

ADDITIONAL HOMINOID MATERIAL FROM THE MIOCENE OF SPAIN AND REMARKS ON HOMINOID DISPERSALS INTO EUROPE

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A hominoid upper molar from Hostalets, recently recognised in collections from the 1920s housed at the Museu i Laboratori de Geologia del Seminari (Barcelona) is assigned to the genus *Dryopithecus*; this may well be the first dryopithecine tooth to have been collected in the Vallès-Penedès. With Hostalets as one of the older European *Dryopithecus* localities, hominoid dispersals into Europe are discussed here as well. These coincided with dispersals of other mammals, and such events were related to eustatic sea level changes and global climate. The first hominoid may have entered Europe 15.5 Ma ago (beginning of MN 5); its affinities are not clear. Since the European remains of *Griphopithecus* are at least 3 Ma younger, they are likely to represent a different species, and might even represent a different genus. *Griphopithecus* entered Anatolia probably not later than 14 Ma ago (late MN 5), and not later than 12.5 Ma ago (late MN 6) it entered Europe. The ages of hominoids from Klein Hadersdorf and Çandir are close; these occurrences might represent the same species. Remains from Neudorf-Sandberg are much younger. *Dryopithecus* may have entered Europe also 12.5 Ma ago, coming directly from Africa.

Key words — *Dryopithecus*, Hominoidea, Vallès-Penedès, stratigraphic age, hominoid dispersals.

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CONTENTS

Introduction	p. 25
Description and comparison of the new material . . .	p. 27
The ages of Turkish and European Miocene hominoids	p. 28
Dispersal of dryopithecines into Europe	p. 34
Summary and conclusions	p. 35
Acknowledgements	p. 37
References	p. 37

INTRODUCTION

When cataloguing and studying fossil suids in the collections of the Museu i Laboratori de Geologia del Semi-

nari in Barcelona (MLGSB), one of us (JvdM) recognised the present specimen amongst suid fossils from Hostalets. The new *Dryopithecus* tooth is from a collection made by M. Guérin in the 1920s, which was later transferred to the MLGSB. At that time, Hostalets was still assumed to be a 'locality', with fossils from a single level only. To date, 'Hostalets' is considered to represent an area, with two stratigraphical levels, a Late Aragonian (Middle Miocene, MN 7 + 8; Neogene Mammal Units, de Bruijn *et al.*, 1992), and an Lower Vallesian (Upper Miocene, MN 9) one, considered to be older than the Can Ponsic and Can Llobateres localities (Agustí *et al.*, 1984). In view of the fact that the present *Dryopithecus* tooth is from an old collection ('Hostalets oc'), its exact stratigraphical provenance remains unknown.

Villalta Comella & Crusafont Pairó (1941) were the first to record a dryopithecine from the Vallès-Penedès.

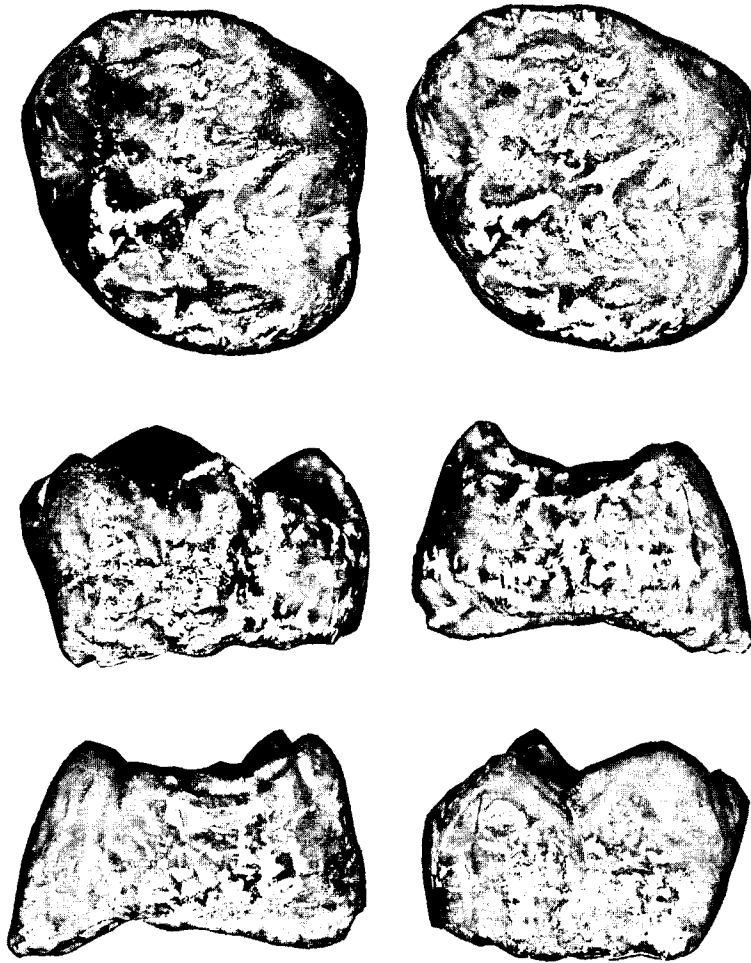


Fig. 1. MLGSB 48486, right M^2 of *Dryopithecus* from Hostalets, x 4; upper figures - stereo pair of occlusal view, middle - buccal and posterior views, lower - anterior and lingual views.

This fossil (IPS 1), the type of *Sivapithecus occidentalis* Villalta Comella & Crusafont Pairó, 1949, originally consisted of two teeth united by a piece of mandible, now lost. The isolated molars are now numbered IPS 1826 (= M_2) and IPS 1827 (= M_3). The specimen was found by Crusafont in the area of Hostalets, near a track leading from Can Vila to Can Mata. Villalta Comella & Crusafont Pairó (1941) considered it to be of Vindobonian (= Late Aragonian) age, and noted that other beds in the Can Mata-Ocata area had yielded *Hipparion*. These authors were already aware of the fact that Hostalets did not represent a single locality. Six other mammal species were stated to have been collected from the beds that yielded the mandible; none of these favours an Aragonian or Vallesian age. Subsequent work has resulted in the consensus that the specimen is considered to be of Aragonian age (Agustí *et al.*, 1984; Begun *et al.*, 1990).

The present specimen is of special interest in being the oldest upper molar of *Dryopithecus* to have been recorded to date from the area. Material from Can Ponsic (= type material of *D. crusafonti* Begun, 1992a) and Can Llobateres (attributed to *D. laietanus*) is younger (Begun *et al.*, 1990). In addition, it represents one of the oldest remains of *Dryopithecus*. In light of this, the time seems right to present additional data on the (relative) ages of European hominoid localities and discuss a model of hominoid dispersal into Europe.

