

Current events

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Some observations on the Miocene hominoids from Spain

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The important collection of *Dryopithecus* specimens from Cataloña, northern Spain has been the subject of a number of brief reports (Woodward, 1914; Villalta & Crusafont, 1944; Crusafont & Hürzeler, 1961, 1969; Crusafont & Golpe, 1973; Peuch *et al.*, 1989) but no comprehensive descriptions of the material have yet been published. Begun *et al.* (1990) have recently provided a detailed survey of the material from Can Llobateres, as well as a good review of the systematic position, chronology and paleoecology of the dryopithecines from the site. This is a welcome and significant addition to the literature on Miocene hominoids from Europe. I have recently been fortunate enough to have had the opportunity to study the Spanish fossil hominoids in some detail and I provide here a brief review of my own observations on the material, in light of the report by Begun *et al.* (1990). These may be summarized as follows:

1. Begun *et al.* (1990) have provided a catalogue of *Dryopithecus* material from Can Llobateres. This will prove to be a useful source of reference, especially as there is much confusion in the earlier literature concerning the identification of individual specimens. However, the Institut Paleontologic Dr M. Crusafont (IPS) in Sabadell, Spain has recently assigned the hominoid material new permanent accession numbers that differ from those published by Begun *et al.* (1990). In order to avoid any further confusion in the literature I have provided a revised catalogue of the material from Can Llobateres that incorporates these changes (Table 1). The list of material was compiled by the author from the original specimens during visits to Sabadell in 1979 and 1989. Although my listing conforms in most details with that presented by Begun *et al.* (1990), some necessary modifications are given in the footnotes to Table 1.

2. Begun *et al.* (1990) argue, quite correctly in my view, that the substantial sample of hominoids from Can Llobateres can all be assigned to a single species that is indistinguishable from the material from the site of La Tarumba, the type locality for *Dryopithecus laietanus* (Villalta & Crusafont, 1944).

However, they further contend that the *Dryopithecus* material from Can Ponsic is sufficiently distinct to merit a species separation (see also Begun, 1989a). I have considered the merits of this suggestion with some care, but can find no strong grounds to support such a taxonomic distinction. For example, Begun (1989a) has suggested that the Can Ponsic sample is characterized by a distinctive lower molar morphology. Only three lower teeth are known from Can Ponsic, an isolated P₄, an isolated M₂ and a fragmentary M₂ (Table 2). Although it is possible to identify minor morphological differences with their homologues from Can Llobateres, these differences are unlikely to prove significant when the samples are expanded to encompass the full range of intraspecific variability. The upper central incisors provide the

Table 1 Catalogue of *Dryopithecus* material from Can Llobateres^a

Published IPS no.	New IPS no.	Specimen
6	1796	Left mandibular fragment with M ₁ -M ₂
7	1764	Mandibular symphysis with right C-P ₄ (♂)
8 ^b	1802	Right mandibular fragment with M ₁ -M ₃
9	1797	Right mandibular fragment with M ₁ -M ₂
10	1794	Left M ¹ (unerupted germ)
11	1822	Left M ₃ (unerupted germ), Holotype: <i>Dryopithecus piveteaui</i> (Crusafont & Hürzeler, 1961)
12	1770	Right I ¹
13 ^c	1771	Left M ²
14	1778	Left M ³
15a ^d	1762	Right P ₃
15 ^d	1763	Right M ₁
16	1765	Left upper canine (♀)
17	1766	Right upper canine (♀)
18	1767	Left lower canine (♀)
19	1768	Left lower canine (♀)
20	1769	Left upper canine (♀)
21	1775	Left P ₄
22	1776	Right P ₄
23	1777	Right P ₃
24	1778	Right I ¹
25	1779	Edentulous right mandibular fragment
37	1781	Left M ¹
38	1782	Left M ₂ (unerupted germ)
39	1783	Right upper dC
41	—	Right upper canine (♂)
42	1784	Right mandibular fragment with dP ₃
43	1785	Left lower dC
44	1786	Left upper canine (♀)
45	1787	Right P ¹ (unerupted germ)
46	1788	Left M ¹
47	1800	Left M ₃

