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A reinterpretation of the taxonomy of *Dryopithecus* from Vallès-Penedès, Catalonia (Spain)

The aim of this paper is to present a critical review of the morphological evidence that has been advanced to support the recognition of two species of *Dryopithecus*—*Dryopithecus laietanus* and *Dryopithecus crusafonti*—in the collections of fossil hominoids from the Vallès-Penedès basin in northeastern Spain. Based on a study of the morphological details of the dentition in the fossils, and comparisons with the ranges and patterns of variation seen in extant hominoids, an alternative interpretation of the taxonomy of *Dryopithecus* from Spain is presented. The main results of this analysis can be summarized as follows: (1) there is no convincing morphological or metrical evidence to support the recognition of more than one species of *Dryopithecus* in the collections from Vallès-Penedès; (2) all of the material from Vallès-Penedès can be attributed to *D. laietanus* (Villalta & Crusafont, 1944); (3) the species *D. crusafonti* Begun, 1992 is considered to be insufficiently distinct from *D. laietanus*, and is recognized here as a junior synonym of the latter; and (4) the El Firal mandible from the Spanish Pyrenees is best attributed to *Dryopithecus fontani*.

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Introduction

The specimens of *Dryopithecus* from late Miocene localities in Catalonia, northeastern Spain, currently provide the largest and most important sample of fossil hominoids from Europe. Much of the early literature on the material consists of brief descriptive and taxonomic reports, but renewed interest in the systematics and phylogenetic status of *Dryopithecus*, and the recent discovery of a partial cranium from Can Llobateres, has led to the publication of a number of more detailed analyses (Begun *et al.*, 1990; Begun, 1992; Moyà-Solà & Köhler, 1993). The collections from Spain have a convoluted taxonomic history. The earliest known specimen, an isolated mandibular fragment from El Firal in the Spanish Pyrenees, has generally been attributed to *Dryopithecus fontani* (Vidal, 1913; Woodward, 1914; Villalta & Crusafont, 1941; Piveteau, 1957; Simons & Pilbeam, 1965; Szalay & Delson, 1979; Kelley & Pilbeam, 1986; Harrison, 1991), whereas the remaining *Dryopithecus* specimens, from sites in the Vallès-Penedès basin, have been assigned, over the years, to a number of different taxa. Villalta & Crusafont (1944) nominated a right P₃–M₃ (IPS 1803) from Viladecavalls (La Tarumba I) as the holotype of *Hispanopithecus laietanus*, and assigned a left mandibular fragment with M₂–M₃ (IPS 1826–27) from Can Vila (Hostalets de Pierola) to *Sivapithecus occidentalis*. Crusafont & Hürzeler (1961, 1969) and Crusafont & Golpe (1973, 1974) recognized three species in the Vallès-Penedès, based mainly on size: a large species, *Dryopithecus piveteaui*; a medium-sized species, *H. laietanus*; and a small species, *Rahonapithecus sabadellensis nomen nudum*. In an attempt to simplify matters, Simons & Pilbeam (1965) included the entire Vallès-Penedès sample in *D. laietanus*. Later, Szalay & Delson (1979) referred the Spanish hominoids to two species, *D. fontani* and *Dryopithecus branchoi*, differentiated mainly on the basis of size. More recently, Begun (1989), Begun *et al.* (1990) and Moyà-Solà *et al.* (1990) have suggested that the material from Can Ponsic is sufficiently different from the specimens from Can Llobateres (and other sites in the Vallès-Penedès) to merit the recognition of a distinct species. This view was countered by Harrison (1991), who argued that the observed differences were due to

intraspecific variation and inter-populational variability. Begun (1992) formally recognized a new species from Can Ponsic, *Dryopithecus crusafonti*, to which he also tentatively attributed the mandible from El Firal.

The aim of this paper is to critically review the morphological evidence that has been advanced to support the claim that two species of *Dryopithecus* are represented in the collections from Vallès-Penedès, and to assess the validity of the newly named species *D. crusafonti* from Can Ponsic. With the discovery of additional craniodental material from Can Llobateres it is now possible to present a revised interpretation of the taxonomic affinities of *Dryopithecus* from Spain, including the somewhat problematic specimen from El Firal.

On the status of *D. crusafonti* from Can Ponsic

According to Begun (1992), *D. crusafonti* from Can Ponsic can be distinguished from *D. laietanus*, represented at all other localities in Vallès-Penedès, in the following respects: (1) it has a higher-crowned and relatively narrower I¹; (2) I¹ has well-developed median and mesial lingual pillars; (3) the male upper canine is broader relative to its mesiodistal length; (4) the upper premolars and molars are relatively broader; (5) M¹ and M² are more similar in occlusal area; (6) molar cingula are absent; (7) the lower molar buccal cusps are broad and low, and are separated by deep, narrow fissures; and (8) the long postmetaconid cristid is continuous with a short preentoconid cristid.

