhyus cf. musculus* TEILHARD DE CHARDIN, semblable à celui de Dormaal (niveau repère MP 7). La composition de ces sites est un mélange entre faunes cernaysiennes et neustriennes, ce qui rend nécessaire la définition d'une nouvelle unité biochronologique mammalienne, le niveau repère MP 6b (Claret 4 comme localité de référence). Une corrélation entre les successions de mammifères nord-américains et européens du Paléocène inférieur est proposé sur la base des stades évolutifs des lignées et des premières apparitions des taxa sélectionnés. La nouvelle unité MP 6b est corrélée avec les Zones Cf 1-2 du Clarkforkien inférieur, les deux épisodes caractérisés par une faible richesse spécifique et une faible diversité par rapport aux associations plus anciennes ou plus récentes. Ce changement de diversité est mis en rapport avec le maximum thermique du Paléocène récent détecté dans une position chronologique voisine en milieux marin/et continentaux. Le début du Neustrien MP 7, avec une grande diversité des faunes, est corrélé avec la Zone Cf 3 du Clarkforkien d'après la composition des faunes et l'anomalie du  $\delta^{13}\text{C}$ .

### VERSION FRANÇAISE ABRÉGÉE

Dans les Pyrénées sud-centrales on observe une épaisse série de dépôts d'âge paléocène, avec passage latéral de dépôts de plate-forme marine à des dépôts côtiers et fluviaux. Quatre gisements de vertébrés ont été découverts immédiatement au-dessous du stratotype de l'étage Ilerdien, qui correspond au Paléocène supérieur-Eocène inférieur [Hottinger et Schaub, 1960; Molina *et al.*, 1992; Serra-Kiel *et al.*, 1994]. Les fossiles de vertébrés sont surtout des mammifères et des oiseaux [López-Martínez *et al.*, 1995, 1996; López-Martínez et Peláez-Campomanes, 1998]. Ces gisements peuvent être replacés dans l'échelle chronostratigraphique générale grâce à la présence de niveaux marins datés (foraminifères benthiques et planctoniques, dinocysts et magnétostratigraphie) qui se trouvent en continuité latérale et qui surmontent les niveaux fossilifères.

Les rares mammifères du Paléocène d'Europe sont surtout concentrés dans les bassins de Paris et de Belgique. Les nouveaux sites à mammifères du Paléocène pyrénéen représentent donc une découverte précieuse, située loin des régions les mieux documentées. De plus ils permettent de compléter l'échelle biochronologique des mammifères du début du Tertiaire, où l'on estime avoir 6 unités (MP1-1) presque dépourvues d'information [Schmidt-Kittler, 1987; BiochroM, 1997].

Les dix espèces de mammifères ont été récoltées dans des gisements situés dans la partie supérieure de la formation Trempe près de la localité type (Pyrénées sud centrales, Lleida, Espagne) [Mey *et al.*, 1968]. La formation Trempe comprend environ 900 m de dépôts côtiers et continentaux datés du Campanien supérieur au Thanétien supérieur. Les faciès principaux sont des lutites bariolées, des marnes grises avec lignites, *Cyrena* et huîtres, des calcaires à *Girvanella* avec foraminifères et charophytes, des grès bioclastiques à stratifications entrecroisées et des conglomérats côtiers. La formation Trempe représente le remplissage du bassin pyrénéen pendant la grande régression qui a affecté la plupart des mers épicontinentales du monde durant la transition Crétacé-Tertiaire.

La formation Trempe est surmontée par des calcaires à *Alveolina* et des marnes du Groupe d'Ager correspondant à la transgression marine ilerdienne qui traversa entièrement la péninsule Ibérique du nord-ouest au sud-est. L'étage Ilerdien [Hottinger et Schaub, 1960] est plus jeune que le Thanétien et comprend tout l'Yprésien ainsi que le hiatus entre ces deux étages [Molina *et al.*, 1992; Serra-Kiel *et al.*, 1994]. Selon ces auteurs, la base de l'Ilerdien appartient

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à la biozone NP 9 de l'échelle des nannoplanctons et au Chron C24r de l'échelle paléomagnétique. La limite Paléocène-Eocène (définie sur la zone BB2 des foraminifères benthiques ou la zone P6b des planctoniques) est située dans l'Ilerdien moyen, plus de 150 m au-dessus de la base du stratotype (fig. 1). La formation Tremp peut être corrélée vers l'ouest avec les formations Laspún et Navarri à Campo (Huesca, environ 50 km au nord-ouest de Tremp, fig. 1B), qui contiennent des charophytes, de grands foraminifères benthiques, du nannoplancton et des mammifères d'âge paléocène [Garrido Megías et Rios Aragüés, 1972; Robador *et al.*, 1990; Gheerbrant *et al.*, 1997; Galbrun *et al.*, 1999]. Entre les deux se développe une séquence de paléosols et de brèches d'effondrement d'évaporites dit «horizon de Tremp-Colmenar» [Eichenseer et Krauss, 1985] qui peut être suivie dans la formation Tremp vers l'est jusqu'à plus de 300 m au-dessus des sites à mammifères (fig. 1B).

Les niveaux fossilifères correspondent à des marnes grises intercalées dans une épaisse série d'argiles rouges avec des conglomérats, des grès et des intercalations de gypse qui forment la transition entre les environnements marins et continentaux. Deux gisements sont situés dans la coupe de Claret (stratotype Ilerdien, route de Tremp à Pont de Montanyana), Claret 0 et Claret 4, respectivement à 80 m et 30 m sous la base de l'Ilerdien (fig. 1B). La coupe de Tendruy est à 2 km au nord et à environ 30 m sous les niveaux à *Alveolina*. La coupe la plus élevée, Palau, est à 5 km au sud, au toit de la formation de Tremp, dans une argile noire, riche en petits foraminifères benthiques et coquilles marines. Les trois localités les plus élevées se trouvent à la base de la séquence transgressive ilerdienne [Krauss, 1990].

Environ 250 dents et un nombre indéterminé d'ossements fossiles de mammifères ont été trouvés après lavage-tamassage de 21 tonnes de sédiments (environ 7 tonnes à Claret 4; 5 à Claret 0; 6 à Tendruy et 3 à Palau). D'autres fossiles ont été trouvés : de nombreuses grosses coquilles d'œufs d'oiseaux géants (*Ornitholithus*), surtout à Claret 4, ainsi que des restes de crocodiles, amphibiens, charophytes, graines et *Microcodium*. Les charophytes de la coupe de Claret sont *Peckichara* gr. *varians*, *Maedleriella* aff. *crustellata* et *Maedleriella michelina*, d'âge thanétien [Feist et Colombo, 1983]. Le taxon maastrichtien *Microchara* cf. *crustata* avait été attribué par erreur à la partie inférieure de la coupe [Médus *et al.*, 1988]. Beaucoup de dents de mammifères sont cassées et corrodées; par contre, les coquilles sont pour la plupart intactes. Ceci suggère que certaines dents de mammifères aient été altérées et/ou digérées avant fossilisation [López-Martínez *et al.*, 1996]. D'autres dents sont bien préservées. Il n'y a pas de signes d'érosion mécanique ou de transport.

Au moins dix espèces de mammifères appartenant à quatre ordres ont été reconnues, la plupart à Claret 4 (table I) : Multituberculata (cf. *Hainina* sp.), Insectivora (*Afrodon ivani* n. sp.; *Adapisorex* sp., aff. *Seia* sp.), Proteutheria? (*Nosella europaea* n.gen. n. sp.) et Condylarthra (*Paschatherium* cf. *dolloi*, *Paschatherium* sp., *Microhyus* cf. *musculus*, et cf. *Pleuraspidothierium* sp.). Les premiers indices de Chiroptera [López-Martínez *et al.*, 1995, 1996] n'ont pas pu être confirmés. Sept de ces taxa sont décrits ici. Le genre *Paschatherium*, de loin le plus abondant dans tous les sites de Tremp, sera décrit dans un travail futur et comparé avec le nouveau matériel de Dormaal (Belgique) collecté et étudié par R. et T. Smith.

Un fragment de p4 à Palau et une P3 complète à Claret 4 (fig. 2, 2) correspondent au multituberculé *Hainina*, sans déterminer son attribution spécifique. Deux espèces, *H. belgica* et *H. godfriauxi*, sont connues dans le Paléocène inférieur de Hainin [Belgique, Vianey-Liaud, 1979]. Une espèce du Paléocène supérieur de Cernay a été attribuée à *H. godfriauxi* par Vianey-Liaud [1986], mais diffère de la population type par une taille plus petite et des couronnes de dents plus compliquées [Peláez-Campomanes *et al.*, 1999]. *Adapisorex* sp. est représenté à Claret 4 par une M3 complète (fig. 2, 1) de taille et morphologie semblable à *Adapisorex gaudryi* de Cernay [Russell, 1964; CR4354, Plate V fig. 5a]. Trois fragments de dents de Claret 0 (fig. 2, 3) ont été rapprochées du genre *Seia*, décrit par Russell et Gingerich [1981] dans l'Eocène inférieur du Pakistan, à cause de fortes ressemblances en taille et morphologie (cingulum complet autour du protocône, paraconule rond à convexité postérieure), mais en diffèrent par l'absence de preprotocrista.

*Afrodon ivani* n. sp. PELAEZ-CAMPOMANES (fig. 2, 1-3), espèce dédiée à Ivan Pérez López, est représentée par cinq exemplaires, dont une M2 droite complète à Tendruy (Holotype : TEN 2, fig. 3.1). Elle est très gracile et élargie transversalement, avec un grand protocône comprimé transversalement et une large plate-forme stylière; paraconule et metaconule sont alignés avec une centrocrista droite, et complètement séparés dès leur base; un cingulum postérieur est présent. Dans un autre spécimen apparaît aussi un petit cingulum antérieur et un léger hypocône. La p4 est peu molarisée, avec une cuspidité sur le talonide; la m2 a un petit paraconide, large talonide et cristida oblique connectée à la partie postérieure du trigonide. Ces caractères coïncident avec la diagnose de Gheerbrant et Russell [1989] pour le genre *Afrodon*, à l'exception du postcingulum et precingulum. Le genre *Bustylus* a aussi une centrocrista droite, mais l'espèce cernaysienne diffère par une taille plus grande et des cuspidités stylières très développées [GHEERBRANT, 1995]. Les trois espèces d'*Afrodon* connues (*A. germanicus* (RUSSELL, 1964), *A. chleuhi* GHEERBRANT, 1988 et *A. tagourtensis* GHEERBRANT, 1993) n'ont pas de cingula ni d'hypocône dans leurs molaires. *A. ivani* n. sp. pourrait représenter une espèce plus avancée du genre *Afrodon* qui aurait acquis des cingula et un hypocône [Gheerbrant et Russell, 1991].

*Nosella europaea* n.gen. n.sp. PELAEZ-CAMPOMANES (fig. 3, 4-7) est nommée sur la base d'un spécimen de Claret 4 (Holotype : M1 dex. CLA4-3, fig. 3.4), qui correspond probablement à un prothétherien aussi présent à Cernay (Synonyme : cf. *Abolylestes* sp. in Russell *et al.* [1966, page 851; Plate XXI, fig. 2]). Sa diagnose est : molaires supérieures à large plate-forme stylière délimitée labialement par un cingulum longitudinal; preparacrista dirigée vers le stylocône, au lieu du parastyle; conules développés; M1-2 avec pre- et postcingulum, le dernier avec un hypocône; postmetaconule-crista près du bord labial de la dent; ectoflexus peu développée. M3 transversalement allongée avec postcingulum mais sans hypocône. Molaires inférieures avec paraconide bien différencié, plus bas que le fort metaconide.