Abbreviations — Numerous collections have been studied; to indicate the repositories of specimens examined the following abbreviations are used:

GML	Geological Museum, Lisbon
HGSB	Hungarian Geological Survey, Budapest

IGGML	Institut für Geowissenschaften/Geologie der Montanuniversität
IPS	Institut Paleontològic Dr M. Crusafont, Sabadell
IPUW	Institut für Paläontologie, Universität Wien
IVAU	Instituut voor Aardwetenschappen, Universiteit Utrecht
MGB	Museo Geológico, Barcelona
MGL	Muséum Guimet, Lyon
MLGSB	Museu i Laboratori de Geologia del Seminari, Barcelona
MNCN	Museo Nacional de Ciencias Naturales, Madrid
MNHN	Muséum national d'Histoire naturelle, Paris
MPZ	Museo Paleontológico de la Universidad de Zaragoza
MTA	Maden Tetkik ve Arama, Ankara
NMB	Naturhistorisches Museum, Basel
NMM	Naturhistorisches Museum, Mainz
NMW	Naturhistorisches Museum, Wien
PIMUZ	Paläontologisches Institut und Museum, Universität Zürich
PDTFAU	Paleoantropoloji, Dil ve Tarih Coğrafya Facultesi, Ankara Üniversitesi, Ankara
SLJG	Steiermärkisches Landesmuseum Joanneum, Graz
SMNS	Staatliches Museum für Naturkunde, Stuttgart
UCBL	Université Claude Bernard, Lyon

DESCRIPTION AND COMPARISON OF THE NEW MATERIAL

The fact that the present tooth (Fig. 1) is bunodont is probably the reason for its being confounded with that of a suid. 'Bunodont molars' occur in suids, ursids and primates, though this descriptive term includes very different morphologies. The low cusps and other morphological features indicate that the present specimen belongs to a primate. The trigon and hypocone are recognisable, indicating that it is an upper molar. Aragonian and Vallesian European primates include pliopithecids, *Dryopithecus* and *Griphopithecus*.

The occlusal surface has a mesio-distally elongated, rectangular outline. The base of the crown has a nearly square outline, being slightly rounded bucco-distally, unlike the M^3 which have a reduced or even absent metacone, resulting in a triangular or trapezoidal outline. The tooth from Hostalets is therefore either an M^1 or an M^2 . Measurements are given in Table 1.

The mesial crista of the paracone is short and adds to the formation of the mesio-marginal crest, which is longer and merges with the mesial crest of the protocone (protocrista). The mesio-lingual crest of the paracone forms part of the anterior transcrista, which ends abruptly at the base of the protocrista. The mesio-marginal crest, protocrista and anterior transcrista converge in one point, a small cusplule, reminiscent of a protoconule. A small disto-lingual crest is directed from the paracone to the buccal crest of the protocone. These two crests do not meet and no second anterior transcrista is formed. The crista obliqua is continuous and connects proto- and metacone.

Mesio-distal diametre	11.3
Bucco-lingual width of the first lobe (= maximum width)	11.5
Bucco-lingual width between the lobes	10.4
Bucco-lingual width of the posterior lobe	9.7
Maximum diagonal of the crown, D1	12.5
Minimum diagonal of the crown, d1	11.5
Maximum diagonal of the occlusal surface, D2	10.2
Minimum diagonal of the occlusal surface, d2	7.2
Mesio-distal length of the anterior fovea	4.6
Mesio-distal length of the posterior fovea	3.5

Table 1. Measurements (in mm) of MLGSB 48486, right M^2 of *Dryopithecus* from Hostalets.

There is no indication of a metaconule in this crest. The crest is in a diagonal direction and separates the large trigonid basin from the smaller talon. The trigonal crest of the hypocone is mesio-buccally directed and ends near the lingual end of the crista obliqua. On the distal side of the metacone there is a small accessory cusp, a 'postmetacone' or 'postero-external accessory cusp'. The hypocone is united to the 'postmetacone' by the posterior transcrista and the marginal-distal crest. There is much variation in the development of the Carabelli cusp in the upper molars of *D. laietanus*; the tooth from Hostalets does not have a Carabelli cusp at all.

The four sides of the tooth are smooth. There is no lingual cingulum, unlike in pliopithecids, which have a wide cingulum along the hypocone. There is a deep furrow on the lingual wall between the protocone and hypocone, and a similar furrow on the buccal wall.

The upper molars of *Griphopithecus darwini* are relatively wide; an upper molar from Neudorf-Sandberg (Dvinska Nova Ves), assumed to be an M^2 (Steininger, 1967), has a length of 11.6 mm and a width of 13.5 mm (IPUW, cast). It is much larger and, in particular, much wider than the *Dryopithecus* upper molars (compare Fig. 2). The tooth is larger than the $M1$ of *Dryopithecus* from the Vallès-Penedès and Rudabánya, but enters into the ranges for the $M2$ (Fig. 2), and is similar in morphology to the M^1 and M^2 of *D. laietanus* (see Golpe Posse, 1993 for a detailed description). The size of MGSB 48486 exceeds that of any of the M^1 of *Dryopithecus* from the Vallès-Penedès and Rudabánya, but is within the ranges of the M^2 (Fig. 2). We believe the tooth is an M^2 of *Dryopithecus*. Ribot (1993; see also Ribot *et al.*, 1996) assigned all material from the Vallès-Penedès to *D. laietanus*.

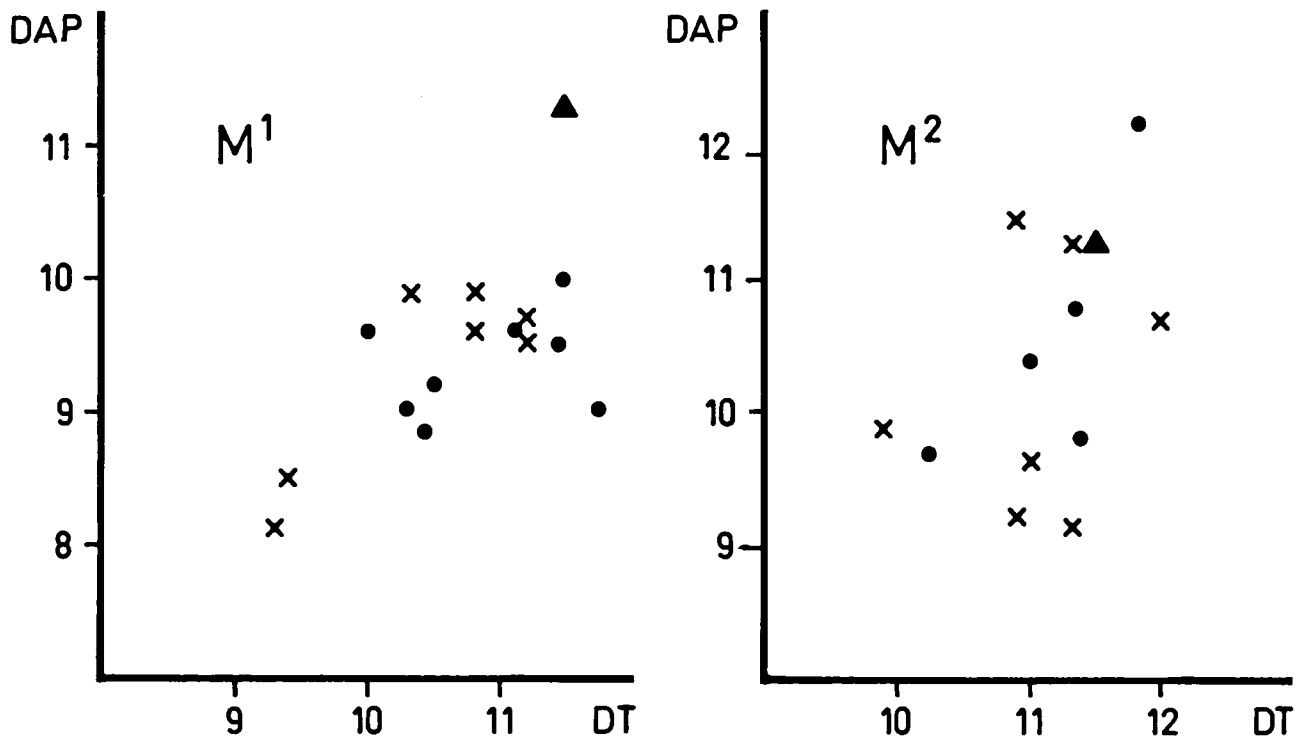


Fig. 2. Bivariate plots of meso-distal diameter (DAP) and transverse diameter (DT) of the tooth from Hostalets (triangles) compared to the M¹ and M² of *Dryopithecus* from Rudabánya and central Europe (dots) and the Vallès-Penedès (crosses); measurements in mm.

