

Dryopithecus crusafonti sp. nov., a New Miocene Hominoid Species From Can Ponsic (Northeastern Spain)

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ABSTRACT Reanalysis of the sample of Miocene Hominoidea from Spain, together with the entire sample of European Miocene Hominoidea, has revealed a number of distinctive traits among the specimens from the early Vallesian locality of Can Ponsic (Crusafont and Hürzeler, 1969; Crusafont and Golpe, 1973; Hartenberger and Crusafont, 1979; Agusti et al., 1984, 1985). The Can Ponsic sample, while sharing characteristics with other samples of *Dryopithecus* from Europe, is sufficiently distinctive to form the basis for a new species. Characteristic of the new species are a distinctive lower molar occlusal morphology, large, broad upper molars, and very high crowned upper central incisors with well-developed lingual pillars. The new species shares characteristics with *Dryopithecus laietanus*, the only other species of the genus in Spain, and lacks derived features of non-Spanish *Dryopithecus*. Four species of *Dryopithecus* are now known (Begun, 1987, 1988a, and in preparation). Their distribution and morphology have significant implications for the biogeography and phylogeny of this early great ape genus.

Hominoid primates have been known from Miocene deposits in northeastern Spain since the early part of this century. The first discovery of a Miocene hominoid from Spain was a mandibular fragment from El Firal (Fig. 1), in Seu d'Urgell in the Province of Lerida (Vidal, 1913; Smith-Woodward, 1914). This specimen was attributed to *Dryopithecus fontani*, a species described earlier from St. Gaudens, on the French side of the Pyrenees (Lartet, 1856).

The Spanish sample of *Dryopithecus* was subsequently greatly increased in size by discoveries from a series of localities in the Vallés Penedés basin, to the south and east of El Firal (Fig. 2) (Villalta and Crusafont, 1944; Crusafont and Hürzeler, 1961, 1969; Crusafont and Golpe, 1973). The hominoids from the Vallés Penedés are now known from seven different localities. In the past, the specimens from these localities were assigned to a large number of different genera and species (reviewed in Simons and Pilbeam, 1965; Szalay and Delson, 1979). These reviews led to the current taxonomic consensus, which places all the Spanish Miocene

hominoid specimens in the genus *Dryopithecus*. Uncertainty persists concerning the exact number of species and their identification, but most authors recognize two species, *Dryopithecus laietanus* and *Dryopithecus fontani* (Simons and Pilbeam, 1965), or *D. brancoi* and *D. fontani* (Szalay and Delson, 1979). In both cases and in other modifications of these general conclusions (Andrews, 1985), the two recognized species are distinguished on the basis of dental size alone, with *D. fontani* always the largest (Simons and Pilbeam, 1965; Szalay and Delson, 1979).

Recent reanalysis of the Vallés Penedés and El Firal specimens along with new specimens from the Vallés Penedés (Begun, 1987, 1988a; Begun et al., 1990) is only in partial agreement with this view. Disagreement centers on which two species are represented and how they are defined. It has been shown elsewhere that size in fact does not distinguish between *Dryopithecus* species

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from Spain (Begun et al., 1990), nor does size distinguish among *Dryopithecus* species throughout Europe (Begun, 1987). These species can, however, be distinguished on the basis of morphological differences, and there is no morphological evidence in the Spanish samples for *Dryopithecus fontani*, known only from France, or *Dryopithecus brancoi*¹ (= *Rudapithecus*, *Bodvapathecus*, *Neopithecus*), known from central and Eastern Europe (Begun, 1987, 1988a). The specimens from Spain, though they are similar in size to these non-Spanish taxa, are morphologically distinctive and represent different taxa. One of these is *Dryopithecus laietanus* (Villalta and Crusafont, 1944; revised diagnosis in Begun, 1987). The second Spanish form represents a new species, which is morphologically distinct from any of the other three species of *Dryopithecus*.

BACKGROUND

The new species comes from the locality of Can Ponsic, the second richest locality in the Vallés Penedés after Can Llobateres (Begun et al., 1990). Can Ponsic is thought to be



Fig. 1. The El Firal mandible of *Dryopithecus*.

¹The Rudabánya hominoids have been attributed to the genera *Rudapithecus* and *Bodvapathecus* (Kretzoi, 1975). *Rangwapithecus* (*Ataxopithecus*) *serus* (Kretzoi, 1984) is represented by a very badly preserved maxillary fragment probably attributable to the pliopithecid *Anapithecus*, contra Begun (1988b). Much or all of the hypodigms of the two hominoid taxa have been included in the genus *Dryopithecus* in Andrews and Martin (1987), Begun (1987), and Tattersall et al. (1988). The Rudabánya hominoid sample is included here in *D. brancoi* (Begun, 1987), based on close similarities to the type specimen of this taxon, a left M_3 from Salmendingen (Germany). This is in contrast to Tattersall et al. (1988), who place it in *D. fontani*. The Rudabánya and Salmendingen samples together are more similar to *D. fontani* (Andrews and Martin, 1987; Begun, 1987; Tattersall et al., 1988) than to *Dryopithecus* from Spain. However, the type M_3 from Salmendingen and three specimens from Rudabánya share enlarged metaconids, absence of buccal cingula, absence of a tuberculum sextum, and a very distally displaced hypoconulid, all of which distinguish these specimens from *D. fontani*. They share with the M_3 of *D. fontani* reduced entoconids. These M_3 comparisons are important to note since the type of *D. brancoi* is an M_3 . In addition, based on more extensive comparisons among the samples from Rudabánya, St. Gaudens, and Spain, *D. brancoi* and *D. fontani* can be distinguished from Spanish *Dryopithecus* in having smaller, more peripheralized molar cusps, lingually steep buccal cusps, larger, deep, enclosed talonids, relatively small entoconids on M_2 - M_3 , more gracile mandibles, a narrow extramolar sulcus, and a deep mandibular symphysis (Begun, 1987 and in preparation; Begun et al., 1990). *Dryopithecus brancoi* is distinguished from *D. fontani* by having more buccolingually compressed lower canines, a broader P_3 with a prominent distolingual cingulum and a large mesial beak, a relatively larger anterior fovea on P_4 , larger premolar metaconids, reduced molar cingula, large anterior and posterior fovea on the lower molars, buccolingually constricted cusps and larger talonids, relatively elongated lower molars, a lateral prominence opposite M_1 - M_2 , and mandibles of constant depth antero-posteriorly (*D. fontani* mandibles become more shallow posteriorly). *D. brancoi* has male upper canines that are buccolingually reduced relative to M^2 , broader female upper canines, and higher crowned female lower canines than *Dryopithecus* from the Vallés Penedés (Begun, 1987 and in preparation; Begun, et al., 1990).

slightly older than Can Llobateres. This sequence is based on a lineage zonation argument involving the three rodent genera *Rotundomys*, *Hispanomys*, and *Muscardinus*, all of which are apparently more primitive at Can Ponsic than at Can Llobateres (Hartenberger and Crusafont, 1979; Agusti et al., 1984, 1985). The fauna from Can Ponsic, which is less abundant but generally similar to the fauna from Can Llobateres, is listed in Table 1.

Both Can Ponsic and Can Llobateres are placed in the MN 9 zone of mammalian biostratigraphy (Mein, 1976, 1986, 1990; Agusti et al., 1984, 1985; Moya-Solà and Agusti, 1990). Based on correlations to dated terrestrial and marine sequences, the early Vallesian, or MN 9, is thought to have begun between about 11.5 and 12.5 MYA (Bernor, 1983; Bernor et al., 1987; Mein, 1986; Steininger, 1986; Steininger and Papp, 1979; Steininger et al., 1990) (Table 2).