La combinaison de caractères de ce taxon est unique, et seulement deux spécimens du bassin de Paris coïncident avec lui : une molaire supérieure (L-121-BR) de Berru décrite par Russell *et al.* [1966] et une autre dent inédite de Cernay (BN CR 11, Muséum d'Histoire Naturelle de Paris). *Nosella* diffère du genre de palaeoryctide *Abolylestes* de Cernay et Walbeck par son hypocône et précingulum bien développés, cuspidités tubulaires, graciles et dents supérieures beaucoup moins élargies transversalement. Szalay [1968] attribua la dent de Berru à un Apatemyidae semblable au genre *Jepsenella*, mais Russell *et al.* [1979] refusent cette attribution. Cette famille a des incisives caractéristiques qui n'ont jamais été trouvées dans les gisements européens, et a des dents à cuspidités moins différenciées des crêtes que *Nosella*.

L'inclusion de *Nosella* dans Pantolestidae par ses ressemblances dans la position et le développement de l'hypocône, des conules et la preparacrista, paroi labiale de P3 droite, et M3 relativement large [voir *Propalaeosinopa* in Krause et Gingerich, 1983] est provisoire, car sa taille est trop petite, les molaires supérieures moins rectangulaires et les couronnes moins robustes.

*Microhyus* cf. *musculus*, TEILHARD de CHARDIN, 1927 (Fig. 3 : 8-9) est représenté à Claret-4 et Tendry par quatre dents et quelques fragments, très semblables aux populations de Dormaal, Suffolk Pebble Beds et Pourcy [MP 7; Teilhard de Chardin, 1927; Louis et Michaux, 1962; Hooker *et al.*, 1980; Sudre et Russell, 1982]: cuspides principales des dents supérieures rapprochées du centre de la dent, conules très petits, hypocône fusionné au métaconule, petit ectoconule antérieur au paraconule, crête postérieure de l'hypocône et M3 réduite. Par contre, la voisine localité de Silveirinha (Portugal) possède un *Microhyus* différent [*M. reisi*, Antunes *et al.*, 1987], de taille plus grande, de dents plus complexes, cuspides stylaires et conules accessoires beaucoup plus développés, cuspides principales moins développées, pre-hypocrista absente [Estravis, 1992]. À Berru on connaît un spécimen attribué à *Microhyus* de très grande taille (approx. 2,8 × 3,6 mm, M1 droite BR-L-3) et de morphologie différente de celle des deux autres espèces: vallées peu profondes, grande plate-forme stylaire, cuspides très proches du centre, sans pré-para-, -proto- et -hypocrista, paroi labiale concave. D'autres formes d'hyopsodontidés des sites cernaysiens diffèrent nettement de *Microhyus*.

Un condylarthre de grande taille est représenté à Palau par une prémolaire inférieure de lait (fig. 2 : 4), attribuée provisoirement à *Pleurospidotherium* par sa forme typiquement lophodonte et gracile, cuspides alternantes et métaconide allongé qui dépasse la cristida obliqua. La taille est bien plus petite que *Pleurospidotherium aumonieri* et *Orthospidotherium edwarsi* du Cernaysien.

La composition de ces faunes est très particulière, avec peu d'espèces et une espèce dominante (70 % de l'association, table I). C'est aussi le cas de la localité voisine de Campo, dominée par *Paschatherium* [Gheerbrant *et al.*, 1997]. La richesse spécifique de Claret 4 apparaît significativement inférieure à celle d'autres localités du Paléocène et de l'Eocène inférieur d'Afrique, d'Europe ou d'Amérique du Nord pour un nombre comparable de spécimens ( $\approx 200$ ) (fig. 4). Pour comparer avec des localités à effectifs plus grands on a calculé la courbe de raréfaction [Hurlbert, 1971], qui montre que Claret 4 n'atteindra pas plus de 15 espèces même si on arrivait à environ 3000 spécimens, c'est à dire un effectif comparable au gisement de Cernay qui lui compte environ 30 espèces. Un échantillon de 157 spécimens de Cernay a été étudié, ce qui permet de vérifier qu'il y a presque 2 fois plus d'espèces qu'à Claret 4 (fig. 4). Ces différences ne sont donc pas dues au nombre de spécimens de l'échantillon. Le biais taphonomique n'est pas non plus une cause probable, car les cinq sites pyrénéens ont des environnements de fossilisation différents, conditions hydrodynamiques très calmes, et pas de tri dû au transport. Les coquilles d'œufs d'oiseaux à Claret 4 sont autochtones, car des fragments ont été recollés. Il est aussi peu probable qu'un tri identique des proies ait opéré sur les cinq types d'environnement. Même si quelques dents appartiennent à des proies digérées, vraisemblablement par les oiseaux, il y a d'autres dents qui ne montrent pas de signe de digestion, et les tailles des mammifères sont beaucoup trop différentes pour avoir été l'objet d'un prédateur unique. L'hétérogénéité des associations est donc une garantie de représentativité de la faune.

Une paléocommunauté de mammifères peu diversifiée pourrait être due à des conditions biogéographiques particulières, comme l'insularité. Cependant, plusieurs des taxons pyrénéens ne sont pas endémiques, mais sont connus dans d'autres régions. Il est donc probable que cette faible diversité soit due à des conditions paléoclimatiques sévères pendant une période de temps significative. Une période de détérioration climatique est également détectée en Amérique du Nord pendant le Clarkforkien. Ces deux épisodes peuvent être corrélés entre eux et avec les changements climatiques enregistrés dans les dépôts océaniques.

En Europe les mammifères cernaysiens (MP6) et neustriens (= « Sparnacien », MP7-9), se distinguent par l'apparition de marsupiaux, carnivores, rongeurs, chauves-souris, dermoptères, euprimates, artiodactyles et perissodactyles [Schmidt-Kittler, 1987; BiochroM, 1997]. Dormaal (localité de référence de MP 7), Silveirinha, Fordones et Rians appartiennent au Neustrien ancien par la présence de ces immigrants, et Cernay et Berru appartiennent au Cernaysien (MP 6) par l'absence des immigrants et la présence de taxons particuliers, surtout des condylarthres. Les localités du Paléocène pyrénéen partagent avec les faunes cernaysiennes les mammifères *Hainina*, *Afrodon*, *Nosella*, *Adapisoorex*, l'abondance de condylarthres et l'absence d'immigrants neustriens. Cependant, les condylarthres *Paschatherium* cf. *dolloi* et *Microhyus* cf. *musculus* sont justement connus à partir de MP 7. La dominance de *Paschatherium* confère une forte ressemblance entre Tresp, Dormaal et Silveirinha. Quelques espèces inédites de ce genre sont aussi présentes à Cernay, mais elles ne sont pas dominantes et ont en général une taille plus grande. Les faunes de Tresp seraient donc chronologiquement intermédiaires entre celles du Cernaysien et du Neustrien. Ceci rend nécessaire la définition d'une nouvelle unité biochronologique mammalienne, MP 6b, dans la succession biochronologique standard de mammifères (Claret 4 comme localité de référence, voir figure 5). Elle est provisoirement incluse dans le Cernaysien car elle est antérieure à la vague migratoire caractéristique du Neustrien.

L'unité MP6b peut être calibrée à l'aide de repères chronologiques. La corrélation des sites de Tresp avec la zone de charophytes *Sphaerochara edda* confirme sa position chronologique plus ancienne que les sites neustriens qui sont corrélés avec la zone *P. disermas* [Hooker, 1996, 1999]. Les sites de Tresp se corrélaient avec le Chron paléomagnétique C24r qui correspond à la base de la séquence ilderienne [Serra Kiel *et al.*, 1994]. La localité de Campo peut également correspondre avec le même Chron C24r, car deux intervalles de polarité normale se trouvent au-dessous, Chrons C25n et C26n [Serra Kiel *et al.*, 1994; Galbrun *et al.*, 1999; fig. 1B, a-b]. Cette localité est dans une intercalation continentale corrélée avec la zone de dinocysts «*Wetzeliella*» *hyperacantha* [Caro *et al.*, 1975] située entre la partie supérieure de la zone *Glomalveolina primaeva* et la zone *G. laevis* [Tambareau *et al.*, 1992]. Les calcaires marins de la zone de nannoplancton NP8 sont au-dessous, non dans l'intercalation continentale [Kapellos et Schaub, 1975 versus Gheerbrant *et al.*, 1997]. Cet épisode régressif se retrouve dans les Pyrénées du Nord et de l'Ouest, et les bassins de Paris et du Nord de l'Europe [Tambareau *et al.*, 1995; Pujalte *et al.*, 1998; Dupuis *et al.*, 1998], représenté par un hiatus entre les zones de nannoplancton NP8 et NP9 qui correspond à un changement majeur entre les zones de dinocysts *Deflandrea speciosa* et «*Wetzeliella*» *hyperacantha* [Caro *et al.*, 1975].

Si cette chronologie est correcte, l'intervalle de temps entre les unités MP 6a et MP 7 doit être plus grand que prévu d'après les corrélations marin-continental des bassins nord européens [Hooker, 1999]. Un hiatus doit exister dans le bassin de Paris entre les grès de Berru – marnes de Montchenot et les plus anciens niveaux neustriens (Marnes à rognons, conglomérat à *Coryphodon*). Ce hiatus correspondrait à celui qui existe entre NP8 et NP9 dans les successions marines.

La nouvelle unité MP 6b aide à corréler les successions de mammifères nord-américaines et européennes du Paléogène inférieur, où deux hypothèses sont opposées : le début du Neustrien en Europe corrélié avec le début du Wasatchien en Amérique du Nord [Wa 0, Gingerich, 1989; Hooker, 1991] ou corrélié avec le Clarkforkien récent [Cf 3, Godinot, 1982; 1996]. Cernay a été corrélié avec le Tiffanien 5 [Krause et Maas, 1990] sur la base des genres communs *Neoplagiaulax* et *Adunator* (= *Mckennatherium*) qui disparaissent au Clarkforkien. L'unité MP6b remplit donc le vide existant dans la succession européenne, représentée en Amérique du Nord par le Clarkforkien ancien-moyen (Cf 1-Cf 2). Cette corrélation s'accorde avec la proposition de Butler *et al.* [1980] et Rapp *et al.* [1983], qui placent les unités Cf 2-3 dans la partie inférieure du Chron paléomagnétique C24r, comme les localités espagnoles. Dans la figure 5 on voit les corrélations proposées entre les faunes de mammifères d'Europe et d'Amérique du Nord basées sur la distribution des taxons sélectionnés.

Les deux épisodes corréliés MP 6b et Clarkforkien inférieur Cf 1-2 sont caractérisés par une faible richesse spécifique et une faible diversité par rapport aux associations plus anciennes et plus récentes. L'épisode ultérieur du début du Neustrien MP 7, avec une grande diversité des faunes, peut être corrélié avec le Clarkforkien Cf 3. Ce changement de diversité peut être interprété comme une réponse à un changement climatique global. Les corrélations entre dépôts marins et continentaux dans le bassin de Tremp-Graus suggèrent que les faunes MP 6b sont antérieures à la limite Paléocène-Eocène, définie par les nannoplanctons, foraminifères benthiques et planctoniques, située plus de cent mètres au-dessus des sites à mammifères de Tremp et Campo (fig. 1B). Les corrélations proposées sont renforcées par la position chronologique de l'anomalie du  $\delta^{13}\text{C}$  (maximum thermique du Paléocène final [Koch *et al.*, 1992; Cojan *et al.*, 1998; Steurbaut *et al.*, 1999; Fig. 5]).

