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Confirmation of rabbit domestication in the 4th century AD at Ambrussum: evidence of morphological change in the pelvis.

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Abstract:

A multivariate analysis of six measurements on the pelvis of rabbits from Ambrussum that had shown evidence of having been kept in captivity revealed that the bones differed morphologically from those of modern wild rabbits as well as being larger in size. The conclusion is that rabbits were already being deliberately bred in the 4th century AD in southern France.

During the excavation of a well, Puits 103, at the site of Ambrussum, near Villetelle (Hérault, France) (see map in Figure 1), numerous rabbit bones were found in a context that suggested that complete rabbit carcasses had been thrown into the well within a short space of time (Fiches, 2012; Gardeisen, 2012). The minimum number of individuals was 35. All parts of the skeleton were well-represented apart from the very small bones such as phalanges and there was no sign of butchery or burning.

A broad spread of ages was represented, suggesting that the bones accumulated from the successive throwing of animals into the well as they died, rather than the result of a sudden disease striking the entire population. This even spread of ages suggested that the rabbits were being kept in captivity (Gardeisen, 2012, 301).

To test whether there was any sign of morphological change that might be the result of domestication, whether by deliberate selection or not, six measurements were taken on the coxal bone of the pelvis (*os coxae*) in those specimens that had the acetabulum fused or in the process of fusion. The minimum number of individuals with the acetabulum fully fused was 13 and the minimum number of individuals with the acetabulum still in the process of fusion was 6. The measurements are described in Appendix I and Figures 2 and 3.

These measurements had previously been taken on modern wild rabbits from various locations in France and the Iberian Peninsula as well as on rabbits from three archaeological sites in the

Peninsula, and unexpected differences had been found between rabbits of different geographical origins (Watson & Davis, 2019).

When the measurements were taken on the Ambrussum specimens it was immediately seen that the shape of the ischium is very different in the larger Ambrussum specimens and in fact the minimum diameter of the shaft, measurement "I", is clearly bimodal in the adults (Figure 4). At first it was thought that this bimodality might represent a difference between the sexes, but the difference is much greater than that seen between the sexes in the specimens from Roissy, the modern sample in which the sexual dimorphism is greatest (Figure 5).

In the study by Watson and Davis, the principal components of the measurements were found and subsequently a linear discriminant function based on the 2nd to 6th principal components was calculated. The first principal component was then plotted against the discriminant score. This is an established technique for separating the variation in the measurements into a size-component, represented by the first principal component, and a shape-component, represented by the discriminant score (see e.g. Burke et al., 2003). Figure 6 shows the mean first principal component plotted against the mean discriminant score for the five largest samples of modern wild rabbits from the subspecies *Oryctolagus cuniculus cuniculus* and the rabbits from three Late Palaeolithic phases at Cova Matutano (Olària, 1999; Watson, 1999), using Roissy as one of the groups for the discriminant function and Matutano A as the other.

Figure 7 shows the individual specimens from Ambrussum compared with the modern wild rabbits as a whole. It can be seen that the specimens from Ambrussum with a thick ischial shaft (i.e. a large "I") were both larger overall and more “Iberian” in shape than the mass of modern wild rabbits, but so were two specimens with a slender ischial shaft. This group will be referred to as the "Large" group from now on, while the specimens that fall amongst the modern wild rabbits will be referred to as the "Small" group. The very large wild specimen to the left of the main part of the “Large” group is in fact an extreme outlier from Roissy in France; the measurements have been retaken and are correct.

Figure 8 shows the individual specimens from Ambrussum compared with the Magdalenian ones from Matutano. Although the “Large” Ambrussum group overlaps with the largest specimens from Matutano, it is on the edge of the mass of Matutano rabbits as a whole. Figure 9 shows the result of adding the means for the two Ambrussum groups to Figure 6. It shows that although the “Small” group fits in well with the wild rabbits the mean for the “Large” group plots out a long way above those for Cova Matutano.