It is important to note from the outset, however, that most of the characteristics used in this diagnosis are based on very few specimens. For example, there is only a single isolated canine and only two lower molars from Can Ponsic, of which only one of the latter (IPS 1816) is in an undamaged state. When dealing with such limited material it is difficult to distinguish between traits that are part of the normal intraspecific variation that segregate out merely as an artefactual consequence of sample size, and those that are taxonomically significant. Obviously, the best solution is to compare the variation seen in the fossils with that in extant primate species. With this in mind, each of the distinguishing characteristics listed above is reviewed in some detail, and comparisons are made with the ranges and patterns of variation seen in modern hominoids.

Proportions of the upper central incisor

Seven hominoid I¹s are known from Vallès-Penedès, of which three are from Can Ponsic (although IPS 1808 is worn, with heavy interstitial wear), and four are from Can Llobateres (two of which are associated with the partial cranium, IPS 18000). As noted by Begun (1992), the upper central incisors at Can Ponsic are higher-crowned than are those from Can Llobateres (Table 1). However, when the relative height of I¹ in *Dryopithecus* is compared with data for extant hominoids, the range of variation in the pooled sample from Vallès-Penedès does not exceed that seen in modern species. The mesiodistal length–buccal height index has a coefficient of variation (CV) for the combined sample of Spanish *Dryopithecus* that is less than that seen in *Hylobates lar* and *Gorilla gorilla*, although the CV for the buccolingual breadth–buccal height index does exceed the range exhibited by all living hominoids. It is important to note at this point, however, that CVs vary widely at small sample sizes, with a tendency to underestimate the extent of variation in the total population (Kay, 1982; Begun *et al.*, 1990; Cope & Lacy, 1992; Cope, 1993). To compensate for the possible effects of small sample size on the CV in *Dryopithecus*, simulations were conducted on the mesiodistal length–buccal height index for the sample of unworn orang-utan I¹s used in this study. CVs were calculated for six

Table 1 Coefficients of variation and range-based indices of the relative buccal height of the I¹ of *Dryopithecus* from the Vallès-Penedès basin

Species	Mean ± S.D.	Observed range	Coefficient of variation	A	B*
Index: MD/buc Ht					
<i>Gorilla gorilla</i> (14)	103.7 ± 15.0	79.1–140.0	14.5	1.8	58.7
<i>Pan troglodytes</i> (41)	89.3 ± 9.3	73.5–110.2	10.4	1.5	41.1
<i>Pongo pygmaeus</i> (26)	91.0 ± 9.3	66.3–106.1	10.2	1.6	43.7
<i>Symphalangus syndactylus</i> (6)	107.6 ± 10.7	100.0–127.5	9.9	1.3	25.6
<i>Hylobates lar</i> (12)	104.4 ± 13.7	87.0–134.2	13.1	1.5	45.2
<i>Dryopithecus laietanus</i> (6)	78.5 ± 10.0	65.8–88.5	12.7	1.3	28.9
Can Llobateres (4)†	84.6 —	79.1–88.5	—	1.1	—
Can Ponsic (2)‡	66.3 —	65.8–66.7	—	1.0	—
Index: BL/buc Ht					
<i>Gorilla gorilla</i> (14)	81.3 ± 12.6	65.5–110.5	15.5	1.7	55.4
<i>Pan troglodytes</i> (41)	71.9 ± 7.4	60.6–89.9	10.3	1.5	40.8
<i>Pongo pygmaeus</i> (25)	74.4 ± 7.4	63.9–97.1	9.9	1.5	44.6
<i>Symphalangus syndactylus</i> (6)	89.9 ± 9.7	76.3–100.0	10.8	1.3	26.4
<i>Hylobates lar</i> (12)	80.8 ± 7.5	68.5–94.7	9.3	1.4	32.4
<i>Dryopithecus laietanus</i> (6)	70.1 ± 12.0	54.1–81.6	17.1	1.5	39.2
Can Llobateres (4)	77.3 —	70.3–81.6	—	1.2	—
Can Ponsic (2)	55.7 —	54.1–57.3	—	1.1	—

*(n), sample size; S.D., standard deviation; A, maximum/minimum; B, range × 100/mean; MD, mesiodistal length; BL, buccolingual breadth; buc Ht, buccal height.

†Includes right and left incisor in IPS 18000.