## INTRODUCTION

Palaeoenvironmental events during the Paleocene are becoming well documented in the marine realm, although they remain poorly known in the continental realm. The geological record in the south-central Pyrenees contains thick deposits of this period, laid down in a laterally continuous setting from the land to the basin. The Ilerdian Stage which spans the Upper Paleocene to Lower Eocene has been defined there, dated by means of planktic and benthic foraminifera, dinocysts and palaeomagnetism [Hottinger and Schaub, 1960; Molina *et al.*, 1992; Serra-Kiel *et al.*, 1994]. Just below this stratotype, four fossil sites have been found containing mammals as well as other vertebrate and plant remains [López-Martínez *et al.*, 1995, 1996; López-Martínez and Peláez-Campomanes, 1998]. Its situation allows to correlate these continental fossil sites with the general chronostratigraphical scale.

Paleocene mammals are rare fossils in Europe, mainly concentrated in the Belgian and Paris basins. A wide gap of information remains to be filled, since the estimated 6 units of the Paleocene mammal biochronological scale still remain largely empty [Mainz congress, Schmidt-Kittler, 1987; Montpellier congress; Biochron'97, 1997]. The new Upper Paleocene Pyrenean mammal sites thus represent a rare discovery situated far from the best documented region.

Here we describe some of these mammals, define two new taxa and discuss their chronostratigraphic and pa-

laeoenvironmental position, using marine-continental stratigraphic correlations and the interpretation of sample diversity in relation with other late Paleocene faunas from North America and Europe.

## GEOLOGICAL SETTING

The four fossil sites are situated in the upper part of the Tremp Formation in the type area, near the city of Tremp (Lleida, Spain, fig. 1A). This formation, also called «Garumnian» facies, has been studied in its type area by many authors but it had never yielded fossil mammals before [see Krauss, 1990 and references therein]. The Tremp Formation red beds consist of up to 900 m of coastal and continental deposits ranging in age from late Cretaceous (late Campanian) to late Paleocene (late Thanetian). Marine influence is detected in the form of transitional lagoonal and estuarine facies among the floodplain variegated claystones (grey marls with *Cyrena* and oysters, *Girvanella* limestones with foraminifera and charophytes, bioclastic sandstones and wave-reworked conglomerates). It represents the infilling of the Pyrenean late Cretaceous foredeep basin, during a major regressive cycle affecting most epicontinental marine basins of the world.

The top of the Tremp Formation is overlain by the *Alveolina*-bearing limestones and marls of the Ager Group, marking the major Ilerdian marine transgression which

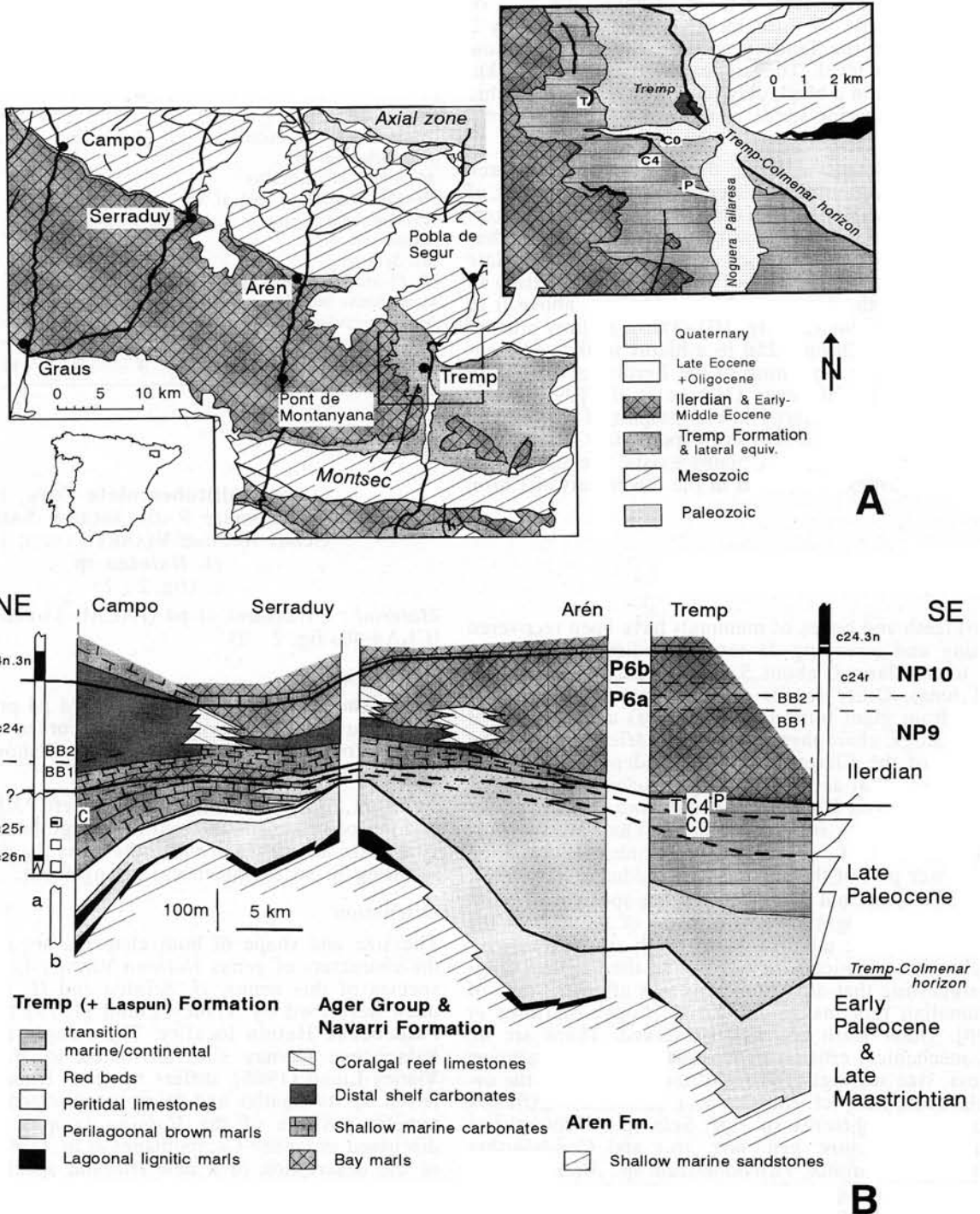
FIG. 1. – Geological setting of the mammalian fossil localities of the Tremp Formation. A) Geological map of the south-central Pyrenees. See location of the fossil sites in the detailed map insert [based in Krauss, 1990]; legend as in fig. 1B; thick lines correspond to conglomeratic levels. B) Stratigraphic cross-section of the northern outcrops of the Tremp-Graus basin (sections located in figure 1A; modified from Eichenseer and Krauss [1985] and Serra-Kiel *et al.* [1994]). The magnetostratigraphic successions are (a) correlated across the entire cross section, according to Serra-Kiel *et al.* [1994] and (b) the Campo section according to Galbrun *et al.* [1999]. Three biochronostratigraphic markers are situated : planktonic foraminifer boundary zones P6a/6b, benthic foraminifer boundary zones BB1/BB2 (Paleocene/Eocene boundary) and nannoplancton boundary zones NP 9/10. C = Campo; C0-C4 = Claret 0 and 4; P = Palau, T = Tendrúy.

FIG. 1. – Situation géologique des gisements de mammifères de la formation Tremp. A) Carte géologique des Pyrénées centrales méridionales. Voir localisation des sites fossilifères dans la carte détaillée de l'encadré [d'après Krauss, 1990; légende *idem* à fig. 1B; les lignes courbes épaisses correspondent aux niveaux conglomératiques]. B) Coupe stratigraphique des affleurements septentrionaux du bassin de Tremp-Graus (coupes localisées sur la figure 1A [modifié de Eichenseer et Krauss, 1985 et Serra-Kiel *et al.*, 1994]). Les successions magnétostratigraphiques sont (a) corréliées à travers toute la coupe, d'après Serra-Kiel *et al.* [1994] et (b) la coupe de Campo d'après Galbrun *et al.* [1999]. Trois limites de zones biostratigraphiques sont positionnées : zones P6a/6b des foraminifères planctoniques, zones BB1/BB2 des foraminifères benthiques (considérée comme limite Paléocène/Eocène) et zones NP 9/10 des nannoplanctons. C=Campo; C0-C4=Claret 0 et 4; P=Palau, T=Tendrúy.

crossed the entire Iberian Peninsula from Northwest to Southeast. The Ilerdian Stage [Hottinger and Schaub, 1960] is younger than the Thanetian Stage, and overlaps the entire Ypresian Stage and the gap between both stages [Molina *et al.*, 1992; Serra-Kiel *et al.*, 1994]. According to these authors, the base of the Ilerdian belongs to the NP 9 nannoplankton zone and is included in Chron C24r, thus late Paleocene in age. The Paleocene-Eocene boundary (either base of benthic zone BB2, or planktic foraminifera zone

P6b) is situated in the middle Ilerdian, more than 150 m above the Ilerdian lower limit.

The Tremp Formation thins westward to Campo (Huesca, about 50 km northwest of Tremp, figure 1B). It is represented by the laterally equivalent Laspún and Navarri Formations, about 150 m thick, dated as Paleocene by charophytes, large foraminifer, nannoplankton and mammals [Garrido Megías and Rios Aragües, 1972; Robador *et al.*, 1990; Gheerbrant *et al.*, 1997; Galbrun *et al.*, 1999].



Between the Laspún and Navarri Formations, a soil catena and evaporite collapse breccias called the «Trempe-Colmeñar horizon» [Eichenseer and Krauss, 1985; figure 1] can be traced eastward within the Trempe Formation, more than 300 m below the level of mammalian fossil sites in the Trempe area (fig. 1B).

The beds with mammalian fossils consist of grey marls, intercalated in a thick succession of red clays with conglomerates, sandstones and gypsum levels transitional between marine and non-marine environments. Two localities are situated in the Claret section (Ilerdian stratotype, road from Trempe to Pont de Montanyana). Of these, the lower locality Claret 0 is 80 m below the base of the Ilerdian, and the upper and richest site Claret 4 is 30 m below the base of the Ilerdian (fig. 1B). A third locality is situated nearly 2 km to the north in the Tendruy section, about 30 m below the first *Alveolina* level. The highest locality, Palau, 5 km south of Trempe, is in a black clay level rich in small benthic foraminifers and marine shells just at the top of the Trempe Formation.

According to Krauss [1990], the position of the three uppermost mammalian localities corresponds to the base of the sedimentary sequence initiating the Ilerdian transgression. The palaeomagnetic polarity of this succession has been measured by Serra-Kiel *et al.* [1994], who correlate the normal interval at the base of the Navarri Formation to Chron C26n, and the reverse polarity sequence above it to Chrons C25r and C24r (see fig. 1B). These authors attributed the absence of Chron C25n to a hiatus in the sedimentation situated at the beginning of the Ilerdian sedimentary sequence (fig. 1B.a). However, Galbrun *et al.* [1999] report a sample with normal polarity in the midpart of the Navarri Formation, which thus would correspond to Chron C25n (fig. 1B.b). Whether or not a hiatus exists, the uppermost mammalian localities would fall in the lower part of Chron C24r.

## SYSTEMATIC PALAEOLOGY

The fossil teeth and bones of mammals have been recovered by washing and screening 21 tons of sediments (Claret 4 about 7 tons, Claret 0 about 5 tons, Tendruy, 6 tons and Palau, 3 tons). Other fossils are abundant thick eggshell fragments from giant birds (*Ornitholithus*) and remains of crocodiles, frogs, charophytes, seeds and *Microcodium*. The charophytes of the Claret section were identified by Feist and Colombo [1983] as *Peckichara* gr. *varians*, *Maedleriella* aff. *crustellata* and *Maedleriella michelina*. These authors dated this assemblage in the Thanetian. The Maastrichtian taxon *Microchara* cf. *crustata* was erroneously reported from the lower part of the section [see Médus *et al.*, 1988].