The depositional environment at Can Ponsic was similar to that described for Can

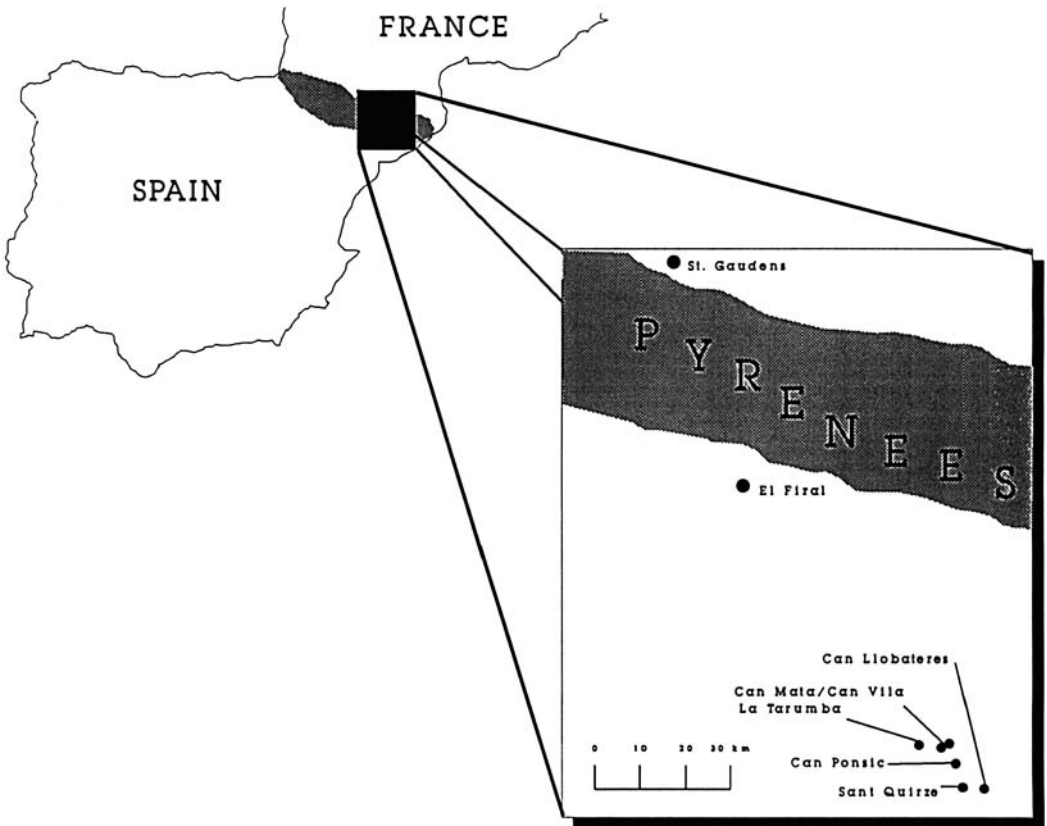


Fig. 2. *Dryopithecus* localities in Spain and the French Pyrenees.

TABLE 1. *Can Ponsic* faunal list, modified from Crusafont and Golpe (1973)

Mammalia

<i>Plesiodimylus chantrei</i>	<i>Mesomephictis medius</i>
<i>Heterosorex sansaniensis</i>	? <i>Promephitis pristinidens</i>
? <i>Palerinaceus</i> sp.	<i>Grivasmilus jourdani</i>
<i>Talpa vallesiensis</i>	<i>Amphicyon major</i>
<i>Talpa minuta</i>	<i>Pseudaelurus quadridentatus</i>
<i>Galerix exilis</i>	<i>Macrotherium grande</i>
? <i>Lantanoherium sanmigueli</i> sp.	<i>Hyotherium palaeochoerus</i>
Erinaceinae ind.	<i>Conohyus simorreensis</i>
Talpinae ind.	<i>Parachleuastochoerus crusafonti</i>
<i>Sciurus</i> cf. <i>spermophilinus</i>	<i>Dorcatherium</i> sp.
<i>Miopetaurista</i> aff. <i>grimi</i>	Cfr. <i>Euprox furcatus</i>
<i>Cryptopterus crusafonti</i>	<i>Cervidae</i> indet.
<i>Cricetodon</i> cfr. <i>ibericus</i>	<i>Miotragocerus chatrei</i>
<i>Cricetodon sansaniensis</i>	<i>Palaeotragus</i> sp.
<i>Ruscinomys thaleri</i>	<i>Dryopithecus crusafonti</i>
<i>Rotundomys</i>	<i>Hipparion catalaunicum</i>
<i>Hispanomys</i>	<i>Aceratherium incisivum</i>
<i>Muscardinus</i>	<i>Dicerorhinus sansaniensis</i>
<i>Monosaulax minutus</i>	<i>Tapirus priscus</i>
<i>Prolagus</i> cfr. <i>oeningensis</i>	" <i>Mastodon</i> " sp.
<i>Lymnonyx sinerizi</i>	<i>Deinotherium laevius</i>
<i>Machairodus aphanistus</i>	
<i>Progenetta</i> sp.	
<i>Indarctos vireti</i>	
<i>Ursavus primaevus</i>	
<i>Micromeryx flourensianus</i>	

TABLE 2. Miocene hominoid localities in Spain

MYA	Neogene continental chronology	Units	Vallés Penedés	Lerida
10	Vallesian	MN 10	La Tarumba Polinya II	
11		MN 9	Can Llobateres Can Ponsic	El Firal
12.5	Aragonian	MN 8	Sant Quirze Can Mata Can Vita	

Llobateres (Begun et al., 1990) and consisted of channel and floodplain or deltaic sediments, though details of the sedimentology and microstratigraphy have yet to be fully analyzed. The fauna from Can Ponsic, like that from Can Llobateres, suggests a relatively moist, forested biotope, which is compatible with the geologic evidence, although detailed work on this faunal material has also not yet been undertaken. Evidence from analyses of large scale paleoclimatic changes in the northwest Mediterranean area, and in particular in the Vallés Penedés and other fossiliferous basins in Spain, is also consistent with this picture. For example, comparative analysis of rodent faunas in Spanish middle/late Miocene sedimentary basins (Daams et al., 1988; Agustí et al., 1984), Mediterranean microplankton (Muller, 1984), clay minerals, stable isotopes and planktonic foraminifera (Chamley et al., 1986) and other geologic evidence (Lopez-Martinez et al., 1987) all suggest cooling and higher humidity during the transition from late Aragonian to early Vallesian in the northwest Mediterranean. Increased humidity at this time coincides with the introduction of hominoids into these faunas. Subsequent decline of cool, humid conditions in the Turolian occurs as the hominoids disappear from the Spanish fossil record.

SYSTEMATICS

The characteristics of the Can Ponsic hominoid sample are sufficiently distinctive to warrant the identification of a new species of the genus *Dryopithecus*.

Order Primates Linnaeus, 1758
Superfamily Hominoidea Gray, 1825
Species *Dryopithecus crusafonti* sp. nov.

[= *Dryopithecus fontani* (Lartet, 1856); *Hispanopithecus laietanus* (Villalta and Crusafont, 1944; Crusafont, 1958); *Dryopithecus (Dryopithecus) fontani* (Simons and Pil-

TABLE 3. Features of *Dryopithecus crusafonti* compared with other *Dryopithecus*

Distinguishing features of <i>Dryopithecus crusafonti</i>	
Very high crowned, relatively narrow I ¹	
Well developed I ¹ median and mesial lingual pillars	
M ¹ and M ² ln × bd the same	
Elongated (mesiodistally) upper premolars ¹	
Broad male upper canine	
Absence of molar cingula	
Lower molar buccal cusps, separated by deep, narrow fissures	
A long molar postmetaconid cristid continuous with a short preentoconid cristid	
Broad upper molars ²	
?Delayed molar enamel perforation	
Features shared with <i>Dryopithecus laietanus</i>	
Robust mandibular corpora ³	
Broad extramolar sulci ³	
Molars with relatively broad, rounded cusps	
Shallow, restricted talonid basins and premolar fovea	
Long premolars relative to breadth	
Narrow upper central incisors relative to breadth	
Features shared with <i>Dryopithecus</i>	
Thinner enamel	
Narrow I ¹ (exceptionally narrow in the new species)	
Peripheralized cusps	
M ¹ close in size to M ²⁽⁴⁾	
Large elongated premolars ⁴	
Elongated upper molars ⁴	
Reduced premolar cusp heteromorphy ⁴	
Reduction or absence of molar cingula ⁴	

¹Distinct from *Dryopithecus brancoi*.

²Distinct from *Dryopithecus laietanus*.

³Known from El Firal.

⁴Great ape and human synapomorphies.

beam, 1965; Szalay and Delson, 1979); *Dryopithecus (Dryopithecus) laietanus* (Simons and Pilbeam, 1965); *Dryopithecus (Dryopithecus) brancoi* (Szalay and Delson, 1979); *Dryopithecus* sp. (Crusafont and Golpe, 1973); *Hispanopithecus* sp. (Crusafont and Golpe, 1973).]