most striking contrast (Begun, 1989a). Those from Can Ponsic are slightly higher-crowned than those from Can Llobateres, and the lingual pillar is more prominent. However, the general morphology is similar, and the apparent differences between the two samples have been accentuated somewhat by differential wear. The upper canine is known only from a single broken and worn male canine from Can Ponsic, and from a very worn male canine and several female canines from Can Llobateres. The preservation and sample size makes adequate comparison difficult. The upper canine from Can Ponsic is smaller than the extremely robust male canine from Can Llobateres, although it appears to be compatible in size with the male lower canines from the site. The upper cheek teeth from Can Ponsic are closely similar in morphology and proportions to those from Can Llobateres, although the latter appear to be very slightly smaller in size. In my opinion these minor dental differences do not merit the recognition of a separate species. They are best interpreted as intraspecific differences that stem from the small size of the sample, and from inter-populational variation. My assessment of the taxonomic affinities of the Spanish hominoids would suggest that all of the *Dryopithecus* material from Vallès Penedès (i.e., from the sites of Can Ponsic,

Table 1 (Continued)

Published IPS no.	New IPS no.	Specimen
48	1780	Right mandibular fragment with ?M ₁
53	1789	Left upper dC
54	1790	Right I ²
55	1791	Left P ₃ (unerupted germ)
56	1792	Right P ³
57	1839	Left dP ³
58 ^c	1838	Right I ₁
59	1841	Right I ₁
61	1837	Left lower dC
62	1840	Right lower dC
63	1835	Left lower canine (♂; unerupted germ)
64 ^f	1842	Right upper dC
65	1836	Right upper dC
66 ^g	1846	Left dP ⁴
67	1844	Right M ¹ (unerupted germ)
68 ^h	—	Right M ¹ (unerupted germ)
69	1793	Edentulous right mandibular fragment
70	—	Left mandibular fragment with M ₁ –M ₂

^aThe following specimens, previously identified as hominoids, have been excluded from this catalogue because they are not considered by the author to be primates: IPS 40/1795, possibly a premolar germ of a suid; IPS 40/1801, possibly a deciduous incisor of a ruminant; and IPS 60, an incisor of uncertain affinities.

^bThis specimen is identified on the associated museum label as the holotype of "*Rahonapithecus sabadellensis*". However, in the initial description of the species by Crusafont & Hürzeler (1961) no type specimen was nominated. The name is therefore considered to be a *nomen nudum* (see Simons & Pilbeam, 1965; Szalay & Delson, 1979).

^cIPS 13/1771 has a distal contact facet. It is therefore most likely to be an M² rather than an M³ (*contra* Begun *et al.*, 1990).

^dIPS 15 and IPS 15a are unlikely to belong to the same individual judging from the difference in wear. The two specimens have therefore been assigned separate permanent accession numbers, IPS 1762 and IPS 1763 respectively.

^eIPS 58/1838 is most likely a central incisor rather than a lateral incisor (*contra* Begun *et al.*, 1990).

^fIPS 64/1842 is from the right side rather than from the left (*contra* Begun *et al.*, 1990).

^gIPS66/1846 is considered by Begun *et al.* (1990) as a non-primate. There is no doubt, however, that this is a dP⁴ of *Dryopithecus*.

^hI thank Lawrence Martin for providing details of this specimen.

Can Llobateres, La Tarumba, Can Vila, Can Mata, Polinyà II, Sant Quirze and Castell de Barbera; See Table 3) can be assigned to a single species, *D. laietanus*.