About 250 teeth and fragments of ten species of mammals have been recognized so far, most of them from the locality Claret 4 (see table I). Many teeth are badly corroded by abrasive chemicals, in contrast to the eggshell fragments, suggesting that digestion processes affected some of the mammalian remains before burial [López-Martínez *et al.*, 1996]. Other teeth are well preserved. There are no signs of mechanical erosion or traction by lateral transport (roundness, size sorting). The fossil teeth belong to the orders Multituberculata (cf. *Hainina* sp.), Insectivora (*Afrodon ivani* nov. sp.; *Adapisorex* sp., aff. *Seia* sp.), ?Proteutheria (*Nosella europaea* nov. gen. nov. sp.) and Condylarthra (*Paschatherium* cf. *dolloi*, *Paschatherium* sp., *Microhyus* cf. *musculus*, cf. *Pleuraspidothierium* sp.). The first poor indices of the presence of Chiroptera have not yet been confirmed [López-Martínez *et al.*, 1996]. We figure and describe here seven out of the ten taxa, namely two new

taxa (*Afrodon ivani* n. sp. and *Nosella europaea*) and five other taxa already known or poorly characterized (cf. *Hainina* sp., *Adapisorex* sp., aff. *Seia* sp., cf. *Pleuraspidothierium* sp. and *Microhyus* cf. *musculus*). The genus *Paschatherium*, by far the most abundant in the Trempe assemblages will be described in a future work, and compared with the new material from Dormaal (Belgium) collected and studied by R. and T. Smith.

TABLE I. – Mammalian taxa and number of specimens identified in the four localities of the upper part of the Trempe Formation, Upper Paleocene (Spain).

TABLE I. – Mammifères et nombre de spécimens identifiés dans les quatre localités de la partie supérieure de la formation Trempe, Paléocène supérieur (Espagne).

Taxa	Claret 0	Claret 4	Tendruy	Palau	Total
<i>Paschatherium</i> cf. <i>dolloi</i>	3	160	4	2	169
<i>Paschatherium</i> sp.		20			20
<i>Microhyus</i> cf. <i>musculus</i>		7	2		9
<i>Nosella europaea</i> n. gen. n. sp.		12			12
<i>Afrodon ivani</i> n. sp.		1	4		5
<i>Adapisorex</i> sp.		1			1
aff. <i>Seia</i> sp.	3				3
cf. <i>Pleuraspidothierium</i> sp.				1	1
Condylartha indet.	2	9	1		12
Multituberculata cf. <i>Hainina</i> sp.		1		1	2
Total	8	211	11	4	234

Order **Multituberculata** COPE, 1884

Family Kogaionidae RADULESCU & SAMSON, 1996

Genus *Hainina* VIANEY-LIAUD, 1979

cf. *Hainina* sp.

(fig. 2 : 2)

*Material* : a fragment of p4 (PALAU-1) and a complete P3 (CLA4-40, fig. 2 : 2)

### Description

**p4.** The fragment of a blade-shaped p4 preserves the anterior part of the crown with four curved ridges, and the anterior root. The border of the enamel shows a strong expanded inflexion over the root.

**P3.** (1,52 × 0,86 mm). Complete left P3 having four buccodent, paired cusps in front of a large basin. The two lingual cusps are closer to each other than the two labial cusps, resulting in an asymmetrical arrangement.

### Discussion

The size and shape of both elements are compatible with the characters of genus *Hainina* VIANEY-LIAUD, 1979. Two species of this genus, *H. belgica* and *H. godfriauxi*, have been described by Vianey-Liaud [1979] from the Lower Palaeocene Hainin locality. The sample from the Upper Palaeocene Cernay site, attributed to *H. godfriauxi* by Vianey-Liaud [1986], differs however from the type population by its smaller and more complicated teeth. The systematic position of the *Hainina* sample from Cernay is discussed in Peláez-Campomanes *et al.* [1999], in the frame of the description of a new *Hainina* species from the lowermost Paleocene of the Pyrenees, and the revision of the phylogeny and systematics of this genus. The small sample from Trempe does not allow to determinate its specific attribution.

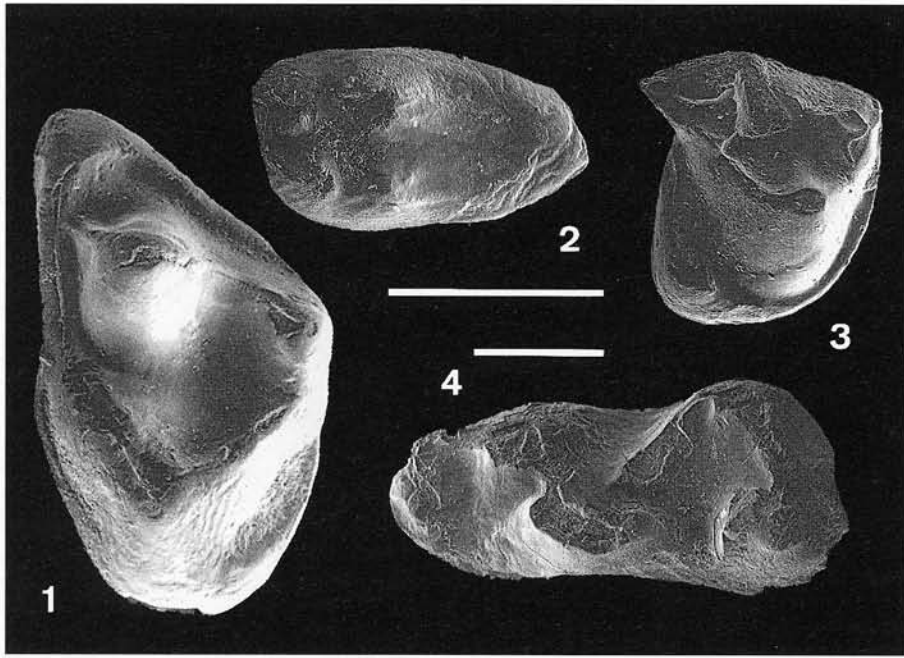


FIG. 2. – Mammals from the Upper Paleocene of the Tremp Formation. 1 : *Adapisorex* sp., left M3, CLA4-9, Claret 4. 2 : cf. *Hainina* sp., left P3, CLA4-40, Claret 4. 3 : aff. *Seia* sp., labial fragment of a left M2, CLA0-1, Claret 0. 4 : cf. *Pleuraspidothierium* sp., right dp4, PALAU-1, Palau de Noguera (Lleida). Collections in deposit at the Departamento de Paleontología, Universidad Complutense de Madrid (Spain). Scale bar = 1 mm.

FIG. 2. – Mammifères du Paléocène supérieur de la formation Tremp. 1 : *Adapisorex* sp., M3 gauche, CLA4-9, Claret 4. 2 : cf. *Hainina* sp., P3 gauche, CLA4-40, Claret 4. 3 : aff. *Seia* sp., fragment labial d'une M2 gauche, CLA0-1, Claret 0. 4 : cf. *Pleuraspidothierium* sp., dp4 droite, Palau-1, Palau de Noguera (Lleida). Collection déposée au Département de Paléontologie, Université Complutense à Madrid (Espagne). Echelle = 1 mm.

Order **Lipotyphla** HAECKEL, 1866  
 Suborder **Erinaceomorpha** SABAN, 1954  
 Family ? Erinaceidae BONAPARTE, 1838  
 Genus *Adapisorex* LEMOINE, 1883  
*Adapisorex* sp.  
 (fig. 2 : 1)

**Material** : a right M3 (CLA4-9, fig. 2 : 1).

#### Description

**M3** (1,14 × 1,95 mm) is a robust molar with a triangular shape. The three main cusps are connected by ridges isolating a triangular basin in the middle of the crown. The metacone is reduced in relation with the paracone. The paraconule is weak and the metaconule is absent. A strong parastyle in anterolabial position is connected to the preparaconule-crista. The preparacrista joints this crest and is longitudinally oriented, aligned with the straight centrocrista. A low hypocone and postcrista are well formed in the posterior wall of the teeth.

#### Discussion

The M3 from Claret-4 is easily distinguished from other M3 attributed to *Paschatherium* from the Tremp sample by its larger size, more robust shape, stronger protocone, preparaconule-crista obliquely oriented, and by the absence of metaconule and premetaconule-crista. Its size and morphology coincides well with CR4354 from Cernay, attributed to *Adapisorex gaudryi* by Russell [1964, Plate V, Fig. 5a]. Although the documented evidence is scarce and the specific attribution is not reliable in this case, the characters observed in this element coincide well with the generic pattern and thus it is called *Adapisorex* sp.

Order **Lipotyphla** HAECKEL, 1866  
 Suborder ?**Erinaceomorpha** SABAN, 1954  
 Family indet.  
 Genus ? *Seia* RUSSELL & GINGERICH, 1981  
 aff. *Seia* sp.  
 (fig. 2 : 3)

**Material** : a fragment of a right upper second molar (CLT0-2, fig. 2 : 3), a lower premolar (CLT0-1) and a fragment of lower molar (CLT0-4).

#### Description

**M2**, (1,10 × – mm). Only the lingual part of the tooth is preserved. The high, sharp protocone is completely surrounded by a cingular crest, which connects the precingulum to the hypocone. The paraconule is round-shaped, close to the protocone but not connected to it. The postparaconule-crista is only a shallow convexity of the posterior wall of the paraconule. There is not preprotocrista. The straight postprotocrista connects with a sharp metaconule with well developed crests. The postcrista reaches the posterior part of the postmetaconule-crista. The position of the metaconule is somewhat labial in relation to the paraconule.

**p3** (1,36 × 0,66 mm). A simple morphology with a single protoconid and a very small talonid.

**m1-2**. (– × 1,3 mm). A fragment of trigonid with sharp cusps, a protoconid obliquely directed forwards and a low but massive paraconid. A short cingulid is present on the anterolabial wall of the protoconid.

#### Discussion

The peculiar morphology of this upper tooth, with a complete cingulum around the protocone, has been compared

with different taxa, such as Paraprimates (*Berruvius*) and Insectivora (*Seia*), both sharing this character with the Claret-0 sample. The size of the Tremp specimens is however much larger than the described *Berruvius* species. The size of the erinaceoid *Seia shahi*, described by Russell and Gingerich [1981] from the lower Eocene of Pakistan, is very close to our specimens. The first molar of *Seia shani* shows a paraconule more labial than the metaconule, while its second molar has a reversed position. The Tremp specimen coincides thus with the shape of the second molar. This taxon shares also with that from Claret-0 the complete labial cingulum and the peculiar rounded paraconule with a shallow convexity instead of postparaconule-crista. It differs by the absence of preprotocrista and by the more proximal position of the protocone in the Spanish specimen. The lower teeth of this taxon are unknown; the two specimens from Claret-0 are associated with the upper ones because of their congruent size.

The peculiar taxon from Claret-0 shows closer affinity to the Asiatic *Seia* than to any other European, African or American taxa known by us, although the similarities between them can be considered not enough for an assertive identification. The differences in morphology between both samples lead us to name our material aff. *Seia* sp.