Diagnosis

A species of *Dryopithecus* that is distinguished from other species of the same genus by the following features (Table 3): very high crowned, relatively narrow I¹, with well developed I¹ median and mesial lingual pillars; M¹ and M² length × breadth that are nearly identical (Table 4); a male upper canine that is broad relative to mesiodistal length; absence of molar cingula; lower molars with broad, low buccal cusps separated by deep, narrow fissures; shallow, restricted talonid basins; and a long molar postmetaconid cristid continuous with a short preentoconid cristid (Table 3a). *Dryopithecus crusafonti* differs from *D. brancoi* in having large, relatively narrow (mesiodistally elongated) upper premolars (Figs. 3, 4) and from *D. laieta-*

TABLE 4. *Dryopithecus crusafonti* tooth dimensions (mm)

Upper teeth	Acc. no.	Mesiodistal	Buccolingual	Height
I1	IPS 1807	7.6	6.2	11.4
	IPS 1808	7.7	6.2	10.7 (worn)
	IPS 1809	7.8	6.7	12.5
C	IPS 1799	12.2	9.6	
	IPS 1798	7.7	10.0	
	IPS 1806	7.3	9.7	
	IPS 1810	7.5	9.8	
P3	IPS 1817	7.4	10.0	
	IPS 1798	6.9	10.4	
	IPS 1798	8.8	10.7	
M1	IPS 1815	9.5	11.1	
	IPS 1818	9.6	11.4	
	IPS 1798	9.1	10.4	
M2	IPS 1814	—	11.0	
	IPS 1820	10.6	12.0	
	IPS 1821	9.6	11.0	
	IPS 1812	10.5	12.0	
Lower teeth				
P4	IPS 1781	7.4	6.6	
M1	IPS 1813	—	9.3	
M2	IPS 1816	11.5	9.4	

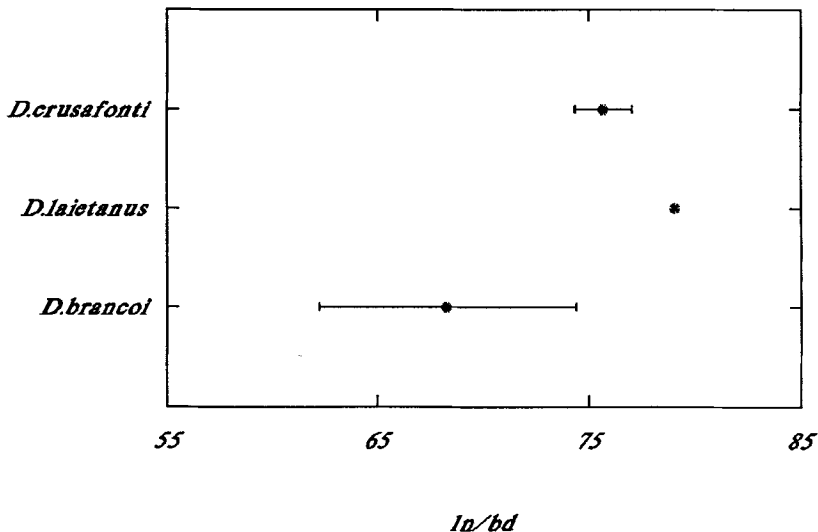


Fig. 3. Means and standard deviations for P^3 $(\ln/bd) \times 100$ in three species of *Dryopithecus*. Samples are: *D. crusafonti*, $n = 4$; *D. brancoi*, $n = 5$; *D. laietanus*, $n = 1$. The *D. crusafonti* and *D. brancoi* samples are significantly different at the $P \leq 0.05$ level, Mann-Whitney U test statistic = 2.00, chi-square approximation = 3.84.

nus in having relatively broader upper premolars and molars (Fig. 5). *D. crusafonti* shares with other species of the genus *Dryopithecus* thinner enamel (compared to such thickly enamelled forms as *Kenyapithecus* and *Sivapithecus*), and narrow I^1 (exceptionally narrow in the new species). *D. crusafonti*

shares with other *Dryopithecus* and with living great apes an M^1 close to size to M^2 , relatively large, elongated premolars and elongated upper molars, reduced premolar cusp heteromorphy, and reduction or absence of molar cingula, all of which distinguish *Dryopithecus* and the living great apes

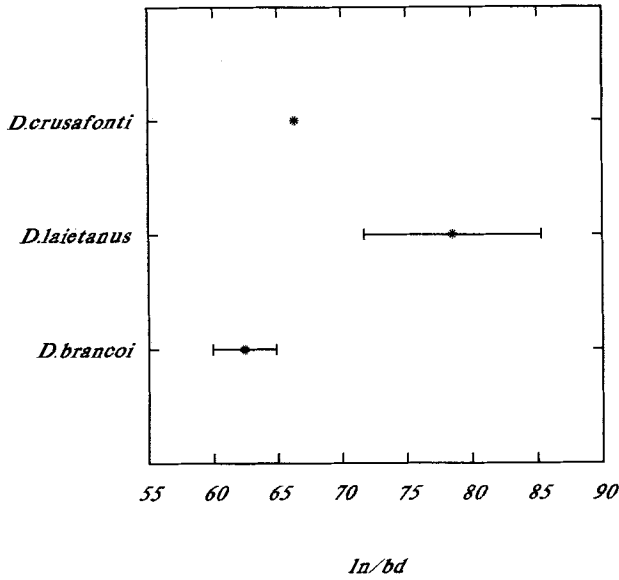


Fig. 4. Means and standard deviations for $P^4 (ln/bd) \times 100$ in three species of *Dryopithecus*. Samples are: *D. crusafonti*, n = 1; *D. brancoi*, n = 6; *D. laietanus*, n = 2.

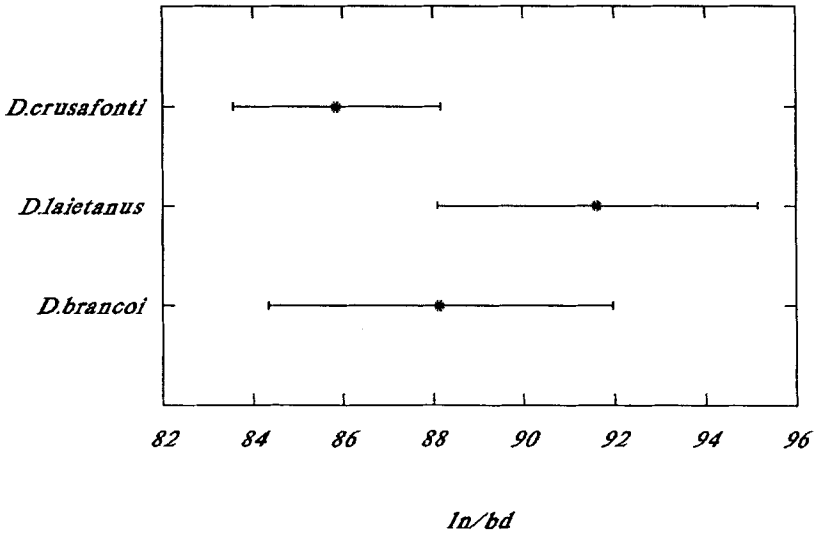


Fig. 5. Means and standard deviations for $M^{1-2} (ln/bd) \times 100$ in three species of *Dryopithecus*. Samples are: *D. crusafonti*, n = 6; *D. brancoi*, n = 12; *D. laietanus*, n = 4. The samples (probably *D. crusafonti* and *D. laietanus*) are significantly different at the $P \leq 0.05$ level, Kruskal-Wallis test statistic = 6.033.

from Early Miocene East African catar-rhines (Andrews, 1985).

Holotype

The holotype is IPS 1798/1799 (27), a crushed maxillary fragment with the left

C-M². The specimen and all material included in the hypodigm are part of the collections of the Institut Paleontologic Miquel Crusafont in Sabadell, Spain. Numbers in parentheses refer to old IPS catalogue numbers, some of which have appeared in print.



Fig. 6. IPS 1798-1799, the holotype of *Dryopithecus crusafonti*.

Type locality

Can Ponsic, Vallés Penedés, Spain.

Distribution

The late Miocene (early Vallesian) of Can Ponsic.

Hypodigm

IPS 1781 (30) rt. lower P4; IPS 1806 (33) lt. upper P3; IPS 1807 (34) rt. upper I1; IPS 1808 (36) lt. upper I1; IPS 1809 (35) lt. upper I1; IPS 1810 (32) rt. upper P3; IPS 1812 (3) rt. upper M3; IPS 1813 (72) rt. lower M1 fragment; IPS 1814 (47 or 74) rt. upper M2 fragment; IPS 1815 (4) lt. upper M1; IPS 1816 (71) rt. lower M2; IPS 1817 (52) rt. upper P3; IPS 1818 (29) lt. upper M1; IPS 1820 (28) lt. upper M2; IPS 1821 (31) rt. upper M2.