THE AGES OF TURKISH AND EUROPEAN MIOCENE HOMINOIDS

For several reasons it is important to have a good stratigraphic control of the hominoid localities. Hominoid type material is often incomplete, and for that reason material from several localities which are geographically and stratigraphically close, frequently is united. This is obviously a subjective element, but may be limited by precise stratigraphic (and palaeobiogeographic) information. The reconstruction of hominoid history is another reason. Before arriving in Europe, hominoids passed through Anatolia; correlations between these two areas are obviously important.

There are still many problems in the correlations of the important European hominoid localities; there are

problems with individual localities and with the estimation of the age of the commonly used Neogene Mammal Units (MN units; de Bruijn *et al.*, 1992). For instance, de Bruijn *et al.* (1992), without explanation, placed Klein Hadersdorf and Neudorf-Sandberg in MN 6, whereas Mein (1986), in a study of the ages of European hominoid localities, put forward arguments to place the localities in MN 8. There was a tremendous difference in the estimate of the age of the lower boundary of MN 5. There has been discussion on the content of MN 5. In Spain and France, where the reference localities of the MN units tend to be situated, palaeontologists included faunas of Aragonian zone D (Daams & Freudenthal, 1988) in MN 5, but in central Europe similar faunas were placed in MN4.

Fig. 3. Correlation scheme; left column - eustatic sea level cycles of Haq *et al.* (1987), and ages (in Ma) of onset of each cycle, the second age indication in this column being the corrected age by Miller *et al.* (1996). Each cycle starts with a sea level low, which is assumed to have allowed for intercontinental dispersals of terrestrial animals. The thick black horizontal lines indicate these dispersal events. The next columns give the zonation of the Aragonian and Vallesian (Daams & Freudenthal, 1988) and the MN units with dates of the lower limits according to Krijgsman *et al.* (1994, 1996). The last column gives the Faunal Sets of Pickford (1981) and African localities with their radiometric ages (Pickford, 1986; other references given by Van der Made, 1996a). The central columns show suoid and bovid lineages and their European and Turkish localities. Double lines in a column indicate that in that particular lineage, the samples above the double lines are more advanced than those below; generally this is reflected in a taxonomic change. The lineages are described in detail elsewhere: *Bunolistriodon lockharti* lineage (Van der Made, 1996a), *Taucanamo* lineage (Van der Made, 1997a, 1998), *Bunolistriodon latidens* lineage (Van der Made, 1996a), *Listriodon splendens* lineage (Van der Made, 1996a), *Conohyus* lineage (Van der Made, 1989, 1990a, 1999b), *Schizochœrus* lineage (Van der Made, 1997a, 1998), *Tethytragus langai* lineage (Fig. 5; Van der Made, 1994), *Tethytragus koehlerae* lineage (Van der Made, 1994), *Parachleuastochoerus* lineage (Van der Made, 1990a, 1999b).

As a compromise, zone D was included in MN 5 (Krijgsman *et al.*, 1996). Still, there is a great difference between the estimates of the ages of the MN units based on correlations with marine strata in the western Paratethys and Spanish sections with superimposed mammal localities and long palaeomagnetic sequences. Units MN 7 and MN 8 have been united into MN 7+8 (de Bruijn *et al.*, 1992). In the present paper, MN 7 and MN 8 are used in an informal manner to indicate early or late MN 7+8, respectively.

The stratigraphy and dispersal events are synthesised in Fig. 3. The MN units, the Aragonian and Vallesian zones and the estimated ages of their lower boundaries are given in columns on the left, while Faunal Sets (Pickford, 1981), selected African and Arabian localities and their ages are given in the right column. The central columns present a selection of suoid and bovid lineages and their localities. The evolution in these lineages is gradual, though fluctuations in evolutionary rates are likely to have occurred. Besides, the samples are not evenly spaced in time. In both cases a clear difference in evolutionary level can be seen between subsequent samples. Double lines in a column indicate that for that particular lineage, the localities above the line have yielded fossils with a clearly more evolved aspect than those below. Generally, but not invariably, this coincides with a change in taxonomy.

Andrews *et al.* (1996, table 12.7) placed Engelswies and Pasalar in MN5-6 and Neudorf-Sandberg, Klein Hadersdorf and Çandır in MN6. They assigned the hominoids from Neudorf-Sandberg and Klein Hadersdorf to *Griphopithecus darwini*, those from Pasalar and Çandır to *G. alpani* and the one from Engelswies to ?*Griphopithecus* sp. This classification is maintained in subsequent papers (*e.g.* Köhler *et al.*, 1999). Engelswies yielded only a fragmentary tooth (Heizmann *et al.*, 1996), which of course is a difficult basis for an assignment to species or genus. Although Heizmann (1992) placed Engelswies in MN5 and, though the current opinion is that Pasalar is placed in MN6, Andrews *et al.* (1996) assigned both localities to MN5-6, which gives the impression that in so doing they wished to minimise the gap between Engelswies and localities for which the presence of *Griphopithecus* has been accepted. The material from Klein Hadersdorf consists of two long bones and cannot be compared directly with the type material from Çandır, nor with that from Neudorf. Nevertheless, Andrews *et al.* (1996) proposed to include *Austriacopithecus weinfurteri*, as defined on material from Klein Hadersdorf, in *G. darwini*. This obviously is not based on a comparative morphological study; the underlying assumption seems to be that a geographical grouping corresponds to a taxonomical grouping. The possibility that one species is present in all four localities or the possibility of different species with different ages was not considered.

Engelswies is in the transition of the lower to the middle unit of the Upper Sweet Water Molasse and the locality of Ravensburg is in the middle unit (Heizmann, 1992). Both localities have yielded the suid *Bunolistriodon loackharti*. The one from Ravensburg is an advanced form, typical of the end of MN5, and that from Engelswies has an evolutionary stage which is more primitive than zone E of the Aragonian (Van der Made, 1996a). The Engelswies locality should probably be placed in the later part of zone D, or low in MN 5, which corresponds to Ziegler's (1995) opinion, based on micromammals. The age is between some 16 and 14 Ma; probably closer to the latter date and therefore 1.5 to 3 Ma older than the accepted *Griphopithecus* localities.

Age estimates for Klein Hadersdorf and Neudorf-Sandberg have varied widely. Klein Hadersdorf was placed in MN 8 because of the presence of '*Gazella stehlini*' (Mein, 1986) and in the top of MN6, far above Neudorf-Sandberg, by de Bruijn *et al.* (1992). The supposed presence of the suid *Bunolistriodon loackharti* (last occurrence in MN 5) at Neudorf-Sandberg has played a role in the estimation of the age of the locality, though these fossils have subsequently been supposed to have been reworked (Mein, 1986). The presence of *Protragocerus* led Mein (1986) to place the locality in MN 8. Nevertheless, de Bruijn *et al.* (1992) placed the locality again very low in MN6, close to the boundary with MN 5. These localities have yielded mainly large mammals. There are few recent revisions of the faunas from these localities, our current knowledge being based mainly on studies published half a century ago. The detailed study of various lineages of large mammals would allow us to place these localities in a stratigraphic framework. The localities Pasalar and Çandır have usually been placed in MN 6, though the former has also been assigned to MN5. Generally, Çandır is placed above Pasalar, though usually no arguments are provided for this. The position of Çandır high in MN 6 suggests that it is much younger than Neudorf-Sandberg.