‡IPS 1808 from Can Ponsic is excluded because of excessive wear.

individuals taken at random from the total sample of 33 individuals, thus corresponding to the sample size for *Dryopithecus*. The results show that the maximum CV possible for these sub-samples of orang-utans was 18.8, and that 12.9% of all sub-samples exceeded the CV (12.7) in *Dryopithecus*. Given these results, the variation in relative height of the upper central incisor in *Dryopithecus* does not exceed the range expected to be found in small samples of single species of extant hominoid. Range-based indices, such as maximum/minimum or range × 100/mean (see Harrison, 1982; Martin & Andrews, 1984, 1993), confirm that variation in incisor proportions in *Dryopithecus* from Vallès-Penedès is considerably less than the maximum extent seen in extant hominoids (Table 1). Importantly, it should be noted that the data on modern hominoids were obtained strictly from specimens with unworn to only slightly worn incisors. The greater degree of wear in some of the *Dryopithecus* incisors would have contributed significantly to a wider range of metrical variation.

We conclude from these data that the observed differences in relative height of I¹ among *Dryopithecus* from Vallès-Penedès is consistent with the normal range of variation seen in a single species of extant hominoid. Nevertheless, it is intriguing that the central incisors from Can Ponsic and Can Llobateres have non-overlapping distributions, and it will be interesting to see if this difference is maintained when additional material is recovered from Spain.

Morphology of the upper central incisors

Begun (1992) noted that a distinctive feature of *D. crusafonti* is the morphology of the lingual face of I¹, and Harrison (1991) has conceded that this is one of the more striking contrasts between the samples from Can Ponsic and Can Llobateres (see also Martin & Andrews, 1993).

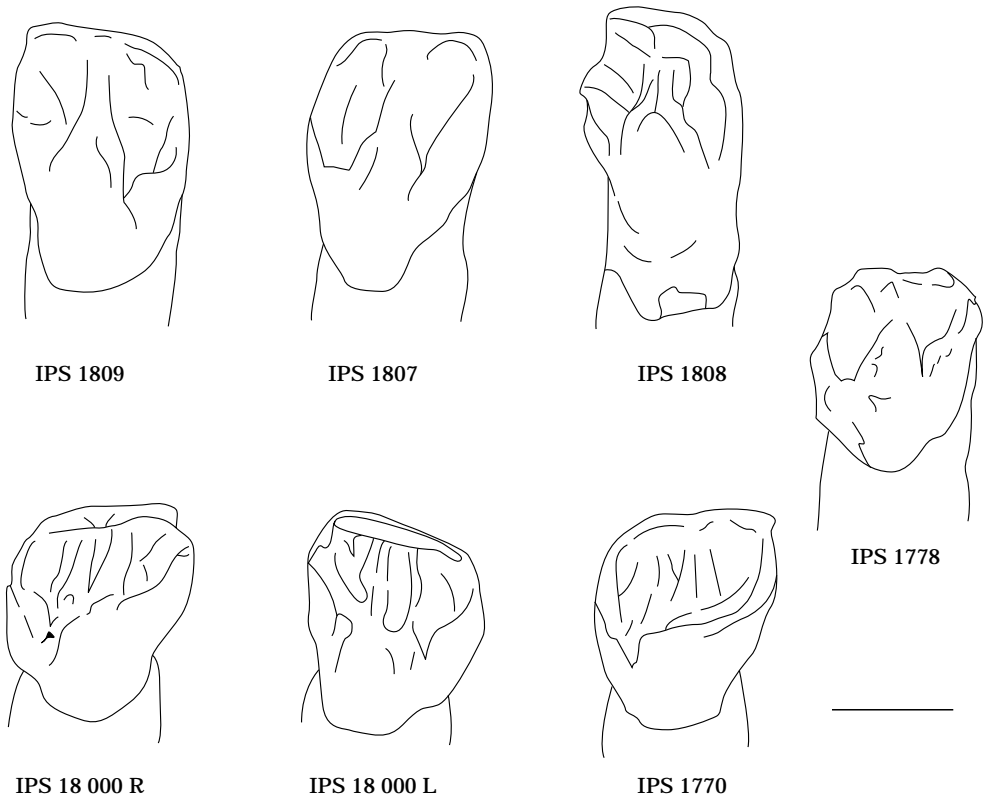


Figure 1. Morphology of the lingual aspects of the upper central incisors in *Dryopithecus* from Vallès-Penedès. Scale bar represents 5 mm.

The three I¹s from Can Ponsic are morphologically uniform, with a prominent lingual pillar separated mesially and distally from the inflated lingual cingulum by deep clefts. In two of the specimens from Can Llobateres, by contrast, the lingual pillar is ill-defined. In IPS 1770, the low, rounded lingual pillar is flanked distally by two narrow crests, and the lingual cingulum forms an almost continuous shelf around the base of the lingual face of the crown. A similar pattern is also seen in IPS 18000. However, in IPS 1778, also from Can Llobateres, an eroded and moderately worn tooth, the lingual surface is sufficiently well-preserved to show that its morphology was generally similar to that of the I¹s from Can Ponsic (Figure 1). The latter specimen shows that the morphology identified by Begun (1992) as being unique to Can Ponsic, does in fact occur in the material from Can Llobateres. In addition, we have made a detailed study of the range of morphological variation in unworn or lightly worn upper central incisors of extant hominoids, and it is evident that the development of the median pillar and lingual cingulum is extremely variable. A well-developed median pillar was found to occur in 72.6% of chimpanzees and 77.4% of orang-utans, while the remaining individuals had pillars that were ill-defined or even, in some cases, entirely absent. A similar range of variation in the development of the lingual cingulum was observed in extant hominoids, ranging from a well-developed shelf across the lingual face of the crown to an incomplete and ill-defined cingular ledge. There is evidently a good deal of variation in the development of both the