Most of these specimens are listed without catalogue numbers in Crusafont and Hürzeler (1969). IPS 1814 is figured in Crusafont and Golpe (1973), although it is mislabelled IPS 53. IPS 1819 (51), also from Can Ponsic and figured in Crusafont and Golpe (1973), is not primate.

Etymology

Etymology is in honor of Professor Miquel Crusafont-Pairo, who contributed greatly to our understanding of Neogene vertebrate evolution.

DESCRIPTION

The type specimen, IPS 1798-1799 (Fig. 6), includes a distorted left upper tooth row with P³ to M² in line, but twisted distobuccally. All

teeth are displaced relative to one another, and are held together by a combination of maxillary fragments and matrix, but no maxillary morphology is preserved. The left upper canine, missing much of its crown, is detached from this matrix. Dimensions of the teeth of IPS 1798-1799 and all other specimens attributed to *Dryopithecus crusafonti* appear in Table 4.

The canine, known only from the type specimen, is broader relative to length than RUD 44 from Rudabánya, attributed to *Dryopithecus branchoi* (Begun, 1987, 1988a) and similar in this regard to IPS 41, a large canine from Can Llobateres. It is large relative to the postcanine dentition, with a robust root and a crown poorly distinguished from the root at the cervix, all of which indicate that the individual was male. A broad, transversely flat wear facet marks the distolingual surface of this tooth, and runs onto a distal cingulum along the distolingual corner of the crown cervix. The cross-section at the cervix is oval with the long axis oriented mesiodistally. The root is strongly curved in buccal or lingual view, especially along the mesial edge.

The P³ of the type is relatively long mesiodistally and high crowned, especially buccally. The buccal edge, which is only moderately longer than lingual edge, is marked by small accessory cusps on the mesial and distal ends of the strong pre- and postparacrista, which are flattened somewhat by wear. The buccal crown surface is flared and extends some distance onto the root. The paracone is slightly more prominent than

the protocone. These are connected by a flattened and mesially convex crest (possibly the lateral protocrista), which also serves to separate a large trigon distally from a well-developed anterior fovea. The pre- and post-protocrista and the protocone are well worn yet no dentine is exposed. The postproto-crista is worn to a large facet continuous with the large talon buccally. Three other upper P³s are known. IPS 1806, 1810, and 1817 (Fig. 7) are all less worn but morphologically quite similar to the IPS 1798 P³. One of these, IPS 1806, had three roots, while the other isolated P³s have two. P⁴, known only from the type, is also mesiodistally long and high crowned. Buccally it is less flared and shorter than the P³. In occlusal view it is rectangular, with protocone and paracone of equal size. The trigon is expanded distobuccally, where it is continuous with a broad, flat wear facet on the postprotocrista, as is the case on the P³. Also similar to the P³ is the pattern of wear, which has formed thick ridges of the P⁴ crista, partially filling the talon and anterior fovea, with only a tiny dentine pit exposed on the protocone tip.

The M¹ of the type is nearly square, being only slightly broader than long. A dentine pit covers much of the protocone, while the hypocone is marked by a tiny dentine pit. The cusps are peripheralized, or shifted toward the edges of the crown, as in *Dryopithecus* generally. A well-developed ectohypocrista traverses the tooth buccally from the hypocone between facets 10 and 12 (Maier, 1984) of the talon. The trigon is large and shallow, and bordered by distinct but flatly worn preprotocrista and crista obliqua. The metacone is slightly smaller than the mesial cusps and is lingual relative to the paracone. The postparacrista and premetacrista are short and meet midway between the buccal cusps. A small lingual cingulum marks the mesiolingual corner of the tooth. A very small anterior fovea occupies the mesiobuccal corner of the occlusal surface. Two isolated upper M¹s are also attributed to *Dryopithecus crusafonti*. Both the M¹ crown germ IPS 1815 and the slightly worn IPS 1818 (Fig. 7) are morphologically very similar to the M¹ of the type.

The M² of the type (IPS 1798) is broadly similar to the M¹ of the same specimen. It is longer but narrower than the M¹, such that the M² surface area as estimated by length \times breadth is actually slightly smaller than M¹ (see Table 4). Other differences include a somewhat larger anterior fovea, reduced

metacone, relatively longer postparacrista, and no entocingulum. A facet for the M³ is preserved. IPS 1820 (Fig. 7) is a slightly worn isolated M² which is larger but morphologically quite similar to the type. Like IPS 1798, IPS 1820 has a large, shallow trigon, somewhat reduced metacone relative to the mesial cusps, a distinct ectohypocrista, a small paraconule, a small, constricted anterior fovea, and a more expanded posterior fovea. Unlike the IPS 1798 M², IPS 1820 has a small entocingulum just mesial to the protocone. IPS 1821 (Fig. 7) is a more strongly worn isolated upper molar that is most likely to be an M², based on its reduced metacone relative to the mesial cusps and its better developed paraconule. IPS 1814 (Fig. 7) is a slightly worn upper molar fragment probably assignable to M², lacking the distolingual corner of the crown. It is similar to IPS 1812 (Fig. 7), an M³ (see below), in crown height but closer to IPS 1798, 1820, and 1821 in having, relative to IPS 1812, a relatively larger metacone, a smaller paraconule, a small entocingulum (IPS 1798 and 1820), a less constricted trigon, and a less distally oriented postmetacrista.

M³ is represented by a single specimen, IPS 1812. IPS 1812 is a slightly worn and very low crowned M³. The metacone is greatly reduced, while the hypocone is expanded, being the largest cusp, and filling in the talon lingually. A large paraconule, as large as the paracone, is present mesiobuccally. The trigon is shorter than in the more anterior molars, the anterior fovea slit-like, and the crista obliqua truncated and less well defined. All of these characteristics are typical of hominoid last upper molars.

Perhaps the most distinctive features of the dentition of *D. crusafonti* are the upper central incisors, of which three are preserved (Fig. 8). IPS 1807 and IPS 1809 are right and left I¹s, respectively. They are morphologically very similar, though IPS 1809 is somewhat larger and slightly more worn. Both are very high crowned relative to length and breadth (Table 4; Fig. 9) and have very strongly developed mesial and median pillars and distal cingula.

The mesial and median pillars are constricted mesiodistally and are separated by deep fissures, which also separate the median pillar from the distal cingulum. The crowns are very narrow and asymmetrical, the incisive edges having more rounded distal corners. The crowns extend substantially onto the root labially and lingually causing