Order ?**Lipotyphla** HAECKEL, 1866

Family Adapisoriculidae VAN VALEN, 1967

Genus *Afrodon* GHEERBRANT, 1988

*Afrodon ivani* n. sp. PELAEZ-CAMPOMANES  
(fig. 3 : 1-3)

*Holotype*. – M2 dex. TEN-1 (fig. 3 : 1).

*Type locality*. – Tendrú (Lleida, Spain).

*Etymology*. – In honour to Mr. Iván Pérez López for his help during the field work.

*Diagnosis*. – Taxon similar in size and morphology to the other species included in the genus *Afrodon* but differing in having small postcingulum and precingulum.

*Material*. – A fragment of M1-2 (TEN-18), a complete M2 (TEN-1, holotype, fig. 3 : 1), a complete m2 (TEN-2, fig. 3 : 2) and a fragment of a lower molar very corroded in which only the trigonid without enamel has been preserved. This taxon may also be present in Claret-4 as inferred from a lower p4 (CLA4-17, fig. 3 : 3) of corresponding size.

#### *Description*

**M2** (1,23 × 1,86 mm). – Molar very elongated transversally, with stylar shelf well developed; large protocone compressed antero-posteriorly; paracone and metacone well individualised, and connected longitudinally by a centrocrista. The long preparacrista and postmetacrista run transversally, almost parallel to one another. It is not possible to observe the presence of styles in the labial border because the enamel in this region is missing. However, a swelling is present in the position occupied by the stylocone in other adapisoriculids. The pattern of the dentine indicates that this molar probably had a stylar cingulum with strong styles. The conules are well developed and both have distinct anterior and posterior crests. The postmetaconule-crista reaches only the lingual base of the metacone. The paraconule is closer to the protocone than is the metaconule. The lingual side of the paracone reaches a more lingual position than that of the slightly smaller metacone. A small posterior cingulum is present.

**M1-2** (0,63 × --- mm). Only the lingual half of the tooth is present. The protocone is high and sharp. The paraconule and metaconule are well developed and both have distinct anterior and posterior crests. There are a small lingual cingulum and a small hypocone-like posterior cingulum.

**p4** (1,3 × --- mm). Poorly molarized premolar, with a low paraconid anterior to protoconid and metaconid. The

latter is slightly more posterior than the protoconid. It shows a posterior crest running towards the entoconid. The talonid is broadly open labially and not basined, with only a cusp which represents probably the entoconid.

**m2?** (1,28 × 0,9 mm). – The trigonid and the talonid have approximately the same width. The cusps are sharply pointed. The precingulid is well developed. The paraconid is broken, but seems to have a lower position than the other two trigonid cusps. The metaconid is slightly more posterior than the protoconid and both have a similar height. The metaconid shows a postero-lingual crest descending towards the entoconid. The hypoconid is the most voluminous cusp of the talonid. The hypoconulid is slightly closer to the entoconid than to the hypoconid. The talonid basin is rather deep and semicircular. The cristid obliqua connects to the posterior wall of the trigonid in a low and lingual position.

#### *Discussion*

The assignment of this material to the family Adapisoriculidae seems clear after the diagnosis proposed by Gheerbrant and Russell [1989]. The diagnostic characters are: upper molars transversally elongated; stylar cusps well developed; stylar shelf rather wide and preparacrista and postmetacrista long; paracone and metacone completely separated at their base; lower molars with moderate difference in height between trigonid and talonid; cristid obliqua extended up onto the lingual side of the posterior wall of the trigonid. All these diagnostic characteristics are present in our material, even if the well developed stylar cusps can be only inferred because of the preservation of the material.

*Afrodon ivani* n. sp. shows a more primitive dental pattern than *Adapisoriculus* or *Remiculus* do, because it does not have either the mesostyle or the dilambdodont morphology typical of these genera [Gheerbrant, 1995]. The genera *Bustylus* and *Afrodon* show a straight centrocrista mesiodistally oriented as in the Tremp sample. *Bustylus*, however, differs from *Afrodon ivani* by its larger size and by its strongly-developed stylar cusps.

The main morphological difference between *Afrodon ivani* and the other three species of the genus (*A. germanicus* (RUSSELL, 1964), *A. chleuhi* GHEERBRANT, 1988 and *A. tagourtensis* GHEERBRANT, 1993) is its small anterior and posterior cingula in the upper molars. According to Gheerbrant and Russell [1991] the presence of a hypocone and a lingual cingulum could be interpreted as a derived character. This difference could then be interpreted as a more derived stage of *A. ivani* in relation to *A. germanicus* [RUSSELL, 1964] from Walbeck. The lower p4 pattern with a single cusp in the talonid has been observed in *A. chleuni* and in one doubtful specimen of *A. tagourtensis* from the Eocene locality of N'Tagourt 2 [Morocco, Gheerbrant, 1993]. Thus, the Tremp localities contain a new species of *Afrodon* which could be considered in this particular character closer to the African species than to the European one. However, the morphological differences observed in the talonid of the lower p4 are subjected to a high intraspecific variability, as pointed out by Gheerbrant [1993], and this structure is poorly represented in the fossil record.

#### Order ?**Proteutheria**

Family indet. aff. Pantolestidae

***Nosella*** nov. gen., PELAEZ-CAMPOMANES

*Type species*. – *Nosella europaea* nov. sp.

*Etymology*. – From the Spanish “no sé” that means “I don't know”. Due to the difficulty for inferring the affinities of this material with other described taxa.

*Diagnosis*. – Upper molars having a rather broad stylar shelf, labially delimited by a longitudinal cingulum. The preparacrista is directed toward the stylocone instead of the



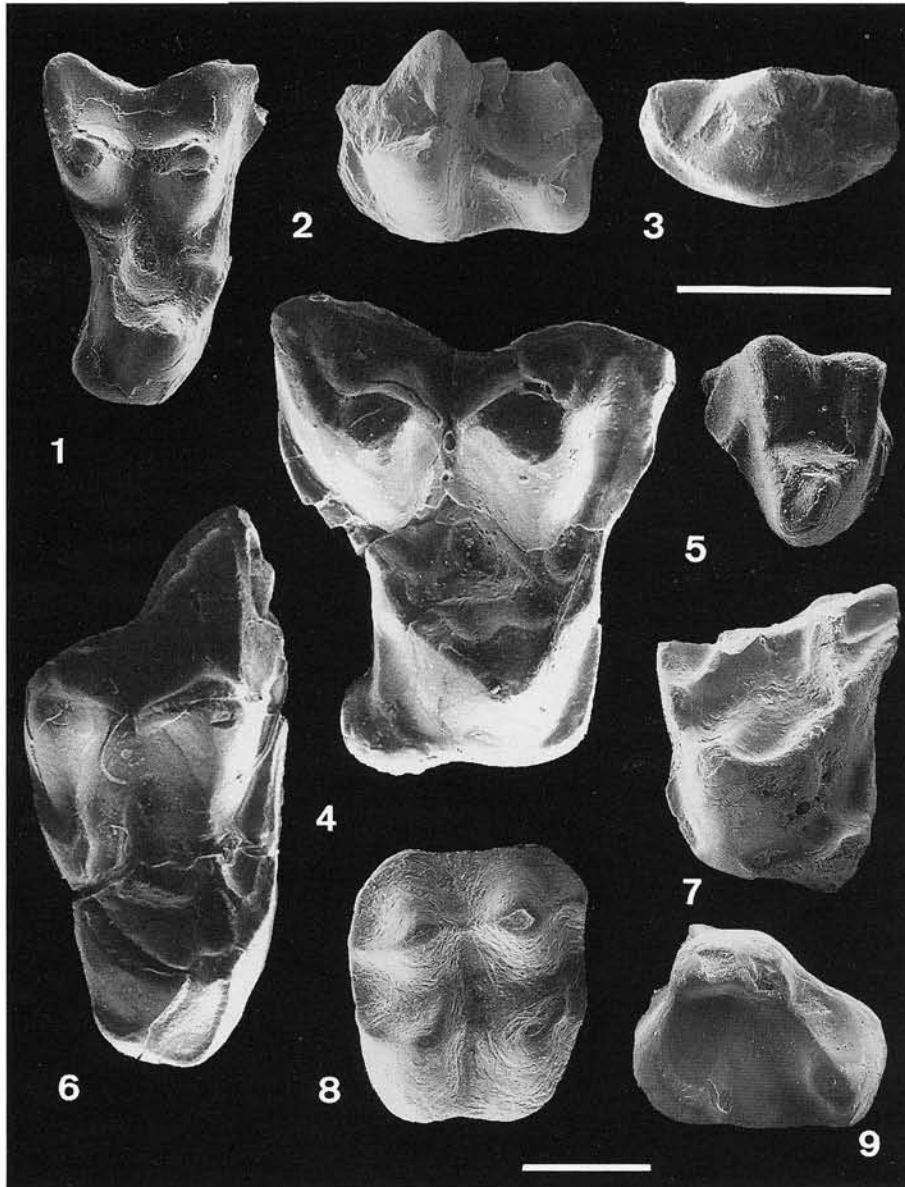


FIG. 3. - Mammals from the Upper Paleocene of the Tremp Formation. *Afrodon ivani* nov. sp. - 1 : holotype, M2 dex. TEN-1, Tendruy; - 2 : m2 sin. TEN-2, Tendruy; - 3 : p4 sin CLA4-17, Claret 4. *Nosella europaea* nov. gen. nov. sp. - 4 : holotype, M1 dex. CLA4-3; - 5 : fragment of dp4 dex. CLA4-33; - 6 : M3 dex. CLA4-10; - 7 : M2 sin. CLA4-50; all samples from Claret 4. *Microhyus* cf. *musculus* Teilhard de Chardin, 1927. - 8 : M1 dex. TEN-3, Tendruy; - 9 : M3 dex. CLA4-11, Claret 4. Collections in deposit at the Departamento de Paleontología, Universidad Complutense de Madrid (Spain). Scale = 1 mm.

FIG. 3. - Mammifères du Paléocène supérieur de la formation Tremp. *Afrodon ivani* nov. sp. - 1 : holotype, M2 dex. TEN-1, Tendruy; - 2 : m2 sin. TEN-2, Tendruy; - 3 : p4 sin CLA4-17; *Nosella europaea* nov. gen. nov. sp. - 4 : holotype, M1 dex. CLA4-3; - 5 : fragment de dp4 dex. CLA4-33; - 6 : M3 dex CLA4-10; - 7 : M2 sin. Cla4-50; tous les échantillons sont de Claret 4; *Microhyus* cf. *musculus* TEILHARD DE CHARDIN, 1927. - 8 : M1 dex; Ten-3, Tendruy; - 9 : M3 dex. Cla4-11, Claret 4. Collection déposée au Département de Paléontologie, Université Complutense à Madrid (Espagne). Echelle = 1 mm.

parastyle. The conules are well developed. M1-2 having pre and postcingulum, the latter bearing an hypocone. The well-developed postmetaconulecrista almost reaches the labial border of the tooth. Ectoflexus poorly developed. M3 elongated transversally and showing a postcingulum but no hypocone. Lower molars with a well differentiated paraconid, lower than the strong metaconid.

*Nosella europaea* nov. gen. nov. sp.,  
PELAEZ-CAMPOMANES  
(fig. 3 : 4-7)

*Synonym* : *Abolerylestes* (?) sp. in Russell *et al.*, 1966 (page 851; Plate XXI, fig. 2).

*Holotype* : M<sup>1</sup> dex. CLA4-3 (fig. 3 : 4).

*Type locality* : Claret 4 (Lleida, Spain)

*Diagnosis* : same as the genus.

*Other localities* : Berru and Cernay (Paris basin, France).

*Distribution* : Upper Paleocene of Spain and France.