In accordance with Bergmann's rule (Bergmann, 1847; Davis & Moreno-García, 2007), which states that mammals from colder environments tend to be larger, one explanation for the large size of the “Large” Ambrussum rabbits might be an origin in a cold part of the Peninsula, which would not be impossible, given that Ambrussum lies on the main line of communication between the Peninsula and Italy, the Via Domitia.

The other explanation would be that the difference in shape is the result of domestication or the processes leading to it. This is supported by the observation that measurement "I" is disproportionately large in all but four of the "Large" Ambrussum specimens compared with measurement "H" when the Ambrussum specimens are compared with the modern wild ones (Figure 10). Although this difference is much less marked when the Ambrussum specimens are

compared with the Magdalenian ones from Matutano, it is still noticeable (Figure 11).

It should be stressed that both measurements "H" and "I" are very dependent on age up to the point at which the acetabulum is fully fused. After this, growth appears to slow sharply. Figure 12 shows the Ambrussum specimens classified according to their stage of development (Gardeisen, 2012). There is little difference between Gardeisen's Stades 4 and 5 but the Stade 3 specimens are markedly smaller. For this reason only adult specimens, i.e. those in Stades 4 and 5, are included in the study, but even so the possibility that differences in "H" and "I", especially "H", might correspond to differences in age needs to be borne in mind. However, it is clear that the Stade 3 specimen with a value of 37 for "I" (3.7 mm) must belong with the "Large" group, not only because of its position in Figure 12 but also because of its behaviour in the multivariate analyses.

Nevertheless, given that measurement "I" is so large in the "Large" Ambrussum specimens, it is difficult to escape the conclusion that the differences between them and all the wild specimens studied, both modern and ancient, are the result of domestication and subsequent genetic selection, whether deliberate or not.

What is surprising is the direction of the change in shape. Figure 13 shows the Ambrussum specimens together with the modern wild ones, as in Figure 10, but with the addition of specimens from two domestic breeds, the Gris de Vienne and the Papillon (Watson & Davis, 2019). These modern breeds are very much larger and so the scale of the figure has had to be altered. The striking feature of the figure is that there is a disproportionate increase in measurement "H" in the modern domestic breeds, which is exactly the opposite to what is observed for the "Large" Ambrussum specimens.

This difference between the "Large" Ambrussum specimens and the modern domestic breeds is also seen in the plot of the the mean first principal component against the mean discriminant score. The two domestic breeds plot out on the opposite side to the Ambrussum specimens and have mean discriminant scores similar to those for the French wild specimens (Figure 14). This is partly the consequence of the differences in the relationship between measurements "I" and "H" shown in Figure 10, but it is also influenced by differences in the ilium.

That the modern domestic rabbit breeds resemble the French wild rabbits in shape is not surprising given that they are thought to be descended from French wild stock and have been shown to resemble modern French wild rabbits genetically (Carneiro et al., 2011). Studies of the mitochondrial DNA show that the B1 type, widespread in France, predominates in all the main domestic breeds and that no exclusively Iberian types occur in them (Queney et al., 2002). But what then might be the genetic affinities of the "Large" Ambrussum rabbits?

This unexpected discovery of a presumably domestic strain with a morphology different from present-day domestic breeds raises the question of whether there could have been two separate episodes of domestication (in the sense of morphological change), the well-documented one in the 11th-12th centuries AD leading to the spread of warrens ("garennes") across France (Callou, 2003, 255-256) and another one in the 4th century AD or earlier. In the intervening centuries the strain or strains developed could have died out or could simply have been absorbed into the much larger later expansion of domesticated rabbits.

The specimens in the “Small” group from Ambrussum also raise many questions. Although they are

clearly differentiated from the “Large” group on the shape of the ischium, there are also important similarities, namely their rather “Iberian” shape and the large overall size of some of them. It needs to be asked whether they might not represent the population from which the “Large" group had been bred or had mutated. The smaller ones are indistinguishable from modern samples from Navarre but very different from the modern sample from Tour du Valat, which is less than 50 kilometres away from Ambrussum on the far side of the Camargue. Unfortunately there is no modern material available from the Hérault apart from a single wild rabbit from Lattes, which falls into the middle of the “Small” Ambrussum group. It could be that the modern wild rabbits are different from those in the Camargue and closer in shape to those from Navarre and that the wild rabbits of the 4th century AD were similar.