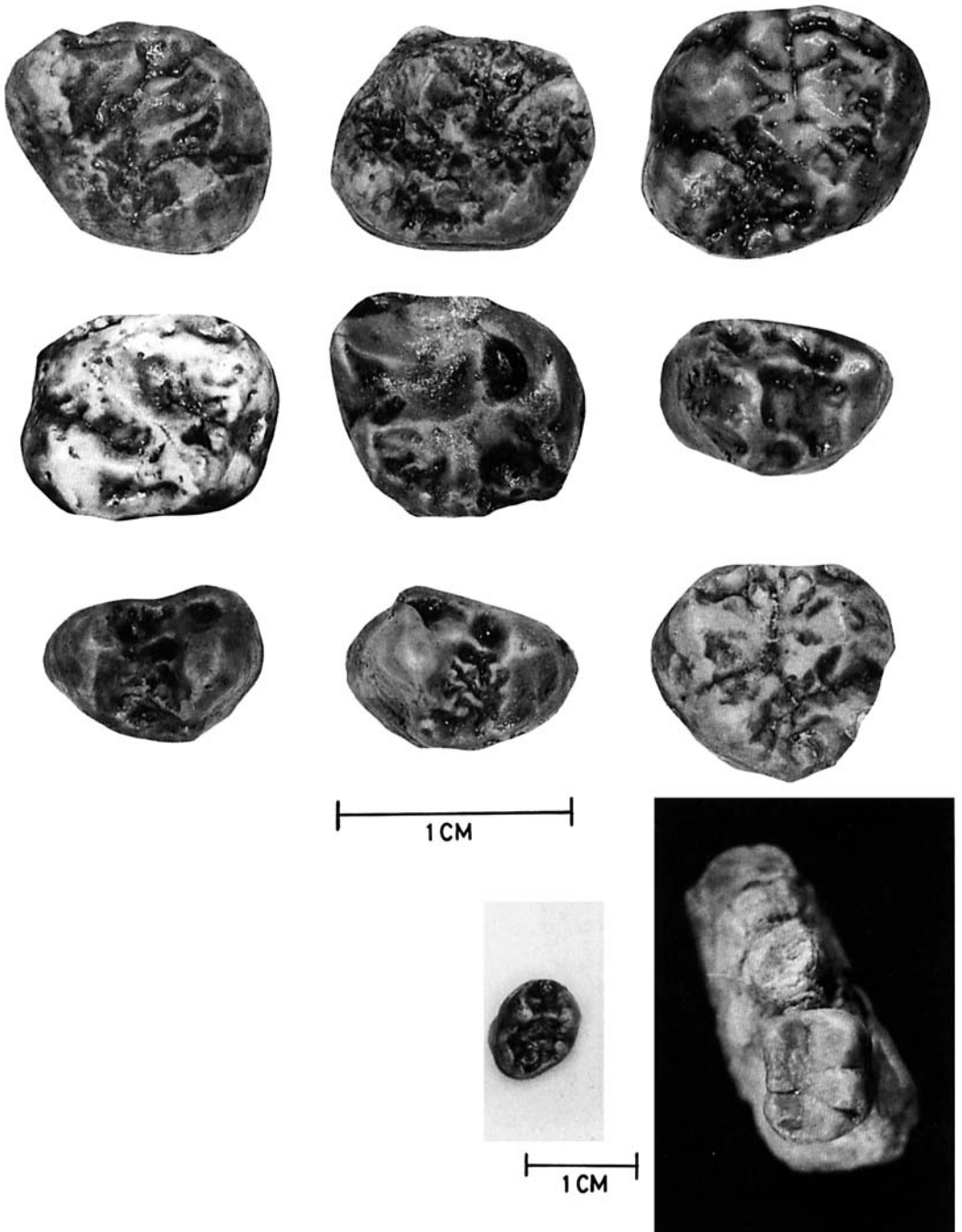


Fig. 7. Postcanine specimens attributed to *Dryopithecus crusafonti*. From left to right, top row: IPS 1812 (RM³), 1815 (LM¹), 1820 (LM²); second row: IPS 1818 (LM¹), 1821 (RM²), 1810 (RP³); third row: IPS 1806 (LP³), 1817 (RP³), 1814 (RM²). All casts. Bottom row, left to right: IPS 1781 (RP₄, cast), IPS 1816 (RM₂, original).



Fig. 8. Upper central incisors of *Dryopithecus crusafonti* and *Dryopithecus laietanus*. Column one, from left to right, first row: IPS 1807 labial, lingual; second row: IPS 1809 labial, lingual; third row: IPS 1808 labial, lingual. Column two, first row: IPS 1770 labial, lingual; second row: IPS 1778, labial, lingual. Original specimens, natural size.

the cervical line to curve strongly on the root from close to the level of the median pillar mesially and distally to well up toward the root tip labially and lingually. IPS 1808 is a left I^1 that in most respects is identical to the

other two, but with a curious pattern of occlusal wear. The interstitial facet for the right I^1 is much larger than on the other specimens and is concave and tilted distally off the long axis of the tooth, whereas in IPS

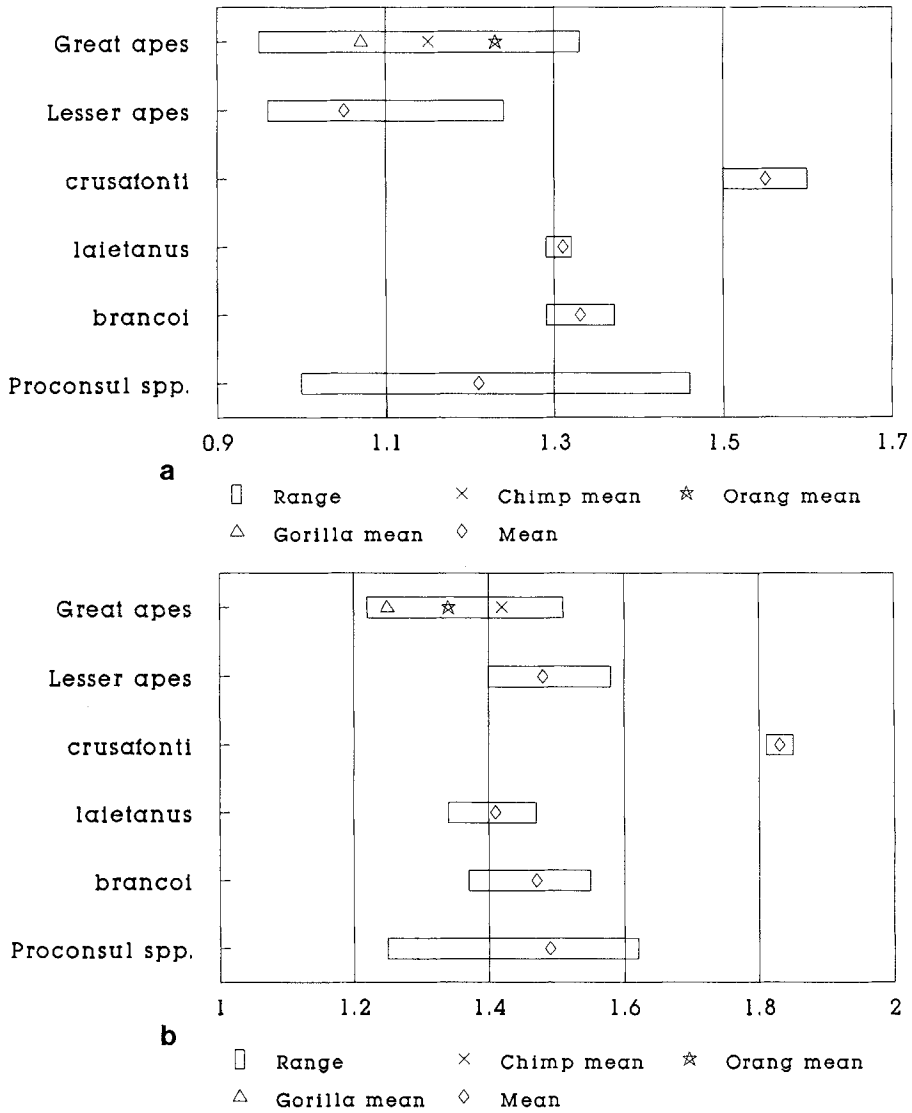


Fig. 9. a: Means and ranges of upper central incisor crown height relative to crown mesiodistal length in apes (n = 38), *Dryopithecus crusafonti* (n = 2), *D. laietanus* (n = 2), *D. brancoi* (n = 4) and in *Proconsul* (n = 13). Data from Andrews (1978) and personal observations.

IPS 1808 excluded due to excessive crown wear. b: Means and ranges of upper central incisor crown height relative to buccolingual breadth in apes, three species of *Dryopithecus*, and *Proconsul*. Data sources and sample sizes as in Fig. 9a.

1807 and 1809 it is aligned with the long axis. The lingual face has been worn nearly flat and bears a broad occlusal facet oriented obliquely from the sharpened incisive edge labially to flattened mesial and median pillars lingually. The distolingual corner of the crown has been removed by wear, which has formed a very large, deeply concave facet. The distolingual facet appears to have been

formed by occlusion with the lower canine, which normally occludes with I², and which might suggest that IPS 1808 is an upper lateral incisor (in fact, it was initially identified as such [Crusafont and Hürzeler, 1969]). However, the overall morphology of the tooth, which is very similar to the other upper central incisors from Can Ponsic, and the angle of the interstitial facet and its size

and concavity are all consistent with the view that IPS 1808 is an upper central incisor that was implanted strongly obliquely, with its root pointing laterally and occupying part of the space normally reserved for the upper lateral incisor alveolus. Reorienting the long axis of the tooth in this manner brings the surface of the interstitial wear facet into alignment with the sagittal plane. Because this upper central incisor was implanted in this way, the upper lateral incisor must either have never erupted, or was lost or displaced, all of which are known to occur in living primates.

The lower dentition of *Dryopithecus crusafonti* is represented by only three isolated specimens. IPS 1781 (Fig. 7) is a small, unerupted, relatively long lower P4 crown. The protoconid and metaconid are of equal size, buccolingually constricted and small relative to the large, low talonid. These mesial cusps are linked by well-defined, transversely straight medial and lateral protocristids, which are separated by a deep fissure. The protocristids separate a large anterior fovea, defined mesially by a low, weak preprotocristid and premetacristid, from a long talonid, which is surrounded by well-developed accessory cusps. The entoconid is large, being similar in size to the mesial cusps, which causes the crown to bulge distolingually. The hypoconid is small and linked to the entoconid by a well-developed posthypocristid, which is long and oriented distolingually, giving the talonid a truncated, lingually displaced appearance.