3. I agree with Begun *et al.* (1990) that the Spanish taxon, *D. laietanus*, can be distinguished from the type species, *D. fontani* Lartet, 1856 from Saint Gaudens in southern France. *Dryopithecus fontani* differs from *D. laietanus* in its lower molar morphology, especially the presence of a much better developed buccal cingulum, and in having a deeper mandibular corpus with a more strongly developed inferior transverse torus (see also Begun *et al.*, 1990). It is significant to note, therefore, that the hemi-mandible from Seu d'Urgell ("El Firal"), a site located on the Spanish side of the Pyrenees about 100 km northwest of Vallès Penedès, is morphologically consistent with *D. fontani*. It has a deep mandible, with a shelf-like inferior transverse torus and strong buccal cingula on the molars (Woodward, 1914). The Seu d'Urgell specimen differs from the Saint Gaudens mandibles in having slightly narrower and more rectangular molars. However, these differences are rather minor when compared with the wide range of variation in molar size and proportions exhibited by the small sample

Table 2 Catalogue of *Dryopithecus* material from Can Ponsic^a

Published IPS no.	New IPS no.	Specimens
3	1812	Right M ³
4	1815	Left M ²
27 ^b	1798	Left maxillary fragment with P ¹ -M ²
27 ^h	1799	Left upper canine (♂)
28	1820	Left M ²
29	1818	Left M ¹
30	1781	Right P ₄ (unerupted germ)
31	1821	Right M ³
32	1810	Right P ³
33	1806	Left P ³
34	1807	Right I ¹
35	1809	Left I ¹
36	1808	Left I ¹
52	1817	Right P ³
71	1816	Right mandibular fragment with M ₂
72	1813	Fragmentary right M ₂ (or M ₁)
74 ^c	1814	Right M ³

^aIPS 51 from Can Ponsic, described by Crusafont & Golpe (1973, p. 22 and Plate 5) as *Dryopithecus* cfr. *indicus*, is excluded from this catalogue as a non-primate.

^bIPS 27/1798 and IPS 27/1799 are associated specimens.

^cThis specimen has been cited incorrectly by Crusafont & Golpe (1973, p. 22 and Plate 6) as IPS 53.

Table 3 Catalogue of *Dryopithecus* specimens from other sites in Vallès Penedès

Site	Published IPS no.	New IPS no.	Specimen
La Tarumba I (Viladecavals)	2	1803	Associated toothrow comprising right P ₃ -M ₂ , Holotype: <i>Hispanopithecus laietanus</i> (Villalta & Crusafont, 1944).
	2a	1804	Left mandibular fragment with M ₂ -M ₃ (antimere of IPS 1803)
Can Mata I (Hostalets de Pierola)	49	1766	Right lower canine (♀)
Can Vila (Hostalets de Pierola)	1	1827	Left M ₂ and M ₃ , Holotype: <i>Sivapithecus occidentalis</i> (Villalta & Crusafont, 1944)
	1a	-	Left lower molar germ
Sant Quirze	5	1824	Fragmentary molar
Polinya II	50	1805	Left upper canine (♀)
Castell de Barbera (Santa Maria de Barbera)	26	1823	Right upper canine (♀)

available from Saint Gaudens. It seems reasonable to conclude that the Seu d'Urgell specimen should be retained in *D. fontani*, following Woodward (1914) and subsequent revisors (Simons & Pilbeam, 1965; Szalay & Delson, 1979; Kelley & Pilbeam, 1986).

4. It is beyond the scope of this brief review to tackle the complex and presently unresolved issue of the alpha-taxonomy of *Dryopithecus* from central and eastern Europe. However, Begun (1989b) and Begun *et al.* (1990) have proposed that an isolated cheek tooth from