The best documented evidence for the relative stratigraphic positions of Pasalar and Çandır comes from the *Bunolistriodon latidens* lineage. The increase in mesodistal diameter of the incisors of these suids indicates that Pasalar is older than Çandır (Van der Made, 1996a; Fortelius *et al.*, 1996).

Similar trends in *Listriodon splendens* incisors and canines and increase in hypsodonty and size in the *Tethyragus langai* lineage (Bovidae) suggest that Pasalar and Çandır are older than Arroyo del Val IV & VI and Manchones I (Fig. 4; Van der Made, 1994, 1996a). Manchones I is in the type section of the Aragonian in zone C2 (Daams & Freudenthal, 1988). Changes in the *Taucanamo sansaniensis-inonuensis* lineage (Palaeochoeridae, Suidae) indicate that Pasalar and İnönü I are younger than Sansan (Van der Made, 1993, 1997a). İnönü I is older than Pasalar on the basis of two listrio-

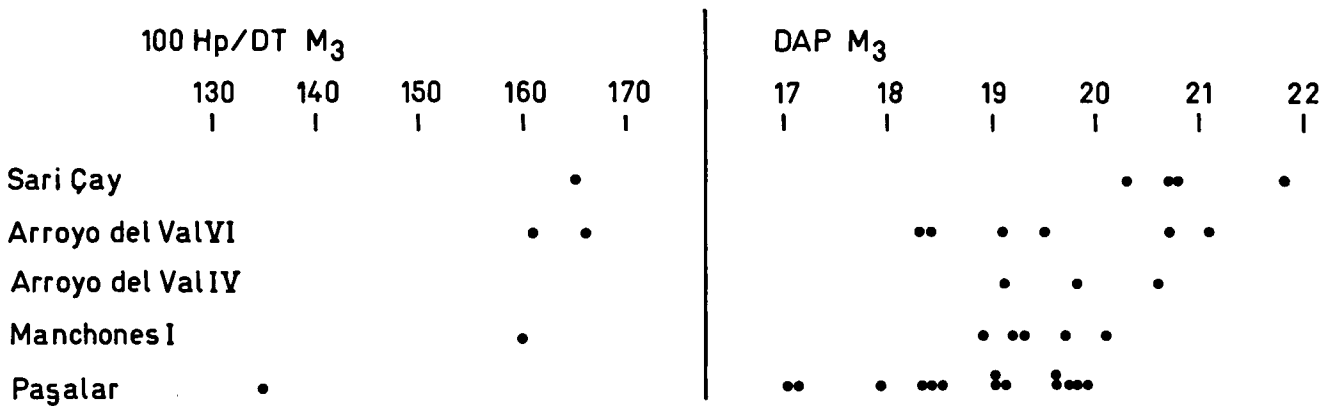


Fig. 4. Increase in length (DAP in mm) and hypsodonty (100 Hp/DT; Hp = height of the entoconid, DT = width) of the M₃ in the *Tethyragus langai* lineage. The localities are in approximate order from old to young: Paşalar (studied while in the IPS), Manchones and Arroyo del Val (IVAU), Sari Çay (studied while in the IPS).

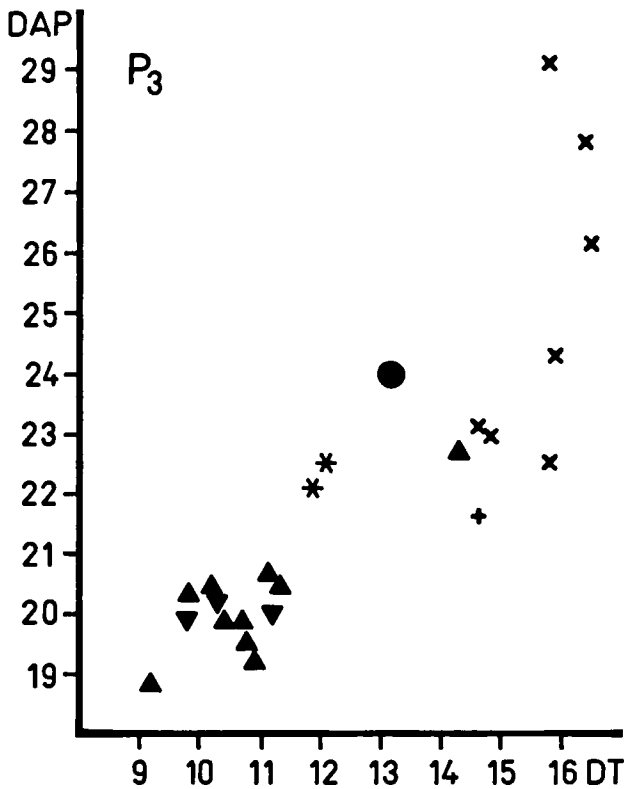


Fig. 5. Bivariate plot of length (DAP; in mm) vs width (DT; in mm) of the P₃ of *Conohyus* and *Parachleua-stochoerus*. Dot = *Conohyus simorrensis* from Klein Hadersdorf (IPUW). Cross = *Conohyus simorrensis* from Paşalar (PDTFAU, MTA, PIMUZ). Oblique crosses = *C. simorrensis* from Goriach (SLJG, NMW). Asterisks = *Conohyus ebroensis* from Fonte do Pinheiro (GML). Triangles = *Parachleuastocherus steinheimensis* from La Grive (MGL, UCBL, NMB). Inverted triangles = *P. steinheimensis* from Steinheim (SMNS, NMB).

dont lineages. Sansan is placed low in MN 6 and in zone F of the Aragonian. A short palaeomagnetic section in Sansan (Sen, 1997) may be interpreted in various ways. The date for the boundary of the G1/G2 zones (Krijgsman *et al.*, 1994, 1996) and the correlations by Van der Made (1996a) suggest for Paşalar and Çandır ages slightly older than and close to 12.5 Ma, respectively.

'*Gazella stehlini*', now referred to *Tethyragus*, is present in Klein Hadersdorf, but is not typical of MN 8; in Europe it is found in late MN 6 and in MN7. The remains from Neudorf-Sandberg that may have given rise to the citation of *Protragoceros*, are too poor for a definite assignment and the genus is likely to have appeared prior to MN 8. The remains from Neudorf-Sandberg, described as *Bunolistriodon lockharti*, belong to *Listriodon splendens*; there is no reason to assume that these fossils are reworked (Van der Made, 1996a).

Trends in incisor width and canine size and morphology (Van der Made, 1996a; using data from Mottl, 1957) of *Listriodon* suggest that:

- Klein Hadersdorf is of about the same age as Çandır and Arroyo del Val IV, *i.e.* close to 12.5 Ma;
- St Stephan is older than San Quirze and of the same age as or older than La Grive oc (oc = old collections);
- Neudorf-Sandberg is about the same age as or younger than La Grive oc (*i.e.* between 12.5 and 11 Ma, but closer to the latter date).