IPS 1816 (Fig. 7) is a lower M₂ with the roots embedded in matrix. The crown is elongated and the cusps peripheralized, the protoconid being the largest. The rounded yet slightly worn buccal cusps are separated by narrow fissures. The hypoconid and hypoconulid are equal in size. The lingual cusps are more buccolingually constricted than the buccal cusps. The postmetaconid cristid is particularly well developed and straight (as opposed to concave buccally, as in most *Dryopithecus*). Between it and the short preentocristid is a well-developed accessory cusp. The talonid basin is shallow and lingually placed, and the foveae are broad and short mesiodistally. The crown is only slightly worn and there is no trace of a facet for the last molar. IPS 1813 is a distal portion of a lower M1 lacking both mesial cusps. Like IPS 1816, the talonid basin is shallow and cusps are broad. The buccal cusps are worn, with dentine pits confined to the tips of the

hypoconid and hypoconulid. The posterior fovea is restricted to the distolingual corner of the tooth.

DISCUSSION

The features listed in Table 3 and discussed above provide evidence that the Can Ponsic sample is distinct from other samples attributed to *Dryopithecus*. These teeth are consistently more distinct from other *Dryopithecus* teeth than are, for example, the teeth of *Pan paniscus* from those of *Pan troglodytes* (Kinzey, 1984). In some features, such as incisor morphology, the Can Ponsic specimens are strongly divergent. Despite these species-level distinctions in dental morphology, the sample from Can Ponsic is clearly attributable to *Dryopithecus*. As noted above, the sample shares with other *Dryopithecus* such features as peripheralized molar cusps, narrow, labiolingually robust upper central incisors, and an occlusal wear pattern that produces isolated dentine pits.

Spatulate upper incisors

Among the unique attributes of the sample from Can Ponsic is the wear on IPS 1808 (Fig. 8), which causes this tooth to superficially resemble a spatulate upper lateral incisor (see above). Andrews (1985) lists spatulate upper lateral incisors as a characteristic of *Dryopithecus* shared only with chimpanzees and humans among living hominoids. Therefore, the re-identification of the spatulate IPS 1808 as an upper central incisor is of some importance. Removing this specimen from the sample of *Dryopithecus* upper incisors leaves only two specimens (IPS 1790 (54), from Can Llobateres and RUD 15 from Rudabánya). Both of these specimens resemble the upper lateral incisors of Miocene hominoids generally, which are peg shaped with asymmetrical crowns. Thus there is no evidence that *Dryopithecus* shares spatulate upper lateral incisors with chimps and humans.

Occlusal wear

The pattern of wear shared among *Dryopithecus* species includes the presence of isolated dentine pits appearing at the cusp tips after relatively little occlusal wear. This is commonly explained by suggesting either that the teeth have a relatively thin enamel layer, or that they have prominent dentine horns, or both. The enamel thickness of the Can Ponsic teeth and the configuration of the enamel dentine junction have yet to be

examined directly. However, the morphology and the pattern of occlusal wear on Can Ponsic molars suggest some differences from other *Dryopithecus*. Nearly all the specimens from Can Ponsic show some occlusal wear, yet only three molars have any sizeable perforations of their enamel layer. In both IPS 1798 and IPS 1821 dentine pits are confined to the protocone and in IPS 1813 pits occur at the tips of the hypoconid and hypoconulid. The enamel rims that surround these perforations are thicker and very flat compared to most other *Dryopithecus* molars. This pattern of wear is most similar to that seen on *Pongo* molars and on the molars of the El Firal mandible. In other specimens of *Dryopithecus*, such as *Dryopithecus brancoi* from Rudabánya, molars are much more strongly worn in general, and among less worn specimens, perforations occur on all cusps with very little wear. These perforations appear to have coalesced earlier (i.e., after relatively little wear as opposed to rapidly following a longer period of wear), and the rims of enamel surrounding them are narrow and rounded or inclined into the pit. This pattern of occlusal wear is most similar to that seen on the molars of African apes and gibbons. The wear pattern differences between *Dryopithecus brancoi* and *Dryopithecus crusafonti*, plus several morphological differences distinguishing Can Ponsic from other *Dryopithecus* molars, (shallower, more restricted basins, and broader, more rounded cusps), suggest that enamel thickness and patterns of occlusal wear may have differed among *Dryopithecus* species. It is currently not possible to say in precisely what manner the enamel on *Dryopithecus* teeth was developed (Martin, 1985). Nevertheless, a single pattern of occlusal wear, enamel thickness, and enamel-dentine junction morphology may not serve to adequately describe variation in *Dryopithecus*.

Size diversity

The sample attributed here to *Dryopithecus crusafonti* is relatively homogeneous in size. However, Martin (personal communication, and cited in Kelley and Pilbeam, 1986) has suggested that two species are present at Can Ponsic, primarily on the basis of size variation. Szalay and Delson (1979) tentatively assign the sample from Can Ponsic to two species of *Dryopithecus* again on the basis of size. Within the subsample of each tooth type (e.g., within the sample of upper first molars), there is no indication of size

variation in excess of that expected within a single species (Begun et al., 1990). Between tooth types, however, the difference in size between P_4 and M_2 is relatively large, and is perhaps the major reason for the view that more than one taxon might be represented.

The only P_4 from Can Ponsic, IPS 1781, is quite small relative to IPS 1816, an M_2 , the only other complete lower tooth, and one of the largest molars in the Vallés Penedés collection. The breadth of the Can Ponsic P_4 is 70% of the M_2 breadth, and its length just 64% of the M_2 length. However, comparisons to modern hominoids and to other samples of *Dryopithecus* reveal that even these size differences are not indicative of the presence of more than one species. Both fossil length and breadth ratios are between the minima (smallest P_4 /largest M_2) and maxima (largest P_4 /smallest M_2) of modern hominoids and two of three *Dryopithecus* species (Fig. 10a). Thus, although small, the lower fourth premolar from Can Ponsic is well within the expected range of variation in relative size among isolated teeth of a single species.

It is not possible to be certain whether or not P_4 was small in general within individual dentitions or if the Can Ponsic collection just happens to sample different individuals toward opposite extremes of size variation. The fact that the upper premolars of the type specimen (IPS 1798) are large relative to the molars suggests that the lower premolars were probably not excessively reduced in size compared to lower molars of the same individuals. Thus, the apparently small size of IPS 1781 is probably an artifact of small sample size.

When dental measurements from the Can Ponsic sample are applied to the formulas for estimating body weights provided by Gingerich et al. (1982), the body weight estimates based on most of the postcanine teeth fall between 23.3 and 31.2 kg. Differences in the reliability of different teeth as predictors of body weight as well as the presence of other sources of taxon specific dental size variation (diet, social organization, etc.), make the absolute values of these estimates of uncertain significance. However, the fact that most of the postcanine teeth from Can Ponsic predict similar body weights means that they probably come from individuals of similar size, which is consistent with the view that they can all be attributed to a single taxon, regardless of exactly what size it was. The tooth that predicts the lowest body weight is the upper second molar of the type