The "Large" coxal bones from Ambrussum, although they form a striking cluster, include both left and right bones. Some of these, if not all, are paired bones from the same individual, so that the actual number of individuals represented is only between 5 and 8. Since the rabbits all appear to have been deposited in the well within a short space of time, it is quite possible that all these individuals were closely related. It might be thought, therefore, that these bones were just the result of a chance mutation that went no further, were it not for the fact that a very similar bone occurs in a 4th century AD level at the nearby site of Lunel Viel (Raynaud, 1990). The value of measurement "I" is 39, which puts it into the group with a thick ischial shaft (see Figure 4). Unfortunately measurement "F" is slightly damaged, but the damage is not enough to affect the measurement by more than three tenths of a millimetre, so upper and lower limits for the value have been used and the first principal component and discriminant function calculated in each case. The result is shown in Figure 15 and it can be seen that the specimen clearly falls into the "Large" group. The site at Lunel Viel is only 7 km away from Ambrussum, so there is still a faint possibility that the animal was closely related to the "Large" Ambrussum rabbits, but it seems more likely that it represents a general phenomenon and that large rabbits were being deliberately bred in the eastern Languedoc in the 4th century AD.

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Figure 1. Map showing the location of the site of Ambrussum.

(This figure is based on the map created by Eric Gaba and made available at https://commons.wikimedia.org/wiki/File:France_map_Lambert-93_topographic-blank.svg under the GNU Free Documentation License and is therefore subject to the same licence.)