Following Thenius (1952), Rabeder (1978) cited *Conohyus simorrensis steinheimensis* from Klein Hadersdorf. However, it has been shown that *Parachleuastocherus steinheimensis* actually is no subspecies of *Conohyus simorrensis*, but a different species in a different genus (Chen Guanfang, 1984; Fortelius *et al.*, 1996). Although *Conohyus* reduced premolar size from *C. simorrensis* (crosses in Fig. 5) to *C. ebroensis* (asterisks), *Parachleuastocherus* has still smaller premolars (triangles).

gles). The large size of the premolar from Klein Hadersdorf (dot) indicates that these suid fossils represent *Conohyus*. Within *Conohyus*, molar size increased from *C. simorreensis* (MN 5-7) to *C. ebroensis* (MN 8-9) (Van der Made, 1989, 1998; Fortelius *et al.*, 1996). The size

of the molars from Klein Hadersdorf (Fig. 6) suggest an evolutive level between Pasalar (early MN 6) and Le Fousseret (MN 7). Data on *Listriodon* and *Conohyus* corroborate a position late in MN 6 for Klein Hadersdorf.

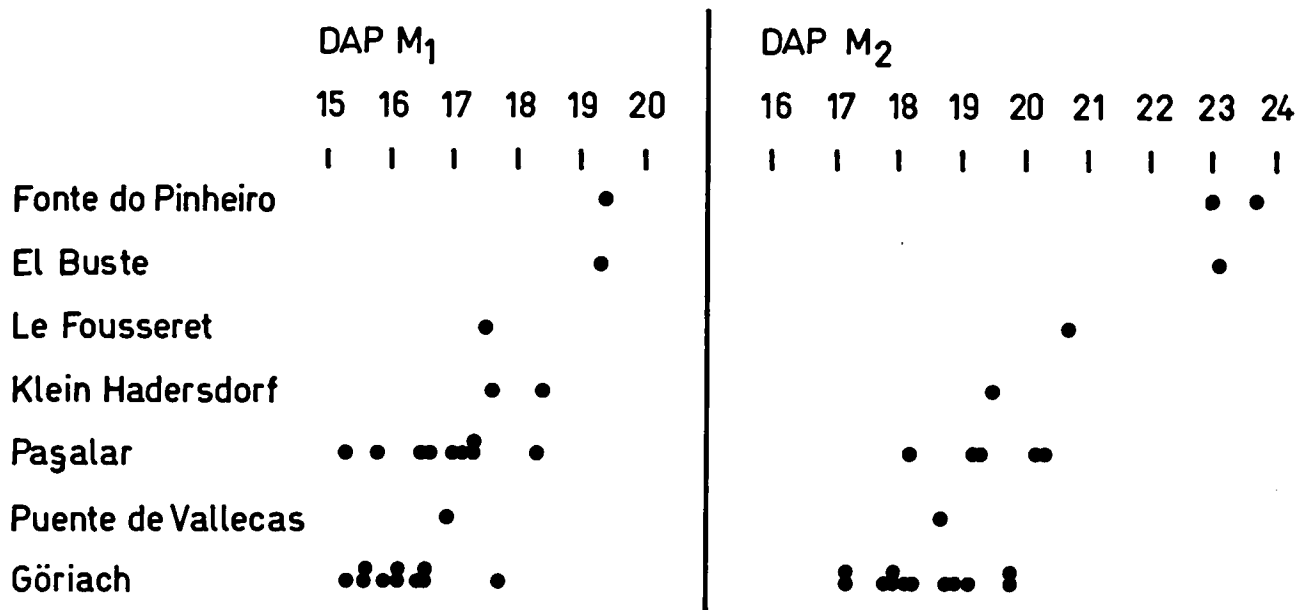


Fig. 6. Increase in length (DAP; in mm) in the first and second molars in the *Conohyus simorreensis-ebroensis* lineage. The localities are in approximate order from old to young: Göriach (SLJG, NMW, IGGML, NMB), Puente de Vallecas (MNCN), Pasalar (PDTFAU, MTA, PIMUZ), Klein Hadersdorf (IPUW), Le Fousseret (MNHN), El Buste (MPZ), Fonte do Pinheiro (GML).

At Neudorf-Sandberg, there are two small suoids, and the figures and descriptions by Thenius (1952) suggest that these do not represent *Taucanamo pygmaeus* and *Taucanamo sansaniensis*, as stated by that author, but the palaeochoerid *Taucanamo grandaeuvus* and possibly the suid *Albanohyus castellensis* (see Van der Made, 1996b, for systematics). If this observation is correct, this would corroborate a late MN 7+8 age. *A. pygmaeus* (MN 7) evolved into *A. castellensis* (MN 8) and *T. grandaeuvus* replaced the *T. sansaniensis* lineage late in MN 6 or in MN 7.

Neudorf-Sandberg is late in MN7+8, Çandır and Klein Hadersdorf are late in MN6 and Pasalar is earlier in MN6. The difference in age between Çandır and Neudorf-Sandberg might be over 1 Ma. Considering a realistic rate of evolution, the possibility exists, that the older localities have one species (*G. weinfurteri*) and Neudorf-Sandberg another (*G. darwini*). This is of course a speculation, but it is more realistic than the one by Andrews *et al.* (1996).

Dryopithecus is present in St Stephan and in the old collections from La Grive; these localities are as old as or older than Neudorf-Sandberg. The stratigraphic and geographic ranges of *Dryopithecus* and *Gryphopithecus* overlapped.

The lower levels of Hostaletts (including Can Mata) are assumed to be younger than Sant Quirze (Agustí *et*

al., 1984). St Gaudens was placed in MN 8, when MN 7 and MN 8 were still treated as different units. Lithostratigraphically, the locality is placed high in the Aragonian of the local sequence and *Propotamochoerus palaeochoerus* is cited from this locality (Ginsburg, 1971). This species appeared just prior to *Hipparion* and indicates that the locality is younger than most of the MN 7+8 localities. However, we did not succeed in finding the *P. palaeochoerus* fossils on which the citation is based.

Agustí *et al.* (1996) correlated Rudabánya with Can Llobateres on the basis of a list of supposedly shared taxa. However, taxa such as *Aceratherium incisivum* (range MN 9-12), *Hipparion primigenium* (range MN 9-11), *Dorcatherium naui* (MN6-11/12), *Listriodon splendens* (MN 6-9, but not present at Rudabánya), *Korynochoerus palaeochoerus* (MN 8-9/10), *Myoglis meini* (MN5-10), *Eomyops catalaunicus* and *Glirulus aff. lissiensis* are not particularly useful for such a precise correlation.

The use of the entry of *Cricetulodon* to subdivide MN 9, originally used by Agustí *et al.* (1984) and the evolution of the suid *Parachleuastochoerus huenermanni* into *P. crusafonti* during the later part of the *Cricetulodon* zone gives the following sequence: Hostaletts, Can Ponsic I, Can Llobateres and La Tarumba (Fig. 7; Van der Made, 1990a).