lingual cingulum and median pillar in modern apes, and the results of our comparative survey show that the range of variation seen in the Vallès-Penedès sample can be easily encompassed by the morphological diversity seen in any one species. It could be argued, with some justification, however, that simply matching individual traits of *Dryopithecus* with those seen in living hominoids does not take into account the possible occurrence of unique combinations of traits in the fossils that may imply species-specific differences. Nevertheless, even when data on relative crown height, development of the cingulum, and development of the lingual pillar are considered in combination, it is evident that the total morphological pattern that purportedly distinguishes the Can Ponsic and Can Llobateres incisors are found as part of the normal range of intraspecific variation in extant hominoids (Figure 2).

Relative breadth of the upper canine

Only one upper canine is known from Can Ponsic (IPS 1799), although eight additional specimens have been recovered from other localities in Vallès-Penedès (Table 2). Based on its size and structural characteristics, the canine from Can Ponsic can be identified as belonging to a male individual (see Kelley, 1995 for details of sexing individuals based on canine morphology). A comparison of its dimensions shows that it is very similar in its breadth-length proportions, although slightly smaller than the large male upper canine from Can Llobateres (IPS 1801), whereas it is slightly narrower than IPS 18000, but similar in size (Table 2). Considering the range of variation exhibited by both male and female canines in extant hominoids, the observed differences in size and proportions in the specimens from Can Ponsic and Can Llobateres are evidently very minor.

Relative breadth of the upper premolars and molars

A re-analysis of the relative breadth of the upper cheek teeth confirms the findings of Begun (1992) that there are differences in the proportions of the crowns between the samples from Can Ponsic and Can Llobateres, but this relationship is apparently not such a simple one (Table 3). The P³s from Can Llobateres (especially IPS 18000), for example, are relatively broader than those from Can Ponsic, contrary to the suggestion of Begun (1992), whereas the M¹s from Can Ponsic are only slightly broader on average than those from Can Llobateres. On the other hand, the length-breadth index for the M²s, and the only undamaged P⁴, from Can Ponsic fall well within the range of variation for the corresponding teeth from Can Llobateres (Table 3). The ranges for the breadth-length index for all upper cheek teeth in the fossils are less than the maximum limits of variation for modern species. Nevertheless, the CVs for the length-breadth index of P³ and M² do exceed the maximum values seen in extant great apes. Simulations, in which the length-breadth index of the cheek teeth from seven individuals (the number of *Dryopithecus* specimens available for both P³ and M²) were sampled from a large pool of modern orang-utans ($n=66$), confirm that these CVs are relatively high for a single species, but are certainly not excessive. Simulations of the length-breadth index of P³, for example, generated a maximum CV of 13.6, whereas 9.4% of the *Pongo* sub-samples exceeded the CV (8.92) in *Dryopithecus*. A similar analysis of M² provided a maximum CV of 13.3, but only 4.7% of the sub-samples had a higher CV (8.64) than that found in *Dryopithecus*. It is important to note, however, that the relative breadth of M² is not one of the features that distinguishes the Can Ponsic specimens from those from Can Llobateres; indeed, the limits of the range of variation are set entirely by specimens from Can Llobateres. In conclusion, contrary to the indication of Begun (1992), the upper cheek teeth from Can Ponsic do not appear to be significantly broader than those from other sites in the Vallès-Penedès.

(a) **Development of lingual pillar**

		Absent to fine crests	Low to moderate	Strong		
Development of cingulum	Continuous	18.2%	39.3%	3.0%	High	Relative height of crown
		3.0% ■ 1770 ■ 18 000	12.1%		Low	
	Discontinuous		3.0%	6.1% □ 1807 □ 1808 □ 1809	High	
		6.1%	9.1% ■ 1778		Low	

(b) **Development of lingual pillar**

		Absent to fine crests	Low to moderate	Strong		
Development of cingulum	Continuous	4.5%	9.1%		High	Relative height of crown
		13.6% ■ 1770 ■ 18 000	18.2%		Low	
	Discontinuous		4.5%	9.1% □ 1807 □ 1808 □ 1809	High	
		4.5%	27.3% ■ 1778	4.5%	Low	

Table 2 Measurements and relative breadth of the upper canines in *Dryopithecus* from Vallès-Penedès