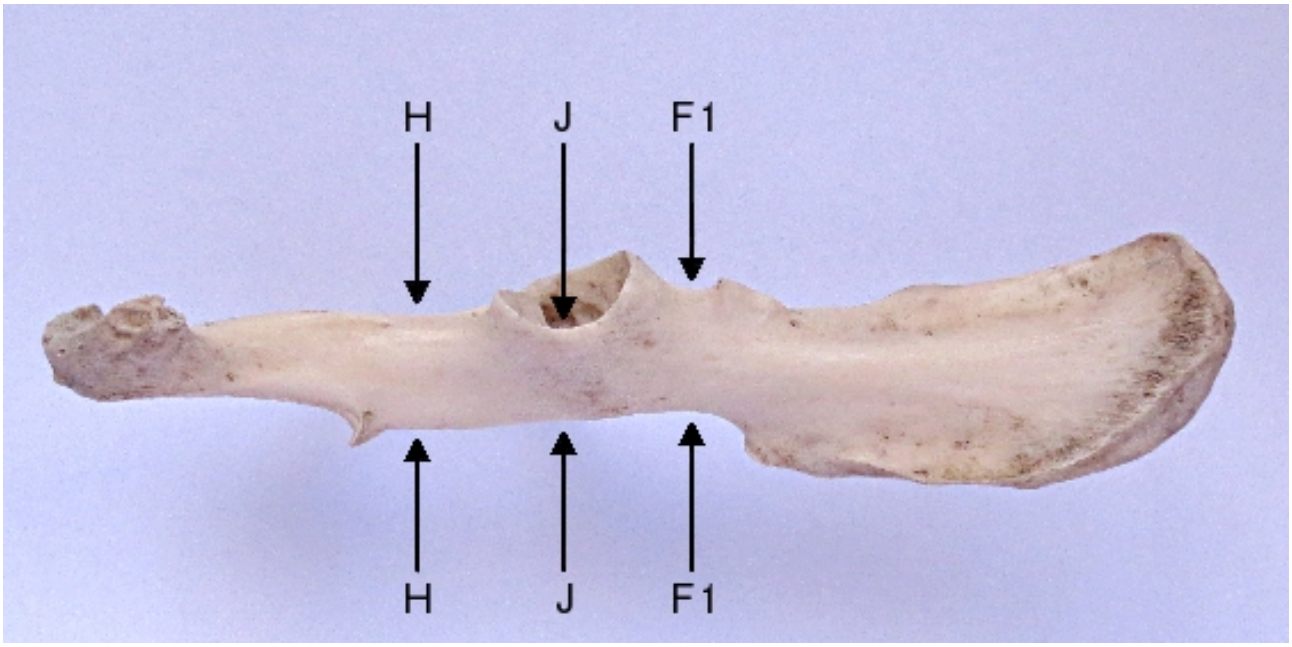

Figure 2. Drawing showing the approximate positions in which measurements H, J and F1 are taken. (N.B. H, J and F1 are not necessarily in parallel planes; they just happen to have that property in the specimen illustrated.)

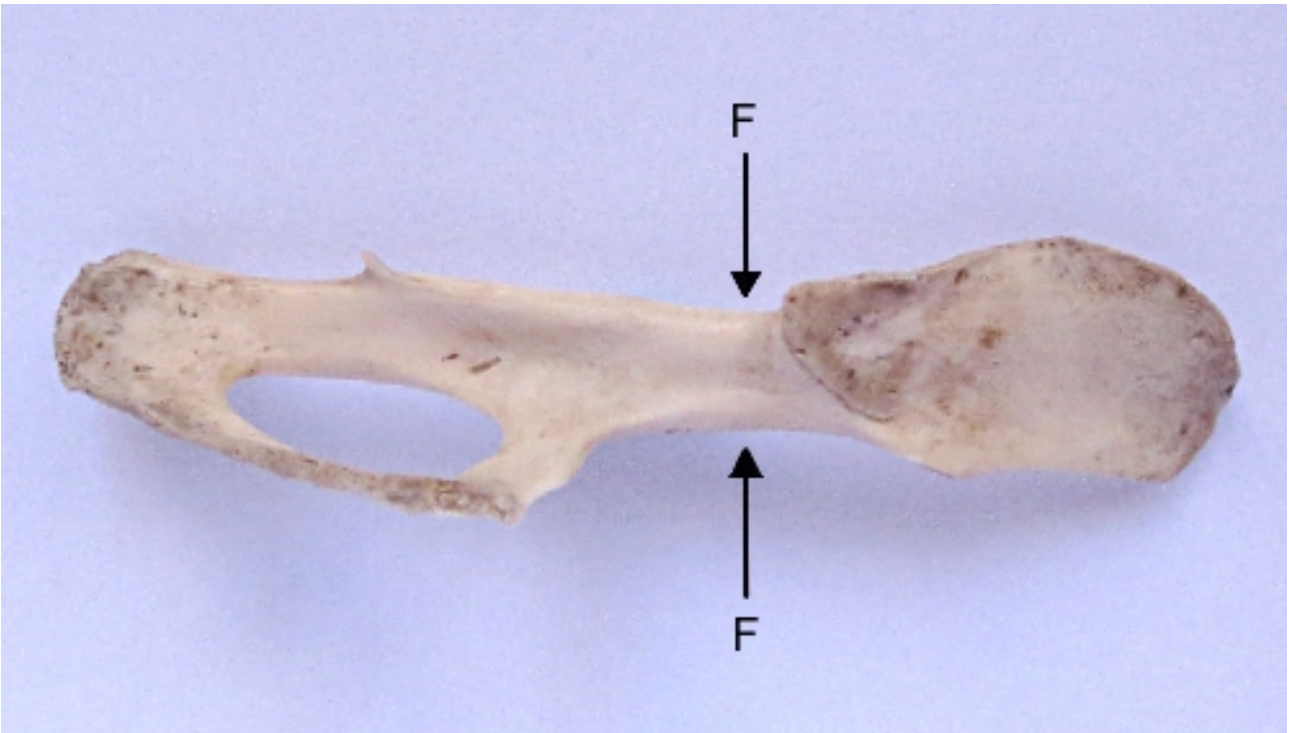

Figure 3. Drawing showing the approximate position in which measurement F is taken.