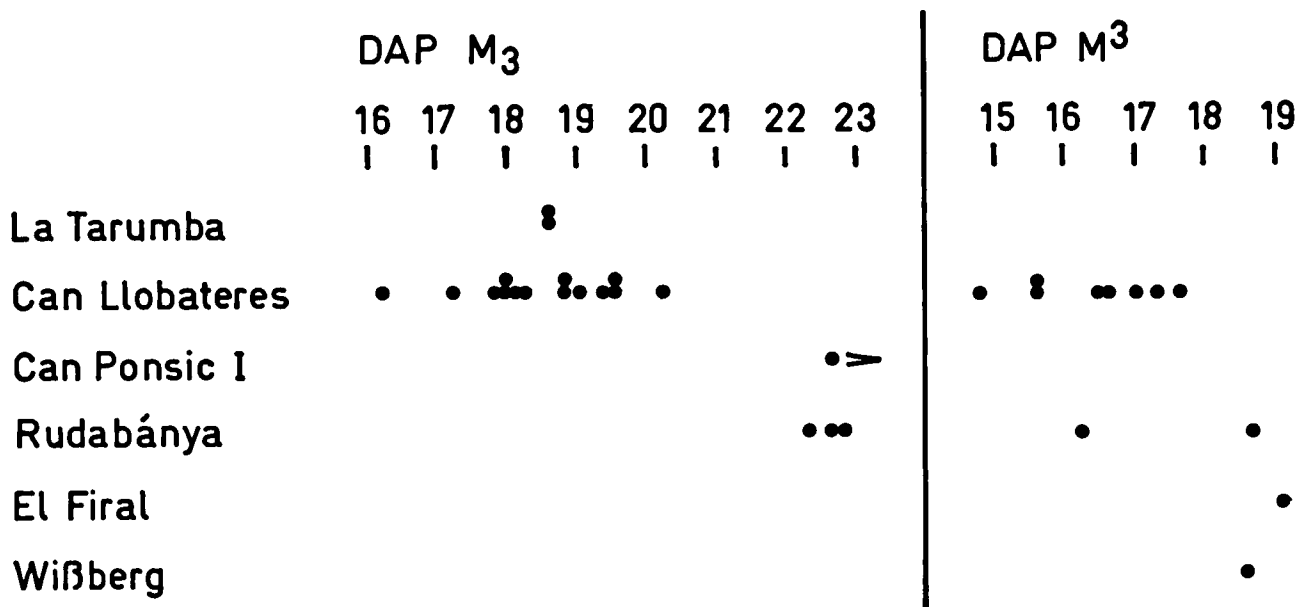


Fig. 7. Decrease in length (DAP; in mm) of the M3 of the *Parachleuastochoerus huenermanni-crusafonti* lineage. The localities are in approximate order from old to young: Wissberg (NMM), El Firal (MGB), Rudabánya (HGSB), Can Ponsic I, Can Llobateres and La Tarumba (IPS).

The presence of *P. huenermanni* and *Cricetulodon* (Agustí *et al.*, 1996, fig. 5) at Rudabánya suggests that this locality is older than Can Llobateres 1 and close in age to Can Ponsic (Fig. 7; Van der Made, 1998) and younger than Hostalets. The transition of *P. huenermanni* to *P. crusafonti* seems to be abrupt, no clearly intermediate samples being known. The Vallesian is a period of important changes and the MN 9-10 transition and the earlier part of MN 10 are marked by important faunal changes, probably caused by important changes in climate. This is called the 'mid-Vallesian crisis' and one of the effects is an important decrease in suoid diversity (Van der Made, 1990a, b; Fortelius *et al.*, 1994). It is possible that these changes caused a short period of rapid evolution in *Parachleuastochoerus*. An alternative explanation could be a gap in the record, implying that there is more time between Can Ponsic (last locality with *P. huenermanni*) and Can Llobateres (first locality with *P. crusafonti*) than we think. It is of interest that authors who recognise more than one species of *Dryopithecus* in the area assign fossils from Can Llobateres and younger localities to *D. laietanus* and the material from Can Ponsic and older localities to *D. fontani* or *D. crusafonti* (e.g. Begun, 1992a), while others assign it also to *D. laietanus* (Ribot *et al.*, 1996).

Middle Sinap has the large suid *Hippopotamodon antiquus*, like Eppelsheim (Fortelius *et al.*, 1996). This

species is replaced by its smaller relative *Microstonyx major*. In Europe this took place in MN 10 (Van der Made & Moyà Solà, 1989) and in Turkey this seems to have been the case at the same moment (Fortelius *et al.*, 1996). The oldest *Graecopithecus* locality is possibly Nikiti 1; this locality yielded *M. major* (Kostopoulos, 1994). Mein (1986), followed subsequently by Andrews *et al.* (1996), placed Melchingen in MN 9 and Salmendingen in MN 11. Mein (1986) based his data on the absence at Salmendingen of *Anchitherium* and the presence of the castorid *Dipoides problematicus*, which is common in the Turolian. Abusch-Siewert (1983) described *Anchitherium* from Salmendingen and believed the locality to be MN 9 (last occurrence of that genus). However, the 'locality' yielded a possible *Microstonyx major* tooth (Fortelius *et al.*, 1996), suggestive of the presence of MN 10-12 elements in the collection from Salmendingen. There are several fissure fillings in the area and it is not clear where the old collections come from (Abusch-Siewert, 1983). It seems more prudent to assume that the hominoid material comes from older associations, *i.e.* from MN 9.

This leaves the latest record of *Dryopithecus* in Europe as early MN 10 (La Tarumba, Polinya II); *Dryopithecus* went extinct during the mid-Vallesian crisis and there is no proof that it extended into MN 11, as suggested by Mein (1986) and Andrews *et al.* (1996).

THE DISPERSAL OF DRYOPITHECINES INTO EUROPE

In Aragonian times, Africa and Arabia were still connected and the Balkan and Anatolia formed a subcontinent, that was not always connected to western and central Europe (Rögl & Steininger, 1983). The Indian Subcontinent was in contact with Asia, but apparently little faunal exchange occurred through the Himalayan area. In the Middle East these land masses were separated by shallow seas, that became land during periods of low eustatic sea levels. At such moments faunal exchange occurred between Africa-Arabia, the Indian Subcontinent, Anatolia-Balkan and Eurasia (Europe minus Balkan and Asia minus the Indian Subcontinent). Five of such events are recognised in the Early and Middle Miocene (Van der Made, 1996a). Hominoid dispersals from Africa to Europe are expected to have taken place in one or two steps through the Turkish-Balkan subcontinent during periods of low eustatic sea level.

Haq *et al.* (1987) studied eustatic sea level fluctuations, named and dated the cycles, each starting with a sea level low. Miller *et al.* (1996) slightly corrected the ages and related eustatic sea level cycles to cyclical changes in global climate. Dispersals of terrestrial mammals that are allowed for by eustatic sea level lows should be simultaneous in the different continents. Dispersal events on the continents correspond to dates of the eustatic sea level lows as given by Haq *et al.* (1987). An intercontinental scheme of correlations was developed on the basis of suoid and bovid evolution (Van der Made, 1992b, 1993, 1994, 1996a, 1997a, b, 1999a, b) and was used to correlate dispersal events in different continents to each other and to the eustatic sea level cycles of Haq *et al.* (1987). This scheme with its corresponding ages was developed independently of the study of the palaeomagnetic sections in the Aragonian type area (Krijgsman *et al.*, 1994, 1996), but the results correspond very well. For instance, new estimates of the age of the MN 4/5 boundary (then placed at the zone D/E boundary) by Krijgsman *et al.* (1994), based on a palaeomagnetic section in the Aragonian type area and the estimates based on suoid correlations (Van der Made, 1992b) and the correlation of mammal dispersals with Haq *et al.*'s cycles (Van der Made, 1996a) are only some hundreds of thousands of years apart and both differ some 3 Ma with previous estimates.

In this model of faunal dispersals (Van der Made, 1995, 1996a, 1997b, 1999a), the first major faunal exchange between Africa and Eurasia took place **21 Ma** ago; this does not seem to have involved primates.