Salmendingen, West Germany probably represents an M_1 of *Anapithecus* cf. *hernyaki*, rather than a dP_4 of *Dryopithecus*, as has been commonly considered in the past (Gregory & Hellman, 1926; Simons & Pilbeam, 1965; Szalay & Delson, 1979). I accept that the tooth from Salmendingen is superficially similar to lower molars of crouzeline pliopithecids, such as *Anapithecus* from Rudabánya, but this is also true of dP_4 s of extant and fossil hominoids. However, there are several important characters of the Salmendingen tooth that suggest to me that it is a dP_4 of *Dryopithecus*, rather than a permanent molar of *Anapithecus*. These are as follows: (a) the occlusal area of the crown is almost 20% greater than the largest first molar of *Anapithecus hernyaki*, but as a dP_4 it is metrically compatible with the isolated *Dryopithecus* molars already known from Salmendingen; (b) the well-defined distal fovea and relatively large hypoconulid in the Salmendingen tooth are more similar to dP_4 s of Miocene large hominoids, such as *Kenyapithecus*, than to permanent molars of *Anapithecus*; (c) *Anapithecus*, like most pliopithecids, has at least a trace of a pliopithecine triangle on M_1 , while in the Salmendingen tooth it is entirely lacking; and (d) the unusual accessory cristid transecting the trigonid basin on the Salmendingen tooth is never found in permanent molars of pliopithecids, but an homologous crest is characteristically very common among dP_4 s of modern great apes, especially *Pongo* and *Gorilla*, and Miocene hominoids, such as *Kenyapithecus*, from East Africa (*contra* Begun, 1989b).

My analysis of the large hominoids from Spain have led me to the following conclusions: (a) the dryopithecine material from Vallès Penedès in northern Spain can all be assigned to a single species, *Dryopithecus laietanus*; (b) *Dryopithecus laietanus* can be distinguished from the contemporary *Dryopithecus fontani* from southern France by details of the morphology of its mandible and lower molars; and (c) the specimen from Seu d'Urgell is the only specimen from Spain that can be attributed with certainty to *D. fontani*.

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References

- Begun, D. R. (1989a). New species of *Dryopithecus* from the Vallesian of Can Ponsic (Northeastern Spain). *Am. J. phys. Anthrop.* **78**, 191.
- Begun, D. R. (1989b). A large pliopithecine molar from Germany and some notes on the Pliopithecinae. *Folia Primatol.* **52**, 156–166.
- Begun, D. R., Moyá-Sola, S. & Kohler, M. (1990). New Miocene hominoid specimens from Can Llobateres (Vallès Penedès, Spain) and their geological and paleoecological context. *J. hum. Evol.* **19**, 255–268.
- Crusafont, M. & Golpe, J. M. (1973). New pongids from the Miocene of Vallès Penedès Basin (Catalonia, Spain). *J. hum. Evol.* **2**, 17–23.
- Crusafont, M. & Hürzeler, J. (1961). Les Pongidés fossiles d'Espagne. *C. r. Séanc. Acad. Sci. Paris* **254**, 582–584.
- Crusafont, M. & Hürzeler, J. (1969). Catalogo comentado de los Pongidos fósiles de España. *Acta Geol. Hisp.* **4**, 44–48.
- Gregory, W. K. & Hellman, M. (1926). The dentition of *Dryopithecus* and the origin of man. *Am. Mus. Anthrop. Pap.* **28**, 1–123.
- Kelley, J. & Pilbeam, D. (1986). The dryopithecines: Taxonomy, comparative anatomy, and phylogeny of Miocene large hominoids. In (D. R. Swindler & J. Erwin, Eds) *Comparative Primate Biology, Vol. 1: Systematics, Evolution, and Anatomy*, pp. 361–411. New York: Alan R. Liss.

- Peuch, P-F., Cianfarani, F. & Trafi, F. R. (1989). Maxillary canine microwear in *Dryopithecus* from Spain. *Am. J. phys. Anthrop.* **80**, 305–312.
- Simons, E. L. & Pilbeam, D. R. (1965). Preliminary revision of the Dryopithecinae (Pongidae, Anthroipoidea). *Folia Primatol.* **3**, 81–152.
- Szalay, F. S. & Delson, E. (1979). *Evolutionary History of the Primates*. New York: Academic Press.
- Villalta, J. F. & Crusafont, M. (1944). Dos nuevos Antropomorfos del Mioceno Español y su situación dentro de la moderna sistemática de los Simios. *Notas Commu. Inst. Géol. Min. España* **13**, 91–139.
- Woodward, A. S. (1914). On the lower jaw of an anthropoid ape (*Dryopithecus*) from the Upper Miocene of Lérida (Spain). *Q. Jl Geol. Soc. Lond.* **70**, 316–320.