Locality	Specimen	Sex	Length	Breadth	Index
Can Ponsic	IPS 1799	Male	12.1	9.4	77.7
Can Llobateres	IPS 1769	Female	8.4	7.2	85.7
	IPS 1773	Female	10.0	9.2	92.0
	IPS 1774	Female	8.8	6.8	77.3
	IPS 1786	Female	8.4	7.0	83.3
	IPS 1801	Male	14.1	11.0	78.0
	IPS 18000	Male	12.4	10.7	86.3
Polinyà II	IPS 1805	Female	8.5	6.3	74.1
Castell de Barberà	IPS 1823	Female	8.2	6.1	74.4
Mean			10.1	8.2	81.0
S.D.			2.21	1.90	6.14
CV			21.9	23.2	7.6

Index, breadth \times 100/length; S.D., standard deviation; CV, coefficient of variation.

Sources: Ribot (1993) and Ribot & Gibert (1996).

Differences in occlusal area between M¹ and M²

A further distinguishing feature of *D. crusafonti* noted by Begun (1992) is that the M¹ and M² length \times breadth are nearly identical. Comparisons confirm that the associated upper molars in IPS 1798 from Can Ponsic are more similar in size (the occlusal area of M¹ is 98.6% of that of M²) than they are in IPS 18000 (83.0% and 82.7% on the right and left sides of the maxilla, respectively). However, differences of this magnitude are not excessive for extant hominoid species. For example, in a sample of 60 orang-utans, the relationship between the occlusal areas of M¹ and M² ranged from 82.3% to 120.4% (mean, 94.1%; S.D., 14.94) (Table 4; Hooijer, 1948; Harrison, unpublished data). In fact, in simulations, where two specimens were drawn randomly from this sample of orang-utans, the difference between them equalled or exceeded that in *Dryopithecus* in 16.7% of trials. The relative size of the upper molars does not seem to be a useful distinction, therefore, to support the recognition of multiple species in the Vallès-Penedès sample.

Development of molar cingula

We have examined 19 upper molars (12 from Can Llobateres and seven from Can Ponsic) and 25 lower molars (14 from Can Llobateres, four from La Tarumba, two from Can Vila, two from Can Ponsic, and three from El Firal) of *Dryopithecus* from Spain in order to ascertain the development of the cingulum. Traces of the lingual cingulum between the protocone and hypocone can be detected on 41.7% of M²s from Can Llobateres and 42.8% from Can Ponsic. A buccal cingulum was not found to occur on any of the lower molars. Contrary to Begun

Figure 2. Comparisons of the patterns of variation in relative crown height, lingual cingulum development, and lingual pillar development in the upper central incisors of *Dryopithecus* from Spain, (a) *Pan troglodytes* ($n=33$) and (b) *Pongo pygmaeus* ($n=22$). The values in the boxes represent the percentage of individuals of living apes that have those particular characteristics. The placement of the *Dryopithecus* incisors is indicated by a square [■] for Can Llobateres and [□] for Can Ponsic] followed by the accession number of the specimen. Note that it is not just in individual traits that the *Dryopithecus* sample is comparable to the intraspecific variation in extant hominoids, but also in the combination of these traits.

Table 3 Measurements and index of relative breadth of the upper premolars and molars in *Dryopithecus* from Vallès-Penedès

Tooth	Locality	Specimen	M-D	B-L	Index		
Upper P3	Can Ponsic	IPS 1798	7.6	10.0	76.0		
		IPS 1806	7.0	9.8	71.4		
		IPS 1810	7.2	10.1	71.3		
		IPS 1817	7.4	9.7	76.3		
	Can Llobateres	IPS 1792	8.1	11.6	69.8		
Upper P4	Can Ponsic	IPS 1798	6.9	10.3	67.0		
		IPS 1787	7.3	9.8	74.5		
	Can Llobateres	IPS 18000 l	6.9	10.7	64.5		
		IPS 18000 r	6.9	10.7	64.5		
		IPS 18000 r	7.2	11.7	61.5		
Upper M1	Can Ponsic	IPS 1798	8.9	10.4	85.6		
		IPS 1815	9.5	11.2	84.8		
		IPS 1818	9.7	11.2	86.6		
	Can Llobateres	IPS 1781	8.5	9.4	90.4		
		IPS 1788	8.1	9.3	87.1		
		IPS 1844	9.9	10.3	96.1		
		IPS 18000 l	9.6	10.8	88.9		
		IPS 18000 r	9.9	10.8	91.7		
		Upper M2	Can Ponsic	IPS 1798	9.2	10.2	90.2
				IPS 1820	10.7	12.0	89.2
IPS 1821	9.6	11.0		87.3			
Can Llobateres	IPS 1771	9.1	11.3	80.5			
	IPS 1794	9.9	9.9	100.0			
	IPS 18000 l	11.5	10.9	105.5			
		IPS 18000 r	11.3	11.4	99.1		

M-D, mesiodistal length; B-L, buccolingual breadth; l, left; r, right; index, $M-D \times 100/B-L$.