*Hypodigme* : a fragment of M2 (CLA4-50, fig. 3 : 7); one M3 (CLA4-10, fig. 3 : 6); three other fragments of upper molars from Claret-4, which only show the protocone and

remains of the conules; four fragments of molariform lower cheek-teeth (CLA4-33, fig. 3 : 5).

*Other material* : A fragment of P3 (CLA4-27) can be tentatively attributed to this taxon.

*Description* :

**P3** (1,57 × ---). – Fragment of a molarized premolar, with a long preparacrista and two well separated labial cusps. Metacone strong and metastyle weak. The lingual wall is parallel to the lingual border.

**M1** (2,12 × 2,47). – Molar with quite robust trigon cusps. Paracone and metacone almost isolated from their bases. Centrocrista short and longitudinally oriented. Paracone slightly larger than metacone. The protocone is robust and poorly compressed antero-posteriorly. Paracrista and metacrista well developed. The ectoflexus forms a bend at the mid-labial part of the tooth. The parastyle is well developed. The conules are both present, but only the paraconule has a crest directed towards the trigon basin. The preparaconulecrista reaches the parastyle. The postmetaconulecrista is long but does not reach the postero-labial side of the tooth. The trigon basin is deep. Although slightly broken, the hypocone is well developed as a cingular cusp. A lingual cingulum is present.

**M2**. – Two molar fragments showing only the lingual part of the tooth, with protocone, hypocone and both conules. The protocone is high and sharp. The conules are small but also sharp. Both internal crests are present and well developed. The metaconule presents an anterior metaconule-crista well developed. The hypocone is small. There is a lingual cingulum, short in one case, and long in the other, running around the protocone and reaching the small hypocone.

**M3** (1,45 × ?2,71). – Molar very elongated transversally. The paracone is larger than the metacone and both are very sharp. A longitudinal centrocrista connects paracone and metacone. The parastyle, paracone and protocone are almost aligned transversally. Paraconule and metaconule are well developed. The latter has a position close to the metacone. The internal crests connect each conule with the lingual base of their respective main cusp. There is a very small posterior cingulum.

Lower molars : only 4 trigonids correspond to *Nosella* in size and shape. The paraconid is cuspidate and individualized from the protoconid. The trigonid basin is triangular in shape and the metaconid is as large as or larger than the protoconid.

*Discussion*

The morphology of this material represent a mixture of characters that individually can be found in different Paleocene taxa, but that all together make this taxon different from any other hitherto known. We have found only two specimens from the Paris Basin related to it. An upper molar (BR- L-121) from the French locality of Berru described by Russell *et al.* [1966] and another specimen from Cernay not yet described (BN CR 11, Muséum Histoire Naturelle de Paris). Both specimens show close similarities with the M1 from Claret 4 in size and morphology : position and development of the cusps; stylar shelf of similar size; development of the hypocone and precingulum, and size and position of the conules. Therefore we assign the teeth from Berru and Cernay to the new taxon *Nosella*, and it is highly probable that they are conspecific with the Tremp species.

The tooth from Berru was assigned with doubt to the palaeoryctid genus *Aboletylestes* (?) sp. indet. by Russell *et al.* [1966]. According to these authors the tooth shows similarities with *Propalaeosinopa* (= *Bessoecetor*) (?) *leveii* from Cernay and with *Aboletylestes* from Walbeck, being in general tooth pattern closer to the latter. In our opinion the assignment of this tooth to the Palaeoryctidae is very

doubtful, since it shows a well-developed hypocone and precingulum in the upper molars, structures generally absent in this family. In addition, this family shows more tubular cusps, their dental pattern is less robust and the upper teeth are relatively more enlarged transversally than in *Nosella*.

Szalay [1968] described three upper molars from Swain Quarry that he assigned to the genus *Jepsenella*. This author also discussed the tooth from Berru (BR- L-121) as being an Apatemyidae similar to *Jepsenella*. The inclusion of this tooth among the Apatemyidae is however refuted by Russell *et al.* [1979]. We agree with these authors and reject the inclusion of *Nosella* in the Apatemyidae. This family includes taxa with a dental pattern in which the cusps are less differentiated from the crests than in *Nosella*. Furthermore, not a single fragment of a lower molar or incisor with the characteristic morphology of the Apatemyidae have been found, either in the Spanish or in the French localities.

*Nosella* shows morphological similarities with the Pantolestidae, although the size of *Nosella* is significantly smaller. The position and development of the hypocone and the preparacrista, the relatively wide M3, and the development of the conules are similar in *Nosella* and *Propalaeosinopa* [Krause and Gingerich, 1983]. Also the P<sup>3</sup> has a parallel labial wall, instead of being oblique as is the case in Insectivora. However, the dental pattern of the Pantolestidae is more robust than in *Nosella* and the upper molars have a more rectangular shape. Therefore *Nosella* should not be referred to that family. Future findings of more material, especially upper and lower P4 are needed to establish its phyletic relationships.

Order **Condylarthra**, COPE, 1881

Family Hyopsodontidae, LYDEKKER, 1889

*Microhyus* cf. *musculus*, TEILHARD DE CHARDIN, 1927  
(fig. 3 : 8-9)

*Material*. – A fragment of right P2 (CLA4-32), a complete right M1 (TEN-3, fig. 3 : 8), two complete left and right M3 (CLA4-11, fig. 3 : 9) and several fragments of isolated, characteristic bunodont cusps.

*Description*

**P2** (2,0 × --- mm). – Only the labial half is preserved, having two roots. A single, high triangular paracone shows a sharp cutting edge. In its posterior crest, an undulation indicates the presence of a small metacone. The labial wall is flattened and there is an anterior cingulum. A fragmented small protocone is present in the lingual side.

**M1** (size measured in the dentine : ?1,9 × ? 2,16; estimation of the enamel is about 0,4 mm additional). – The enamel of this tooth has been lost, leaving the cusp pattern indicated by the intact dentine. The four main cusps are rounded, bunodont, close to each other, and situated near the middle of the crown. The paracone is slightly larger than the metacone and they are separated by a deep valley, although connected by a straight crest which ends anteriorly against a strong parastyle. A low cingulum runs around the anterior, labial and posterior sides. Its lingual ends curve to reach the wall of the lingual cusps. Protocone and hypocone are well separated and show short, curved crests (preprotocrista and prehypocrista) towards the anterior part of the labial cusps. There is no postprotocrista. The accessory conules are absent, apparently included as slight swellings in these crests.

**M3** (1,71 × 2,10 mm). – This tooth has three roots, a triangular shape and a very simplified pattern. A transverse valley isolates the paracone, which is large and slightly higher than the protocone; this last cusp is connected to the strongly reduced metacone, itself connected to a small metastyle.

### Discussion

The very characteristic material attributed to *Microhyus* cf. *musculus* from Claret 4 and Tendrui is closely related to *Microhyus musculus* TEILHARD DE CHARDIN 1927, redescribed by Sudre and Russell [1982] from Dormaal (Belgium) and other northern Neustrian localities, corresponding both in size and shape. The direct comparison with the rich sample of this species from Dormaal, collected by R. Smith, shows they may be conspecific. The Tendrui M1 specimen is closely comparable to the specimen D61 from Dormaal. Both populations have the hypocone fused to the metaconule, very small conules, a small ectoconule anterior to the paraconule, and a ridge posterior to the hypocone. Although all the observed characters coincide, we name the sample from Tremp *M. cf. musculus* because the scarcity of the Spanish material precludes the comparison of most of the tooth types.

The species *Microhyus musculus* has also been reported from other localities of the early Neustrian MP 7 unit [Pourcy, Louis and Michaux, 1962; Suffolk Pebble Beds, Hooker *et al.*, 1980] but only two teeth from the poor original sample has been described so far. The direct observation of this material shows no major differences with that from Dormaal.

The neighbouring Neustrian locality Silveirinha (Portugal) has yielded a different species of *Microhyus*, named *M. reisi* [Antunes *et al.*, 1987]. This species has relatively rather developed accessory cusps (stylar and conules), and less developed main cusps. *Microhyus musculus* differs from this species by its smaller size, more simplified cusp pattern, accessory conules reduced or absent, developed prehypocrista, reduced M3 and by having the main cusps of the upper molars closely spaced near the middle of the crown, instead of being more distant near the borders of the tooth [Estravis, 1992]. Some of these characters (accessory conules reduced or absent, reduced M3, close packing of the cusps) can be considered derived in *Microhyus musculus* in relation to the primitive states present in *Microhyus reisi*.

A single specimen attributed to *Microhyus* has been recovered from Berru (right M1, BR-L-3) having a much more larger size (aprox.  $2.8 \times 3.6$  mm). In addition, it differs from *Microhyus musculus* in having shallow valleys, a large stylar platform, a concave labial wall, the four main cusps much more closely spaced in the center of the crown, and in lacking pre-para-, -proto- and -hypocrista. *Microhyus* may be related to *Monshyus praeivius* SUDRE & RUSSELL, 1982 from the Lower Paleocene from Hainin, both sharing a square pattern of the four main cusps in the upper molars. Most of the bunodont condylarthres recovered from Cernay and Berru similar in size to *Microhyus musculus* belong to the genus *Louisina*, which keeps a distinct trigone in the upper molars.

The Tremp localities contain thus a highly derived condylarth, indistinct from the Neustrian *Microhyus musculus* from Dormaal and other northern localities, and different from the southern Neustrian *M. reisi* and Cernaysian related species.

Family ?**Meniscotheridae** COPE, 1882

Genus *Pleuraspidotherium* LEMOINE, 1878

*Condylarthra* indet., cf. *Pleuraspidotherium* sp.

(fig. 2 : 4)

**Material.** – A lower decidual right molar (dp4, PALAU-3, Fig. 2 : 4).

### Description

**dp4** ( $3.8 \times 1.81$  mm) : has an elongated shape and a lophodont pattern. The main cusps are not paired but alternated : the protoconid is forwardly placed in relation with

the metaconid and the hypoconid in relation with entoconid. All the four main cusps seems to reach a similar size and height. An elongated, sharp paraconid projects anteriorly. Protoconid and hypoconid are flanked by two ridges resulting in a crescent-shaped pattern (selenodont). The cristid obliqua is very long and stops against the middle part of the metaconid. The upper anterior part of the metaconid connects with a high postprotocristid. The metaconid is broken but shows an elongated pattern, protruding the postprotocristid anteriorly and the cristid obliqua posteriorly.

### Discussion

The specimen PALAU-3 is interpreted as a decidual tooth because of its complicated pattern, elongated shape and reduced roots. Its lophodont pattern with two external crescents (selenodont teeth), alternating cusps and elongated metaconid are characters found in the peculiar condylarth family Meniscotheridae with the genera *Pleuraspidotherium* and *Orthaspidotherium* represented in the Upper Paleocene reference levels MP6 and MP7 (?) in Europe [Teilhard, 1927; Russell, 1964; Hooker, 1996].

The size of the Tremp specimen is some 30% smaller than that of *Orthaspidotherium edwardsi*, which itself is 30% smaller than that of *Pleuraspidotherium aumonieri*. The shape of the Tremp specimen is however more similar to that of *Pleuraspidotherium aumonieri*, in having an elongated paraconid and a laterally situated entoconid. We ascribe the Tremp specimen to this later genus because of the shape similarity.

### FAUNAL COMPOSITION

The sample from the four localities of the Tremp Formation is formed by 234 identified specimens and many unidentified fragments. Some of the more complete specimens have been clearly identified, and the rest only tentatively assigned to the identified taxa by comparison with the more complete ones. The distribution of the identified sample is shown in table I.