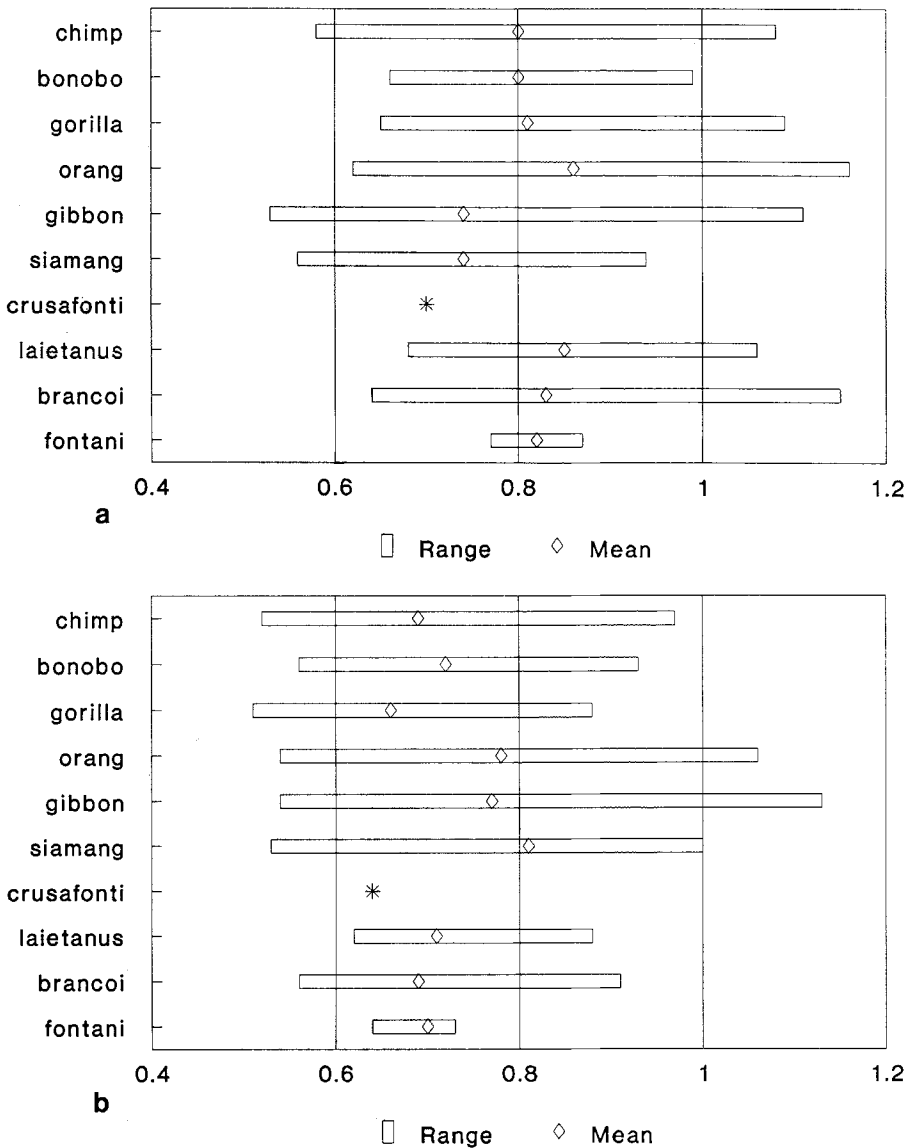


Fig. 10. a: P_4 breadth relative to M_2 breadth in living apes and in four species of *Dryopithecus*. P_4/M_2 sample sizes are: chimp, $n = 121/141$; bonobo, $n = 18/19$; gorilla, $n = 145/153$; orang, $n = 74/90$; gibbon, $n = 61/58$; siamang, $n = 35/20$; *D. crusafonti*, $n = 1/1$; *D. laietanus*, $n = 4/8$; *D. brancoi*, $n = 4/7$; *D. fontani*, $n = 3/4$. The horizontal bars reflect minimum and maximum values using opposite ends of the size ranges of individual teeth (smallest/largest = minimum; largest/smallest = maximum). This is not intended to express a range of variation in the ratio of two dimensions within individuals,

because this aspect of P_4-M_2 size variability is not preserved in the Can Ponsic sample. Instead, it expresses the maximized range of variation in the ratio of two dimensions from two separate samples (premolars and molars, or incisors and molars [see Fig. 11]), which is analogous to the situation at Can Ponsic. Data from Remane (1960) and personal observations. b: P_4 length relative to M_2 length in living apes and in four species of *Dryopithecus*. Same sample sizes and explanations as in Fig. 10a.

(16.7 kg). This is in keeping with the observation (above) that M^1 is slightly larger than M^2 in this specimen, and implies that it is the M^2 that is reduced. First and second upper molars that are close to the same size is a derived characteristic of late Miocene hominoids and living hominids, but second molars are usually larger than first molars. In *Pan*, however, these teeth are very close to the same size and often the first molar is larger.

Diet and feeding strategies

The dentition of *Dryopithecus crusafonti* for the most part lacks indications of any well-developed, specialized dietary preferences. Shearing crests are not well developed, the basins are shallow, and the cusps are relatively low. These traits argue for frugivory as a relatively more important dietary component than folivory (Kay, 1984; Kay and Hylander, 1978; Kay and Covert, 1984).

Incisor morphology and relative size have been used as indicators of food handling preferences (Hylander, 1975; Kay and Hylander, 1978; Kay, 1984; Kay and Covert, 1984), which is of interest given the unusual incisor morphology in *Dryopithecus crusafonti*. Unfortunately, the functional significance of high crowns and well-developed lingual ridges is unclear. It is at least suggestive of some degree of food handling specialization. Increased crown height may add to tooth longevity in response to excessive wear (Kay and Covert, 1984). It may also be related to increasing the space in the jaws for larger canines or to facilitate rotary movements in chewing and ingestion. The prominent lingual ridges of the upper central incisors of *D. crusafonti* may be a response to torsion or bending along the labio-lingual plane, which may have been elevated due to the narrowness of the crowns. The ridges may also have functioned to increase occlusal surface area as wear progressed. Both of these suggestions imply some enhanced incisal preparation during food processing. However, the role of the upper central incisors in food processing in *Dryopithecus crusafonti* probably differed from that of living great apes. Although the incisors are robust they are mesiodistally short relative to the upper molars (Fig. 11). The relative incisor length is similar to a number of hominoids of diverse dietary preferences (gorillas, gibbons, siamangs) and different from frugivorous or omnivorous chimps and oranges,

which have enlarged incisors relative to molar size.

Dryopithecus crusafonti was probably predominantly frugivorous but with anterior dental processing strategies that differed from those seen among living frugivorous great apes. This conclusion is in basic agreement with the conclusions of Puech et al. (1989) based on enamel microwear.

El Firal

The specimens from Can Ponsic differ in the features noted in the diagnosis from all known *Dryopithecus* specimens to which they can be directly compared except one. The molars of the El Firal (Seu d'Urgell) mandible are quite similar in morphology to the lower molars of the Can Ponsic sample (IPS 1813 and 1816). They share such attributes as broad buccal cusps, restricted, shallow talonid basins, long straight post-metaconid cristids, and mesiodistally constricted foveae (see Figs. 1 and 4). In these attributes the El Firal molars can be distinguished from the St. Gaudens dental sample of *Dryopithecus fontani*, the taxon to which the El Firal specimen has been assigned (Vidal, 1913; Smith-Woodward, 1914; Simons and Pilbeam, 1965; Szalay and Delson, 1979). The El Firal molars are also distinguished from the St. Gaudens sample in that the M_3 from El Firal lacks a tuberculum sextum and also lacks the marked reduction of the hypoconids characteristic of the St. Gaudens specimens. In addition, the hypoconulids of M_1 and M_2 are not reduced in size as they are at St. Gaudens (Table 5).

The molar dimensions of the El Firal specimen are much smaller relative to mandibular breadth than in any of the St. Gaudens specimens, or any mandible of *Dryopithecus* (Fig. 12). The mandible, in addition to being very robust for dental size, has a broad extramolar sulcus, unlike the narrow sulci of all *D. fontani* and *D. brancoi* mandibles, and lacks the distal shallowing of all three St. Gaudens specimens. Thus, there are a number of morphological features indicating that the El Firal mandible differs from all three *D. fontani* mandibles, and also from other mandibles attributed to *D. brancoi* (Table 5). It is most similar to other Spanish *Dryopithecus* mandibles (*D. laietanus*) though it also differs from these in the robusticity of its corpus relative to dental dimensions (Table 5; Figure 12). Given these differences, plus the strong similarities between the molars of

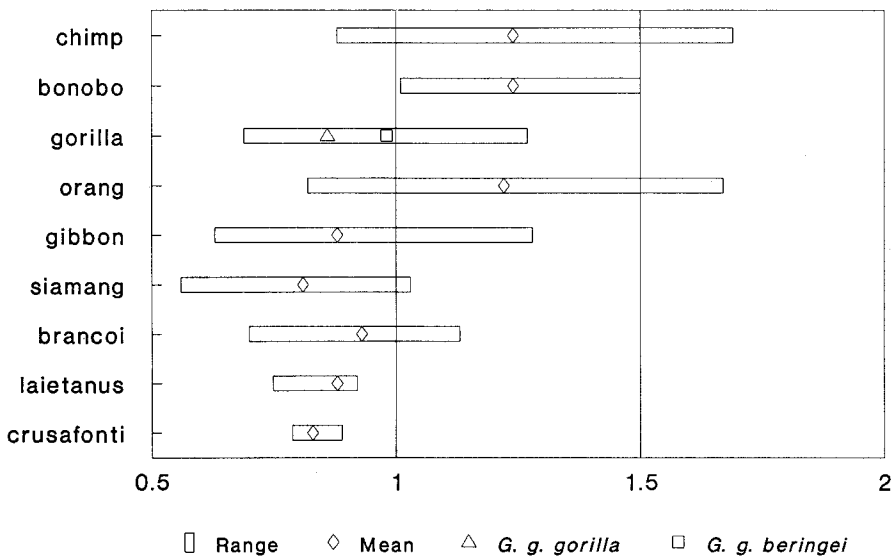


Fig. 11. Upper central incisor mesiodistal length relative to upper first molar length in living apes and in four species of *Dryopithecus*. I¹/M² samples are: chimp, n = 73/185; bonobo, n = 13/19; gorilla, n = 57/172; orang, n = 40/120; gibbon, n = 47/71; siamang, n = 15/39; *D. crusafonti*, n = 3/3; *D. laietanus*, n = 2/3; *D. brancoi*, n = 4/7 (see Fig. 10a legend). Predominantly folivorous

primates fall below an I¹/M¹ length ratio of 1 while the more frugivorous forms fall above 1 in Fig. 11, except gibbons. The small size of gibbons or other factors affecting the size of their molars may account for this discrepancy, or it may be that their strategies of incisal preparation differ from other hominoid frugivores.