About **16.5 Ma** ago (beginning of TB2.3 cycle, zone C, Set IIIa, within MN 4), *Dionysopithecus* of African origin entered the Indian subcontinent. *Dionysopithecus* and *Platodontopithecus* may have entered China at this moment, or during the next cycle (Qiu & Qiu, 1995).

The next event was but one million after the previous cycle (**15.5 Ma** ago, lower boundary zone D, Set IIIb, MN 5). This short time interval makes it difficult to recognise the possible dispersal events. During this cycle or the anterior one the first hominoid seems to have reached Europe (the Engelswies hominoid). There is virtually no record of large mammals of this age in Anatolia and southeast Europe. The locality of Ad Dabtiyah with *Afropithecus leakyi* (= *Heliopithecus*) should be placed in Faunal Set IIIb, on the basis of the presence of the suid *Bunolistriodon akatikubas*, which is typical of this level and which is found also in Maboko (Africa; see Van der Made, 1996a). The possibility of a relationship between the Engelswies hominid, *Platodontopithecus*, *A. leakyi* and *Griphopithecus* is difficult to assess at this moment, but the possibility that the European and Chinese finds represent a single dispersal event by *Afropithecus* into Eurasia merits further investigation.

The event at about **14 Ma** ago (TB2.5 cycle, lower boundary zone E and Set IV, within MN 5) again brought a wave of migrants to Europe that have their origin in Africa (the pliopithecids *Pliopithecus* and *Plesiopliopithecus*), Anatolia (the rodent *Cricetodon*), the Indian Subcontinent (*Conohyus*) and from one or more of these three areas (*Sanitherium*). The bovids *Protragocerus* and *Gentrytragus* entered Africa. Fort Ternan and Pasalar belong to this cycle, though they are closer to the end of it. It is not clear whether Çandir still belongs to this cycle or to the earlier part of the next. Not later than in this cycle, *Griphopithecus* of African origin entered Anatolia. It is possible that some species of African origin had lived already for a long time in Anatolia and southeast Europe. There is virtually no record of large mammals older than 14 Ma. Fossils from the Rotem basin in Israel include a primate (Tchernov *et al.*, 1987) and may be of this age.

Around **12.5 Ma** (TB2.6 cycle, lower boundary zone G and Set V, close to the end of MN 6). The primitive bovid *Hispanomeryx* and the bovid *Tethytragus* with previous records in Anatolia, *Albanohyus*, with a previous record in Fort Ternan, Africa, the bovid *Turcoceros*, of Asian or southeast European and Anatolian origin (Van der Made, 1999a), the suid *Parachleuastochoerus*, of Asian(?) origin, and the deer *Euprox furcatus*, of Asian origin entered Europe (Van der Made, 1993, 1994, 1996a, b, 1997b, 1999a). Around this time, a number of mammal lineages went extinct in western and central Europe; e.g. the suid *Hyotherium* and the deer *Dicrocerus*, and tragulid diversity in Europe was reduced from four to one species. Crocodiles disappeared from central Europe and there seem to have been important changes in the avifauna (Van der Made, 1992a, 1993; Fortelius *et al.*, 1994, 1996) as well.

Dryopithecus was present in Europe prior to 11 Ma (La Grive oc, St Gaudens, St Stephan) and may well have entered Europe as part of the faunal exchange around 12.5 Ma. However, the Aragonian hominoid rec-

ord is very poor in Europe. The Vallès-Penedès is the area richest in hominoid localities in Europe, which possibly is partially for ecological reasons, but for geological reasons it has a very poor fossil record in the range MN5-7. Similarly, the record for this period is poor in several other areas in Europe that might have had favourable environments for *Dryopithecus* (e.g. Styrian basin, southern Germany). Alternatively, *Dryopithecus* may have arrived in Spain in the later part of MN 7+8 (Fig. 9). If this is the case, its arrival seems to coincide

with an increase in humidity in large parts of Spain at the end of MN 7+8, as indicated by the distribution of Castoridae (Daams & Freudenthal, 1988). If the Engelswies hominoid does not represent *Griphopithecus*, this genus may have entered Europe as part of the faunal exchange around 12.5 Ma. Like in the case of *Dryopithecus*, its absence in western Europe may have been due to the lack of record in areas with a favourable environment, though the ecological preferences of both hominoids are likely to have been different.

Cycles Haq et al., 1987 Lower limits Ma	Biozones Aragonian Lower limits Ma	MN units Lower limits Ma	<i>Sivapithecus</i>	<i>Kenyapithecus</i> <i>Afropithecus</i>	<i>Griphopithecus</i>	<i>Dryopithecus</i>	Faunal sets Pickford, 1981
TB3.1 10.5 Ma ± 11.5 Ma		MN 10				La Terumba Polinya Can Llobateres II	
	I	MN 9 11.1 Ma				Can Llobateres I Can Ponsic	
	H 11.1 Ma					Rudabánya El Firal ?Salmendingen ?Melchingen Mariathal Wischberg Eppelsheim	Set VI
TB2.6 12.5 Ma 12.7 Ma	G2-3 13.1-13.5 Ma	MN 7+8 12.5-13.0 Ma	Y76 10.59-11.03 Ma Y495 11.03-11.09 Ma Y663 11.03-11.09 Ma Y498 11.09-11.55 Ma Y500 11.55-11.73 Ma Y499 11.55-11.73 Ma Y496 11.86-12.12 Ma Y494 11.86-12.12 Ma Y767 11.86-12.12 Ma Y775 11.86-12.12 Ma Y750 12.46-12.49Ma	Nachola		St. Gaudens Hostalets inf. Can Mata Can Vila	Set V
		MN6 13.75 Ma			Neudorf Sandberg	St. Stephan La Grive oc	
TB2.5 13.8 Ma 13.6 Ma	F-G1 13.75 Ma			Fort Ternan > 12.6 Ma Nyakach	Pasalar		Set IV
		E 14.01 Ma	MN 5				
TB2.4 14.7-15.5	D 15.975 Ma			Ad Dabtiyah	Engelswies?		Set IIIb
TB2.3 16.5 Ma	C 16.45 Ma	MN 4					Set IIIa
TB 2.2	B			Moruorot > 16.8 Ma Buluk > 17.2 Ma			Set II

Fig. 8. Stratigraphy of European hominoid localities, the oldest *Sivapithecus* localities in the Indian Subcontinent (data from Kappelmann et al., 1991), and selected African and Arabian localities (position according to Pickford, 1986; Van der Made, 1996a).

The 12.5 Ma dispersal event is also noted in the Indian Subcontinent with the entry of *Helicopotax* and *Gazella* (Van der Made, 1996a). 12.5 Ma ago, the hominoid *Si-*

vapithecus entered the Indian Subcontinent (Kappelman *et al.*, 1991). The dispersals of *Dryopithecus* and *Sivapithecus* seem to have been coeval.