Sources: Ribot (1993) and Ribot & Gibert (1996).

(1992), the absence of molar cingula is not a characteristic that distinguishes the Can Ponsic sample from specimens from other sites in Vallès-Penedès.

Configuration of buccal cusps on the lower molars

According to Begun (1992), when compared with other species of *Dryopithecus*, the protoconid and hypoconid on the lower molars of *D. crusafonti* are relatively broad in relation to the width of the crown. However, because only a single undamaged lower molar, an isolated M_2 (IPS 1816), is known from Can Ponsic, comparisons are limited. Nevertheless, we have measured the breadth of these cusps in seven M_2 s from Vallès-Penedès (three from Can Llobateres, two from La Tarumba, one from Can Vila, and one from Can Ponsic), as well as the M_2 in the El Firal mandible, and have related these to the buccolingual breadth and mesiodistal length of the crown (Table 5). The indices for relative protoconid breadth show that the Can Ponsic specimen fits well within the range of variation of specimens from other sites in Vallès-Penedès. However, it is true that the hypoconid is slightly relatively broader in the M_2 from Can Ponsic.

Another feature of the lower molars identified by Begun (1992) as being diagnostic of *D. crusafonti*, is that the buccal cusps are relatively low. We have measured the heights of the protoconid and hypoconid on M_2 (from the cemento-enamel junction to the apex of the cusp) and related these to the mesiodistal length and buccolingual breadth of the crown (Table 5).

Table 4 Coefficients of variation and range-based index of the length-breadth proportions ($M-D \times 100/B-L$) of the upper cheek teeth in *Dryopithecus* from Spain and in extant hominoids

	N	P ³	P ⁴	M ¹	M ²
Coefficient of variation					
<i>Gorilla gorilla</i>	29	5.12	5.62	3.95	4.85
<i>Pan troglodytes</i>	25	8.69	4.44	4.51	7.04
<i>Pongo pygmaeus</i>	64	6.49	5.99	5.18	6.10
<i>Symphalangus syndactylus</i>	12	4.55	5.11	6.26	4.19
<i>Hylobates lar</i>	25	4.68	7.10	4.26	3.83
<i>Hylobates hoolock</i>	12	2.28	9.08	5.36	3.46
<i>Dryopithecus</i> from Spain	—	8.92	6.03	3.94	8.64
Range \times 100/Mean					
<i>Gorilla gorilla</i>	29	17.5	29.9	16.0	18.6
<i>Pan troglodytes</i>	25	30.5	17.3	16.5	34.8
<i>Pongo pygmaeus</i>	64	28.2	27.6	26.0	28.7
<i>Symphalangus syndactylus</i>	12	16.9	14.0	21.4	14.9
<i>Hylobates lar</i>	25	16.9	28.7	17.8	15.7
<i>Hylobates hoolock</i>	12	5.8	30.8	17.1	11.8
<i>Dryopithecus</i> from Spain	—	24.8	14.8	12.7	26.9

Sources: Hooijer (1948) and Harrison (1982, unpublished data).

Table 5 Relative height and breadth of the buccal cusps of M_2 in *Dryopithecus* from Spain

Specimen	Breadth Prot.	Breadth Hyp.	1	2	3	4	Height Prot.	Height Hyp.	5	6	7	8
El Firal												
M_2	6.1	6.9	62.2	54.9	70.4	62.2	6.62	5.98	59.6	67.5	53.9	61.0
Can Ponsic												
M_2 IPS 1816	4.7	6.1	50.5	40.2	65.6	52.1	6.92	5.98	59.1	74.4	57.3	72.1
Can Llobateres												
M_2 IPS 1782							6.76	6.64	62.6	72.7	61.5	71.4
IPS 1796	4.0	5.2	44.9	37.0	58.4	48.1	5.80	5.14	53.7	65.2	47.6	57.7
IPS 1797	4.4	5.5	45.4	37.9	56.7	47.4	7.24	6.56	62.4	74.6	56.5	67.6
IPS 1802							5.06	4.51	56.8	65.7	50.7	58.6
IPS 9001	4.7	5.4	49.5	41.2	56.8	47.4	6.43	6.02	56.4	67.7	52.8	63.4
La Tarumba												
M_2 IPS 1803	4.4	4.7	55.7	45.8	59.5	49.0	5.38	4.60	56.0	68.1	47.9	58.2
IPS 1804	3.7	4.9	46.2	37.7	61.2	50.0	4.69	4.86	47.9	58.6	50.0	60.7
Can Vila												
M_2 IPS 1826	4.0	5.2	45.4	38.1	59.1	49.5	6.43	6.04	61.2	73.1	57.5	68.6

1 Protoconid breadth \times 100/B-L; 2 protoconid breadth \times 100/M-D; 3 hypoconid breadth \times 100/B-L; 4 hypoconid breadth \times 100/M-D; 5 protoconid height \times 100/M-D; 6 protoconid height \times 100/B-L; 7 hypoconid height \times 100/M-D; 8 hypoconid height \times 100/B-L.