The overall composition of these four Spanish assemblages (see table I) is peculiar in having a small number of taxa. Future studies can eventually lead to the identification of more species in the ensemble of unidentified fragments, but even so, the low species/specimens ratio and the highly unbalanced distribution, with one dominant species reaching 70% of the assemblage, indicates a low species richness in the Tremp Paleocene assemblages. This is also the case of the neighbouring Campo Paleocene locality, dominated by *Paschatherium* as well [Gheerbrant *et al.*, 1997].

Other Paleocene and lower Eocene localities from Africa, Europe and North America show a species richness much higher than the South Pyrenean ones for a similar number of specimens. Figure 4 shows that the number of species present in Claret-4 is significantly lower than many other localities from the Paleocene of North America as well as from the Neustrian of Europe (reference level MP 7) for a similar number of specimens ( $\approx 200$ ).

To compare the species richness of Claret 4 with those of other localities having a larger sample size (= number of specimens) we have calculated the rarefaction curve for several localities from Europe and North America [Hurlbert, 1971]. Studying the species abundance distribution of the Claret-4 assemblage (table I) we obtain the rarefaction curve which indicates how the number of species will increase when increasing the number of specimens (fig. 4). It can be observed that the species richness from Claret-4 will not reach more than 15 species even if we reach a sample size similar to that from Cernay (about 3000 specimens), where there are twice more species than the theoretical maximum richness from Claret-4. We have tested a sample of 157 spe-

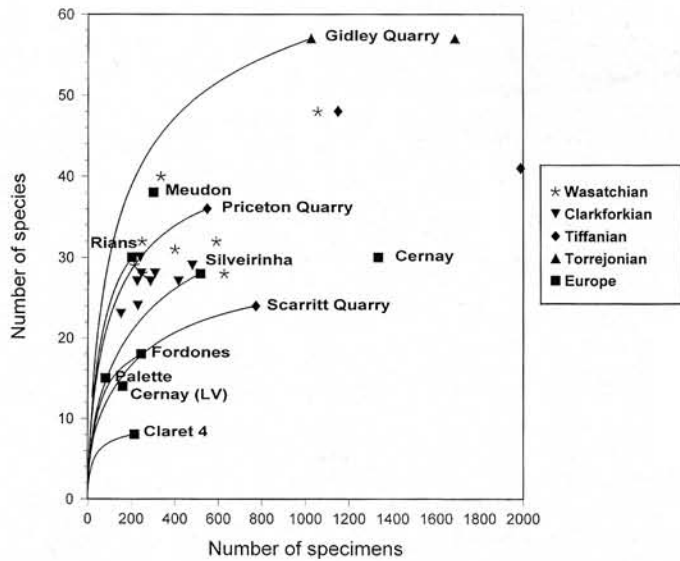


FIG. 4. – Scatter diagram of number of specimens *versus* number of species of mammals in different Paleocene-Early Eocene localities. North American data from Rose [1981 a & b]; Gingerich [1989] and Krause and Maas [1990]; European data from Russell [1964] and papers cited by Marandat [1997]. Rarefaction curve calculated according to Hurlbert [1971]. Curves for localities Cernay and Dormaal (about 40 species) has not been calculated, since abundance data are not available. Cernay (LV) refers to the sample provided by Laurent Viriot (Poitiers University).

FIG. 4. – Diagramme de corrélation entre nombre d'espèces et nombre de spécimens de mammifères dans différents gisements du Paléocène-Eocène inférieur. Amérique du Nord d'après [Rose, 1981 a & b; Gingerich, 1989 et Krauss et Maas, 1990]; données européennes de Russell [1964] et notes citées par Marandat [1997]. Courbes de rarefaction calculées d'après Hurlbert [1971]. Les courbes des gisements de Cernay et de Dormaal (environ 40 espèces) n'ont pas été calculées car le nombre de données n'est pas suffisant. Cernay (LV) correspond à l'échantillon prêté par Laurent Viriot (University de Poitiers).

cimens for Cernay, which contains 14 species (fig. 4). The low diversity of the Spanish late Paleocene faunas cannot thus be explained as a result of a small sample size, but it must be considered instead as a consistent pattern.

The low diversity pattern of the Pyrenean Spanish localities can be attributed to a taphonomic bias either before or after burial. It seems however not probable, since the four localities from the Tremp Formation and the Campo site show a rather different fossilization environment with a similar faunal composition. Palau fossiliferous level is a black clay with marine fossils; Claret-4 is a freshwater grey clay with charophytes and edaphic nodules; Tendruy is a thick light grey clay with fossil seeds intercalated in fluvial sandstones. Claret 0 is a black clay lenticular bed below a conglomeratic level. Campo site is a lenticular dark marly level [Tambareau *et al.*, 1992]. The five localities have sediments indicating quiet hydrodynamic conditions and their fossils show no signs of transport. Claret-4 contains fossils of large eggshell fragments, which would be easily destroyed by erosion; an additional sign of autochthonous assemblage is the perfect connection between two eggshell fragments with old fracture surfaces. Moreover, these fossils assemblages are extremely poor, which is also a common feature of autochthonous assemblages. This eliminates the taphonomic bias of sorting by lateral transport.

A selection of species, such as floating of the corpses (nekrolynesis), predation, etc., can also occur before accumulation, resulting in a biased faunal composition of the assemblage. The predation origin for some of the Tremp fossils can be postulated. Some of the localities have several specimens, mainly the condylarth teeth, with signs of di-

gestion by predators. In Claret 4, the giant bird eggshell fragments with no signs of digestion appear in association with some digested mammal teeth, suggesting that the birds could be the predators of mammals. Not all the species however seems to have the same origin. Some of the smallest mammals are too small for the size of birds. Moreover, many teeth do not show digestion processes. The origin and the preservation state of the fossils are thus heterogeneous. Some of the specimens were probably digested preys, but many of them seem to have a different origin.

Therefore the assemblages from five localities from Tremp and Campo show diverse sources of remains, different fossilization environments, and heterogeneous preservation states of fossils, but a similar composition with few mammal species dominated by *Paschatherium*. This strongly suggests an actually poorly diversified palaeocommunity, the probability of an identical taphonomic bias in the five different localities being very low.

A biogeographic factor can be invoked for explaining the low diversity pattern of the Pyrenean Paleocene faunas. Insularity is a well known factor leading to the depletion of the species richness in isolated areas in relation with similar areas of a more continuous realm. However, the insular faunas have endemic, peculiar species different from that of neighbouring areas. Many of the Tremp Paleocene mammals are instead common to other European regions. There are few signs of endemism in the Spanish faunas, since the majority of the taxa of the Tremp mammals, as well as the birds represented by their eggshells, belong to species also represented in southern France and northern Europe.

It can be argued that these shared taxa were first originated, then migrate out of the island. However, the insular species have a very low immigrant behaviour, and there are not reported cases of species settling out of an island after a severe insulation process.

We favour instead the hypothesis that the low diversity pattern of the Spanish Paleocene faunas has an ecological and chronological significance, representing an episod of severe climatic deterioration, probably related to a larger scale event. We postulate that it represents a global event of ecological alteration as we will discussed below.

## BIOCHRONOLOGY

The mammalian biochronology for the Paleocene in Europe is still unstable due to the lack of good fossil successions. Nevertheless, a major division seems well established between Cernaysian (reference level MP6) and Neustrian (= "Sparnacian", reference levels MP7 to 9) mammal ages on the basis of the first occurrence of marsupials, carnivores, rodents, bats, dermopterans, euprimates, artiodactyls and perissodactyls [Schmidt-Kittler, 1987; BiochroM, 1997]. The localities correlated to Dormaal (reference locality of the MP 7), such as Silveirinha, Fordones and Rians, belong to the early Neustrian because of the presence of these immigrants. The localities of Cernay and Berru belong to the Cernaysian (reference level MP 6) because of the absence of these immigrants and the presence of many particular taxa.

The localities from the Spanish Pyrenees should be assigned to the Cernaysian based on the absence of the Neustrian immigrants, and the presence of *Afrodon*, *Nosella* and *Adapisorex* only recorded in reference level MP 6 and older units. However, the condylarths *Paschatherium* cf. *dolloi* and *Microhyus* cf. *musculus* were until now restricted to reference level MP 7. The first taxon is dominant in Tremp, Dormaal and other Neustrian localities, which gives a strong similarity to these assemblages. The Spanish sites

show thus an intermediate composition between the two reference mammal units.

*Paschatherium* is not a first occurrence in Neustrian times in fact. Several not yet described species of *Paschatherium* were already present in the Cernaysian faunas, although they do not dominate the assemblages. The Cernaysian species were mainly very large forms, twice as large as the largest *Paschatherium dolloi* from reference level MP 7, small-sized species being extremely rare. Likely, the small-sized *Paschatherium* species became dominant after Cernaysian times.

The younger chronological position of the Tremp assemblages in relation to the Cernaysian faunas is reinforced by the morphologically advanced *Afrodon ivani* nov.sp. in relation to *A. germanicus* from Cernay and Walbeck.

On the other hand, the Tremp assemblages can be considered older than Neustrian assemblages. The main criteria supporting this chronological position are the absence in Tremp of Neustrian immigrants and the presence of Cernaysian-related taxa (*Hainina*, *Afrodon*, *Nosella*, *Adapisorex*) which are absent in the Neustrian sites. The correlation of the Tremp localities with *Sphaerochara edda* zone (see below) also reinforce a chronological position older than the Neustrian sites, correlated with the *P. disermas* zone [Hooker, 1996, 1999].

A new biochronological unit is thus proposed here, named reference level MP 6b with Claret 4 as the reference locality, in order to include these new assemblages in the standard Paleogene European mammal succession (see fig. 5). We include provisionally these MP 6b Spanish assemblages in the Cernaysian land mammal age, since there are anterior to the major mammal migratory wave, which is one of the most important features of the Neustrian.

The Tremp localities, and the new MP 6b mammal unit based on them, can be calibrated by means of (a) charophyte biozonation, (b) the overlying marine sediments containing nannoplankton and foraminifera, and (c) by correlation with three magnetostratigraphic successions. On one hand, the charophyte *Peckichara* gr. *varians*, *Maedleriella* aff. *crustellata* and *Maedleriella michelina* present in the upper Claret section can be correlated with the *Sphaerochara edda* zone, on the basis of their association with this taxon in the neighbouring locality St. Salvador de Toló, and the absence of *Peckichara disermas* [Feist and Colombo, 1983; Riveline *et al.*, 1996]. The *Sphaerochara edda* zone has been correlated with the top of nannoplankton zone NP8 and the base of zone NP9. This correlation corresponds well with the situation of the Claret 4, Palau and Tendrue localities overlain by 230 m thick Ilerdian marine deposits assigned to zone NP9 [Serra-Kiel *et al.*, 1994; see fig. 1B].

On the other hand, the base of the Ilerdian stratotype has been correlated with palaeomagnetic Chron C24r [Serra-Kiel *et al.*, 1994]. Although no direct palaeomagnetic measurements have been made below it, the situation of the three uppermost mammal localities (Claret 4, Palau and Tendrue) in the base of the first Ilerdian depositional sequence indicates a correlation with Chron C24r. This correlation is the best fit when both magnetostratigraphic successions from the Campo section are taken into account, that from Serra Kiel *et al.* [1994] and from Galbrun *et al.* [1999, see fig. 1B, a and b]. Either, a hiatus exists comprising the entire Chron C25n, or two normal polarity intervals, Chrons C25n and C26n, are represented in the Navarri Formation.