TABLE 5. Distribution of the El Firal specimen's characteristics among *Dryopithecus* species¹

Comparisons	Spain		Hungary/France	
	D.c.	D.l.	D.b.	D.f.
Broad buccal cusps	X	0	0	0
Restricted, shallow talonids	X	0	0	0
Long straight postmetaconid cristid	X	0	0	0
Mesiodistally constricted fovea	X	0	0	0
Robust mandible (relative to molars)	?	X	0	0
Broad extramolar sulcus	?	X	0	0
Lacks the distal shallowing of the corpus	?	X	X	0
No tuberculum sextum	X	X	X	0
Hypoconid little reduced	X	X	X	0
M ₁ /M ₂ hypoconulids unreduced	X	X	X	0

¹X, shared with El Firal; 0, not present (different character state); ?, unknown for the taxon; D.c., *Dryopithecus crusafonti*; D.l., *Dryopithecus laietanus*; D.b., *Dryopithecus brancoi*; D.f., *Dryopithecus fontani*.

the El Firal specimen and the two isolated molars fragments from Can Ponsic, the El Firal mandible is attributed to *D. cf. crusafonti*.

Relationships among *Dryopithecus* species

Dryopithecus crusafonti most closely resembles *Dryopithecus laietanus*, the only other hominoid from the other Vallés Penedés localities. It shares with *D. laietanus*, as noted above, robust mandibular cor-

pora with broad extramolar sulci, molars with relatively broad, rounded cusps, relatively shallow, more restricted talonid basins and premolar fovea, long premolars relative to breadth, and narrow upper central incisors relative to breadth. None of these features, where comparisons are possible, are characteristic of either *Dryopithecus fontani* or *D. brancoi* (Begun, 1987).

Although *D. crusafonti* shares more features with *D. laietanus* than with other *Dryopithecus*, many of these shared characters

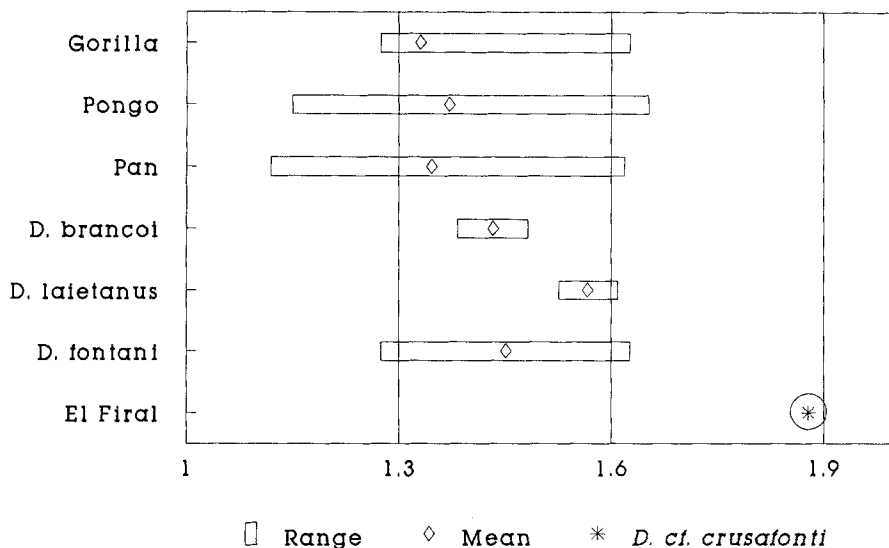


Fig. 12. Mandibular corpus breadth at M_2 relative to M_2 breadth in great apes and *Dryopithecus* species. *Gorilla*, $n = 15$; *Pongo*, $n = 17$; *Pan*, $n = 11$; *D. brancoi*, $n = 4$; *D. laietanus*, $n = 2$; *D. fontani*, $n = 3$.

may be primitive for the genus, since they are present in a number of outgroups, most notably the middle Miocene Hominoidea attributed to *Kenyapithecus* and "*Sivapithecus*" *darwini* (Pickford, 1985; Andrews and Tobien, 1977). These primitive features include traits related to mandibular robusticity and to molars with rounded cusps and shallow basins (the first four of the six traits listed as shared with *Dryopithecus laietanus* in Table 3). Tentatively, then, *Dryopithecus crusafonti* is placed in a clade with *Dryopithecus laietanus*, which together form the sister clade to the clade that includes the two non-Spanish *Dryopithecus* taxa (Fig. 13). This latter clade is defined by a larger number of synapomorphies, described elsewhere (Begun, 1987, 1988a, and in preparation).

CONCLUSIONS

The hominoid sample from Can Ponsic represents a hitherto unrecognized species of *Dryopithecus*, *D. crusafonti*. Though the sample sizes for most of the diagnostic features are quite small, these traits are not found in more extensive collections of *Dryopithecus* from other localities (St. Gaudens, Rudabánya, Can Llobateres). Furthermore, large dental samples of single species of living hominoids do not incorporate a degree of variation in incisor morphology or molar occlusal morphology than would character-

ize a *Dryopithecus* sample that combined the Can Ponsic specimens with samples from other localities. The few metric traits that are available reinforce the conclusion that the Can Ponsic sample is unique. At the same time, the sample does share a number of characteristics with other species of *Dryopithecus* that distinguish *Dryopithecus* from the early Miocene proconsulids. These and other characteristics of the cranium and postcranium of *Dryopithecus* place this genus in the clade of the living great apes and humans (Andrews, 1985; Begun, 1987, 1988a; Morbeck, 1983).

Dryopithecus occurred as locally distinctive species throughout Europe around the periphery of the Paratethys sea during the end of the middle Miocene and the beginning of the late Miocene. *Dryopithecus crusafonti* occurs only in Spain, in the earlier half of the temporal range of *Dryopithecus*, and shares features suggestive of clade affinities with *Dryopithecus laietanus*. The dental morphology of this new species reveals a pattern of frugivory/folivory common within the great apes, without indications of significant specialization toward either extreme. The El Firal mandible (Vidal, 1913; Smith-Woodward, 1914) is attributed to *Dryopithecus cf. crusafonti* based on similarities in molar morphology and differs in many respects from *Dryopithecus fontani*.

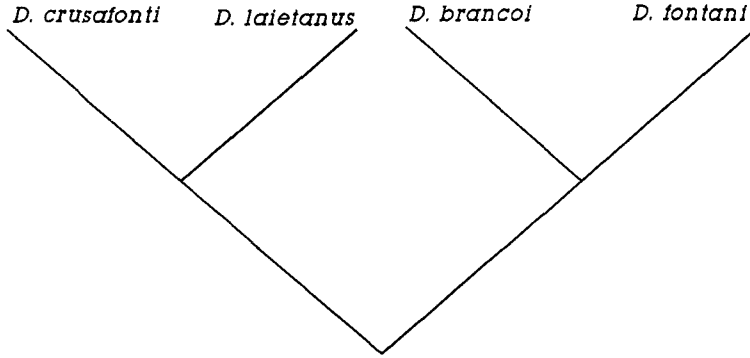


Fig. 13. Cladogram depicting proposed relationships among the species of *Dryopithecus*.

Diversity in *Dryopithecus* represents an early adaptive radiation of forest adapted great apes into the northwestern corner of the range of living and extinct great apes. The species of *Dryopithecus*, possibly derived from the stock of subparatethyan and East African middle Miocene hominoids, all share a suite of characteristics that are likely to have been present in a common ancestor of the living great apes and humans, with none of the derived characteristics of the individual hominid clades. The identification of a new species of *Dryopithecus* and ongoing analysis of new material attributed to the genus increases the data base for interpretations of the earliest phases of the divergence of great apes and humans.

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