Sources: Ribot (1993) and Ribot & Gibert (1996).

The results show that relative protoconid height in the M_2 from Can Ponsic falls within the range of variation of *D. laietanus*. Similar results were obtained for the hypoconid, although when the height of the cusp was related to buccolingual breadth, the index fell slightly above the range of *D. laietanus* (Table 5).

Occlusal morphology of the lower molars

The lower molars of *D. crusafonti* are supposedly characterized by a long postmetacristid and a short preentoconid cristid, associated with the occurrence of a distinct metaconulid or tuberculum intermedium. However, this morphology is not exclusive to the Can Ponsic specimens. A survey of the entire sample from Vallès-Penedès has allowed us to identify the same pattern in M_2 s from Can Llobateres (IPS 9001), La Tarumba (IPS 1804) and Can Vila (IPS 1826). The relative length of the postmetacristid (postmetacristid length \times 100/ M_2 MD) in IPS 1816 is 40.2%, the observed range in the M_2 s from other sites in Vallès-Penedès is 33.6–41.6% ($x=37.3$, $n=6$), whereas in the M_2 from El Firal the index is 34.5%. On the other hand, the relative length of the preentocristid (preentocristid length \times 100/ M_2 MD) in IPS 1816 (13.7%) is somewhat shorter than the sample of M_2 s from Vallès-Penedès (range=16.8–23.7%, $x=19.0\%$, $n=5$), however the preentocristid of the M_2 from El Firal (20.6%) falls within the range of variation of the entire sample.

The distinctiveness of *D. crusafonti*

We have attempted to present here a critical re-analysis of the features identified by Begun (1992) as those that differentiate *D. crusafonti* from *D. laietanus*, two species that apparently occur synchronously at closely neighboring sites in the Vallès-Penedès basin in northeastern Spain. On the basis of our study, we conclude that the majority of traits recognized by Begun as diagnostic of *D. crusafonti* do not, in fact, serve to distinguish the Can Ponsic material from samples from other sites in Vallès-Penedès. Most of the differences noted by Begun are either not confirmed upon closer scrutiny (i.e., relative breadth of the upper canine, development of the molar cingula, and development of the postmetacristid), or are more appropriately explained as the result of the combined effects of very small sample sizes, differential wear, and intraspecific variation (i.e., proportions and morphology of I^1 , relative breadth of the upper cheek teeth, difference in the occlusal area between M^1 and M^2 , the slightly shorter preentocristid, and configuration of the buccal cusps on the lower molars). Based on these results we draw the following main conclusions: (1) there does not appear to be sufficient morphological or metrical distinction between the samples from Can Ponsic and other sites in Vallès-Penedès to justify the recognition of two separate species; (2) all of the fossil hominoid material from Vallès-Penedès is attributable to *Dryopithecus laietanus* (Villalta & Crusafont, 1944), and (3) *D. crusafonti* Begun, 1992 should be recognized as a subjective junior synonym of *D. laietanus*.

On the status of the El Firal mandible

This still leaves open the question of the taxonomic status of the mandible from El Firal, which Begun (1992) attributes to *D. cf. crusafonti*. According to Begun (1992), the specimen shares a number of characteristics with the Can Ponsic specimens, that are not present in *D. laietanus* or *D. fontani*, as follows: (1) broad buccal cusps; (2) long, straight postmetaconid cristids; (3) restricted and shallow talonid basins; and (4) mesiodistally constricted foveae. As our analysis of the Vallès-Penedès material has shown, the first two of these characters do not distinguish *D. crusafonti* from *D. laietanus*, and so cannot be used to assign the El Firal mandible. Interestingly, however, the El Firal specimen does have relatively broad lower molar cusps (Table 5), but this is a feature which distinguishes it from the entire sample from Vallès-Penedès, rather than one that associates it in particular with the material from Can Ponsic.

Table 6 Comparison of the proportions (M-D/B-L) of M_1 and M_2 in *Dryopithecus fontani*, *Dryopithecus laietanus* and El Firal

	M_1		M_2	
	Average	Range	Average	Range
<i>D. fontani</i>	1.07 (5)	1.02–1.12	1.07 (5)	1.02–1.14
<i>D. laietanus</i>	1.27 (7)	1.14–1.33	1.20 (8)	1.16–1.26
El Firal	1.10 (1)	—	1.09 (1)	—

The number in parentheses represents the sample size.