The neighbouring Campo mammalian locality shares with those from Tremp a low diversity assemblage dominated by *Paschatherium* species. This locality is a conti-

mental intercalation situated between the upper part of *Glomalveolina primaeva* zone and the lower part of *Glomalveolina laevis* zone [Tambareau *et al.*, 1992], and correlated within "Wetzeliella" *hyperacantha* dinocyst zone [Caro *et al.*, 1975]. Marine limestones correlated with NP8 nannoplankton zone are situated below the continental intercalation [Kapellos and Schaub, 1975], not in the mammal-bearing level as indicated by Gheerbrant *et al.* [1997]. This regressive episode, also represented in the northern Pyrenees Paleocene deposits [Tambareau *et al.*, 1995], can be correlated with the hiatus dated between zones NP8 and NP9 in the western Pyrenean, NW Paris basin and North Sea platforms [Pujalte *et al.*, 1998; Dupuis *et al.*, 1998]. It also corresponds to a major dinocyst change from *Deflandrea speciosa* assemblages to *Wetzeliella hyperacantha* ones [Caro *et al.*, 1975]. Two normal polarity intervals at the base of Navarri Formation and below the Campo mammal site, can be correlated with Chrons C26n and C25n [Sierra-Kiel *et al.*, 1994, see fig. 1B-a, and Galbrun *et al.*, 1999, see fig. 1B-b]. The situation of Campo mammal site in reference level MP 6b close to the Tremp assemblages, as suggested by its faunal composition, would agree with its correlations with Chron C24r and the chronostratigraphic data.

The new MP 6b faunas can help in the controversial correlation between the European and North American mammalian biochronological scales. Two conflicting hypotheses have been proposed, the beginning of the Neustrian in Europe synchronous with the beginning of Wasatchian land mammal age in North America [Wa 0, Gingerich, 1989; Hooker, 1991], or alternatively synchronous with late Clarkforkian [Cf 3, Godinot, 1982; 1996]. Cernay has been correlated with Tiffanian 5 [Krause and Maas, 1990], as indicated by the shared taxa *Neoplagiaulax* and *Mckennatherium* (= *Adunator*) which disappear in the Clarkforkian. Thus the new MP6b fills a gap in the European succession, represented in the North American succession by early-middle Clarkforkian (Cf 1-Cf 2). This correlation is in agreement with the proposals of Butler *et al.* [1980] and Rapp *et al.* [1983], which place Cf 2-3 units in the lower part of palaeomagnetic Chron C24r, just as the Spanish localities.

If this chronological hypothesis is verified, the time interval between MP 6a and MP 7 must be larger than supposed on the basis on current marine-continental correlations in the northern European basins [Hooker, 1999]. A hiatus can be postulated in the Paris Basin between the Berru Sandstones - marnes de Montchernot and the earliest Neustrian levels (Marnes à rognons, conglomerat à *Coryphodon*). This hiatus would correspond to the already mentioned hiatus between zones NP8 and NP9 in marine successions.

Figure 5 shows the proposed correlations between European and North American mammal faunas based on the ranges of a set of selected taxa. As can be seen, the Neustrian (MP 7) can be correlated with Cf 3 to Wa 1 as we will discuss below. It must be indicated that some Neustrian localities, such as Suffolk Pebble Beds, are probably made of mixed assemblages with reworked fossil mammals.

## PALAEOCLIMATIC INTERPRETATION

The Paleocene localities from the Tremp basin have, as discussed before, a low species richness that contrasts with the much richer localities Cernay, Dormaal and Silveirinha. This characteristic may be the signal of a palaeoenvironmental event that can be recognized in other regions.

There are no other Paleocene localities in Europe that could be correlated with these Spanish assemblages. Indeed the North American Paleocene mammalian record shows a decrease in diversity around the beginning of the Clarkforkian, significantly lower than the Torrejonian, Tiffanian and Wasatchian [Rose, 1981b]. The existence in both continents, Europe and North America, of a decrease in species richness around the reference level MP 6b and the early Clarkforkian would suggest a possible correlation with a general climatic change.

This pattern is reinforced by its relation to the climatic trend recorded in the oceans as a long-term  $\delta^{13}C$  depletion during the late Paleocene until Middle Eocene. Superimposed on this trend, a global rapid short-term shift in the carbon isotope values of the foraminifera ( $\delta^{13}C$  excursion) has been correlated with the lower part of Chron C24r [late Paleocene Thermal Maximum; Kennett and Scott, 1991; Koch *et al.*, 1992; Zachos *et al.* 1994]. A  $\delta^{13}C$  excursion in a comparable palaeomagnetic position has been detected by Cojan *et al.* [1998] in Aix-en-Provence basin (France). It is situated about 80 m below the Neustrian Palette site, around a hiatus between Chron C25r and Chron C24r. Close to the  $\delta^{13}C$  excursion, two horizons have been reported with giant bird eggshells (*Ornitholitus*), similar to that of Claret 4.

The marine-continental correlations in the Tremp-Graus basin suggest that MP 6b faunas occurred earlier than the Paleocene/Eocene boundary defined by nannoplankton, benthic and planktic foraminifera, situated more than hundred metres above the Tremp and Campo mammal sites (fig. 1B).

The chronological relation between European reference level MP6b and North American early Clarkforkian is reinforced when comparing the mammalian assemblages of both continents (fig. 5). The evolutionary stage of the artiodactyl *Diacodexis* [Estravis and Russell, 1989; Smith *et al.*, 1996]

and the paramyid rodents, and the first occurrence of taxa such as *Macrocranion*, *Hyopsodus*, *Phenacodus* and the primates *Cantius* and *Teilhardina*, points out to a correlation of the beginning of the Neustrian with the late Clarkforkian, as suggested by Godinot [1982, 1996] (see figure 5). The position of the the  $\delta^{13}C$  excursion seems to confirm this correlation: in the Paris and Belgium basins it has been situated above the Neustrian Try and Dormaal sites [Sinha *et al.*, 1997; Steurbaut *et al.*, 1999]; in North America, the  $\delta^{13}C$  excursion underlies the Wasatchian Wa 0 unit [Koch *et al.*, 1992]. The  $\delta^{13}C$  excursion would be thus situated within MP7 in Europe, and between Cf 3 and Wa 0 in North America. Therefore, the Neustrian mammalian immigrants in Europe would precede those in North America, as suggested by Godinot [1982, 1996]. Our interpretation situates Spanish MP 6b faunas in relation with American Cf 1-2, before the  $\delta^{13}C$  excursion.

**CONCLUSIONS**

For the first time, fossil mammals have been found in the Tremp Formation in continuity with the marine Ilerdian deposits. The good chronological constraints of these new assemblages allows to interpret them in relation with late Paleocene palaeoenvironmental events. The late Paleocene Thermal Maximum would be chronologically close to the position of the Tremp mammalian assemblages, correlated with the lower part of Chron C24r. These localities, as well as Campo South Pyrenean mammal site, show a low species richness and a low diversity index. Sampling, taphonomic and biogeographic bias factors are discussed and rejected as an explanation of the observed pattern. Instead, this pattern can be the consequence of a climatic change which may be recognized at a global scale.

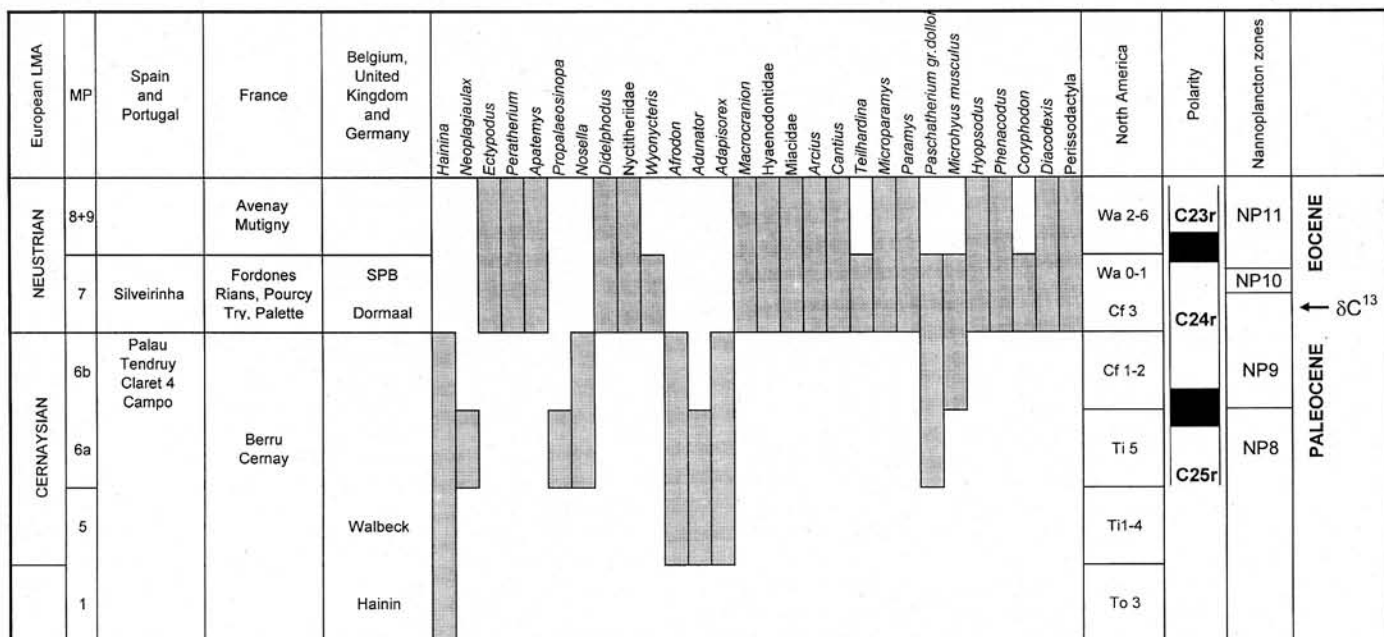


FIG. 5. - Distribution chart of selected mammalian taxa from the European and North American record, and proposed correlations of both biochronological scales. An indication of their calibration with the chronostratigraphic scales is given. The localities included within a MP unit are arranged without chronological order.

FIG. 5. - Graphique de distribution de taxons de mammifères sélectionnés d'Europe et d'Amérique du Nord, et corrélations proposées pour les deux échelles biochronologiques. Une indication de leur calibrage avec l'échelle chronostratigraphique est donnée. Les localités à l'intérieur d'une unité MP sont arrangées sans ordre chronologique.

A new biochronological unit, MP 6b is defined for the new Spanish Paleocene mammal faunas included in the latest Cernaysian European Land Mammal age, situated in an intermediate chronological position between the much more diversified Cernaysian MP 6a faunas (sharing *Hainina*, *Nosella*, *Adapisorex* and *Afrodon* represented by a more primitive species) and the Neustrian MP 7 (sharing *Paschatherium* cf. *dolloi* and *Microhyus musculus*).

A similar succession is found in North America, with rich mammalian faunas from Tiffanian 5 (correlated with Cernaysian MP 6a) followed by poorer Clarkforkian 1 and 2 faunas, then by again richer Clarkforkian 3-Wasatchian 0 assemblages. The Spanish mammal sites allow to fill a gap in the European mammal succession and offers a good agreement with that of North America, both showing a similar event during MP 6b-Cf 1-2 which allow to hypothesize a general palaeoclimatic perturbation in the continental realm. This event can be correlated with the early part of C24r paleomagnetic Chron, just before the Paleocene/Eocene boundary as denoted by nannoplankton and foraminifer biochronostratigraphy. The mammalian faunal depletion is interpreted as a response to a climatic change anterior to the rapid  $\delta^{13}\text{C}$  excursion named LPTM, situated between the North American Cf 3-Wa 0 mammal units, and within the European MP 7 Neustrian unit.

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