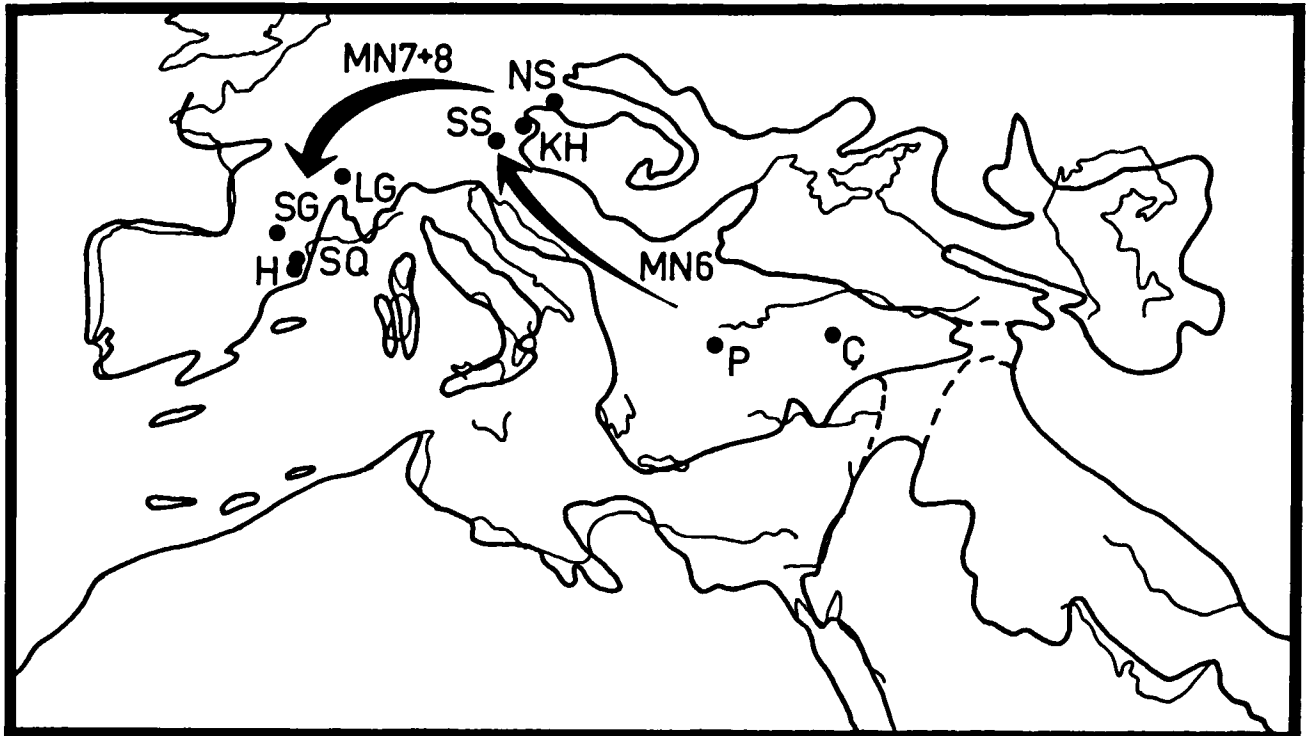


Fig. 9. Dispersal of *Dryopithecinae* into Europe; palaeogeographical reconstruction after Rögl & Steininger (1983) and Cahuzac *et al.* (1992). There are differences of opinion in correlation of continental and marine stratigraphy, which very likely have their impact on the reconstruction of the palaeogeography. Localities: Ç = Çandır, H = Hostalets, inclusive of Can Mata, K = Klein Hadersdorf, L = La Grive, NS = Neudorf-Sandberg (Dvinska Nova Ves), P = Pasalar, SG = Saint Gaudens, SQ = San Quirze, SS = St Stephan. The arrows indicate the dispersal during MN 6 and a possible dispersal during MN 7+8 (but see discussion in main text).

Agustí *et al.* (1996) thought that the common ancestor of *Dryopithecus* and *Sivapithecus* first dispersed outside Africa 15.5 Ma ago. They refer to Steininger *et al.* (1996), who did not discuss the first appearance of *Dryopithecus* in Europe, but who did use old dates for the MN 5-6 boundary (16.5-15.2 Ma) and the date of 12.5 Ma for the MN6-7 boundary. As we have seen, there is no MN 6 *Dryopithecus* locality, so the entry must have been later than 12.5 Ma. The first *Sivapithecus* is also of that age. Whether or not *Dryopithecus* and *Sivapithecus* dispersed independently, the date of the dispersal(s) is 12.5 Ma rather than 15.5 Ma. The 5 Ma period of morphological stasis assumed by Agustí *et al.* (1996) for *Dryopithecus* is therefore much too long, apart from the fact that there are nearly no early *Dryopithecus* fossils to confirm this stasis, even for a much shorter period.

Subsequent dispersals of mammals in Europe show there were few geographical or ecological barriers. In MN 8, *Propotamochoerus palaeochoerus* dispersed in Europe, in MN 9 *Hipparion* and *Hippopotamodon antiquus*, still later in MN 9, hyraxes and murids and in MN 10 *Microstonyx major* and *Schizochoerus*. The distribution of the tapirs seems to have fluctuated and appears to

have coincided largely with that of the hominoids. Many species of *Dryopithecus* with overlapping temporal and geographic ranges have been recognised (*e.g.* four by Andrews *et al.*, 1996). Their morphology and size are rather close and have not been used to demonstrate a separation in habitat and their geographic distribution and the continuous dispersal events are not in favour of geographical separation. It is not clear how parallel lineages should have evolved and maintained themselves, if this is what occurred.

Ankarapithecus from Sinap (MN 9) was supposed to be related to *Sivapithecus* (Andrews *et al.*, 1996), but is now assumed not to be related to *Dryopithecus* and *Graecopithecus*, but rather to *Sivapithecus* (Alpagut *et al.*, 1996). This is suggestive of a southeast European and Anatolian branch that evolved from *Dryopithecus* when it passed through this area on its way to western and central Europe, though alternatively, an *Ankarapithecus-Graecopithecus* lineage may have moved independently of *Dryopithecus* into this area.

The mid-Vallesian crisis occurred either at the transition from MN 9 to MN 10, early in MN 10 or in a short period starting at the MN 9-10 boundary and lasting some time into MN 10. The composition of the bovid

faunas in Spain changed (Alcalá *et al.*, 1988); it is marked by a drop in suoid diversity in Europe, but not in other parts of the Old World (Van der Made, 1988, 1990a, b, 1991), the worldwide extinction of Listriodontinae (Van der Made, 1996a) and the dispersal of murids to Europe (Van Dam, 1997). The event is interpreted as a global change towards a more seasonal climate that is related to the uplift of the Himalayas (Van Dam, 1997). As we have seen above, claims of Turolian (MN 11) dryopithecids on mainland Europe cannot be upheld and it seems that they went extinct during the mid-Vallesian crisis, while *Graecopithecus* survived in southeast Europe.

SUMMARY AND CONCLUSIONS

Suoidea tend to be common in hominoid localities. Suoid and bovid evolution provides a means of correlating of hominoid localities (Fig. 3). The stratigraphic position of most European hominoid localities and a selection of localities from Africa and the Indian Subcontinent is shown in Fig. 8: *Dryopithecus* and *Griphopithecus* probably coexisted for a considerable time in central Europe.

Hominoid dispersals into Europe are related to global events of known chronology (Figs 8, 9). The dates for these events as presented here, tend to be younger than those published previously, but are consistent with the dates from long palaeomagnetic sections in the Aragonian type area and with a model of intercontinental dispersal events and well dated eustatic sea level changes. About 15.5 or 16.5 Ma ago the first hominoid moved into Europe. This hominoid may have been, or might have given rise to, *Griphopithecus*. If this hominoid was not related to *Griphopithecus*, it seems likely that *Griphopithecus* arrived not later than 14 Ma ago in Anatolia and not later than 12.5 Ma ago in Europe. *Dryopithecus* probably entered Europe 12.5 Ma ago, though its dispersal within Europe may have been diachronous.

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