The supposedly restricted nature of the occlusal basins of the lower molars in the El Firal mandible (features 3 and 4 above) is not sufficiently distinct from the patterns seen in either *D. laietanus* or *D. fontani*, especially when differences in the size and proportions of the molar crowns are taken into consideration. In fact, we can find no morphological feature that link El Firal mandible uniquely with the Can Ponsic material to the exclusion of other specimens from Vallès-Penedès. We are, therefore, left with two alternative taxonomic assignments for the El Firal specimen (assuming, of course, that it does not represent a new species). Should it be attributed to *D. laietanus*, along with the other Spanish *Dryopithecus* material, or should it be attributed to *D. fontani*, a species known principally from St Gaudens, located just across the modern-day Pyrenees from El Firal?

Begun (1992) has noted a number of additional features of the lower molars and mandible (i.e., absence of tuberculum sextum and lack of marked reduction of hypoconid on M_3 , lack of reduction of hypoconulids on M_1 and M_2 , more robust corpus in relation to the size of the molars, broader extramolar sulcus, and lack of posterior shallowing of the corpus) that distinguish the El Firal specimen from those of *D. fontani*. There is no doubt, in this case, that Begun is correct in recognizing morphological differences between the El Firal mandible and the material from St Gaudens, but we are less certain that these provide sufficient grounds to justify a taxonomic separation. Although a comprehensive review of the distinguishing characteristics listed by Begun is beyond the scope of our study, we offer the following critical remarks and observations: (1) a tuberculum sextum is absent on the M_3 s from El Firal and those from St Gaudens (Kordos, 1990); (2) the expanded corpus below the molars and the broader extramolar sulcus in the El Firal mandible are not two independent traits, but are part of a suite of related features associated, in this particular specimen, with narrow molars and marked mandibular robusticity; (3) Begun (1992, Begun & Kordos, 1993) presents data to show the distinctiveness of the relative breadth of the mandibular corpus (mandibular breadth at M_2/M_2 breadth) in the El Firal mandible, but his calculation of the index is apparently in error; our own data show that the index in El Firal is only 1.6, which falls within the estimated range for *D. fontani* (range = 1.4–1.9, $x = 1.6$, $n = 3$); and (4) the degree of posterior shallowing of the mandibular corpus in extant hominoids is a variable feature; the range of relative corpus shallowing (height of corpus at $M_3 \times 100/\text{height of corpus at } M_1$) in gorillas, for example, has a range of 78.0–102.3 ($n = 26$, mean = 92.9), easily encompassing the individual values in El Firal (98.6) and the type specimen of *D. fontani* (87.7).

By contrast, as has been noted previously, there are a number of distinctive features that the El Firal mandible shares with *D. fontani* that are not seen in other *Dryopithecus* specimens from Spain; (1) the mandibular corpus is relatively deeper, and the symphysis has a well-developed, shelf-like inferior transverse torus (Woodward, 1914; Harrison, 1991); (2) a narrow, but distinct

buccal cingulum is present on the lower molars; (3) dentine is exposed on all three lower molars more or less synchronously, whereas in the Vallès-Penedès material there is a more marked wear differential on the anterior molars (Bonis & Melentis, 1977; Bonis, 1983); (4) a similar configuration of the postmetaconid cristid and preentoconid cristid is present on the lower molars; (5) as noted above, the tuberculum sextum is absent on M_3 ; and (6) the proportions (MD/BL) of the M_1 and M_2 (Read, 1975) indicate that the molars are nearly square in El Firal and *D. fontani*, whereas in *D. laietanus* (including the M_2 from Can Ponsic) are longer (Table 6). On the basis of these similarities, we concur with the majority of prior workers in recognizing the El Firal mandible as belonging to *D. fontani*.

Summary and conclusions

In this paper we have set out to critically review the morphological and metrical evidence that has been advanced to support the contention that two species—*D. laietanus* and *D. crusafonti*—are represented in the collections from the Vallès-Penedès basin in northeastern Spain. Based on our analysis of the morphology and patterns of variation of individual traits in the sample of fossil hominoids from Spain, including newly recovered specimens from Can Llobateres, we have reached the following conclusions: (1) there is no convincing morphological evidence, given the small samples of fossils available, and based on comparisons with the patterns of variation seen in extant hominoids, to support the recognition of more than one species of *Dryopithecus* in the collections from Vallès-Penedès; (2) all of the fossil hominoid material from Vallès-Penedès can be reasonably attributed to *D. laietanus*; (3) the recently named species, *D. crusafonti* Begun, 1992 is apparently indistinct from *D. laietanus*, and it is considered here to be a junior synonym of the latter species; and (4) the El Firal mandible from the Spanish Pyrenees, attributed to *D. cf. crusafonti* by Begun (1992), is best recognized as belonging to *D. fontani*.

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