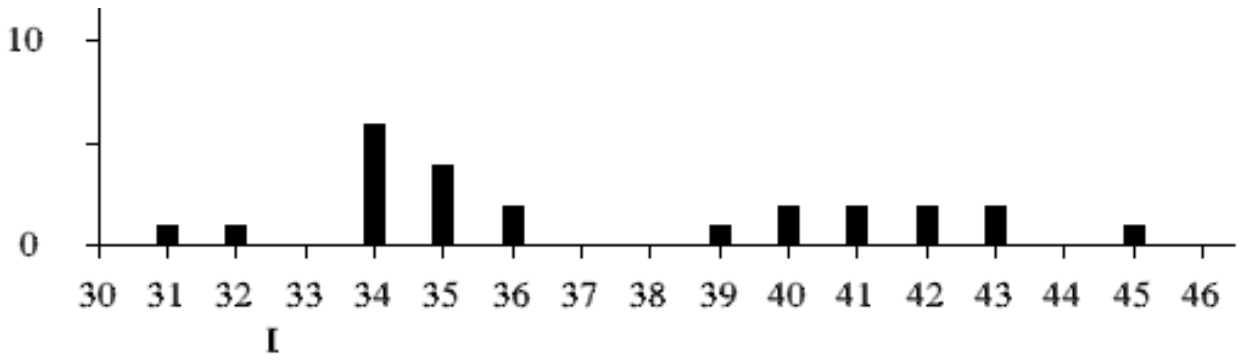

Figure 4. Histogram of measurement "I" for the adult specimens from Ambrussum, showing the marked bimodality. The horizontal axis is in tenths of a millimetre. The specimens classified as "adult" are those belonging to Stades 4 and 5 as defined in Gardeisen & Valenzuela Lamas (2004, Figure 9).

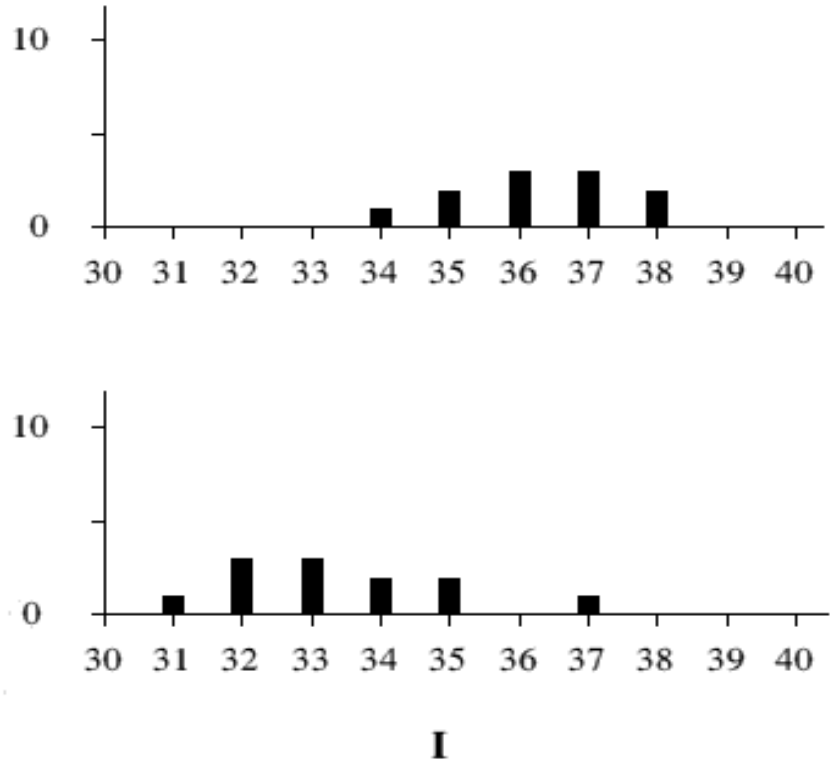

Figure 5. Histograms of measurement "I" for the modern specimens from Roissy. The upper histogram shows the male specimens and the lower histogram the female ones.

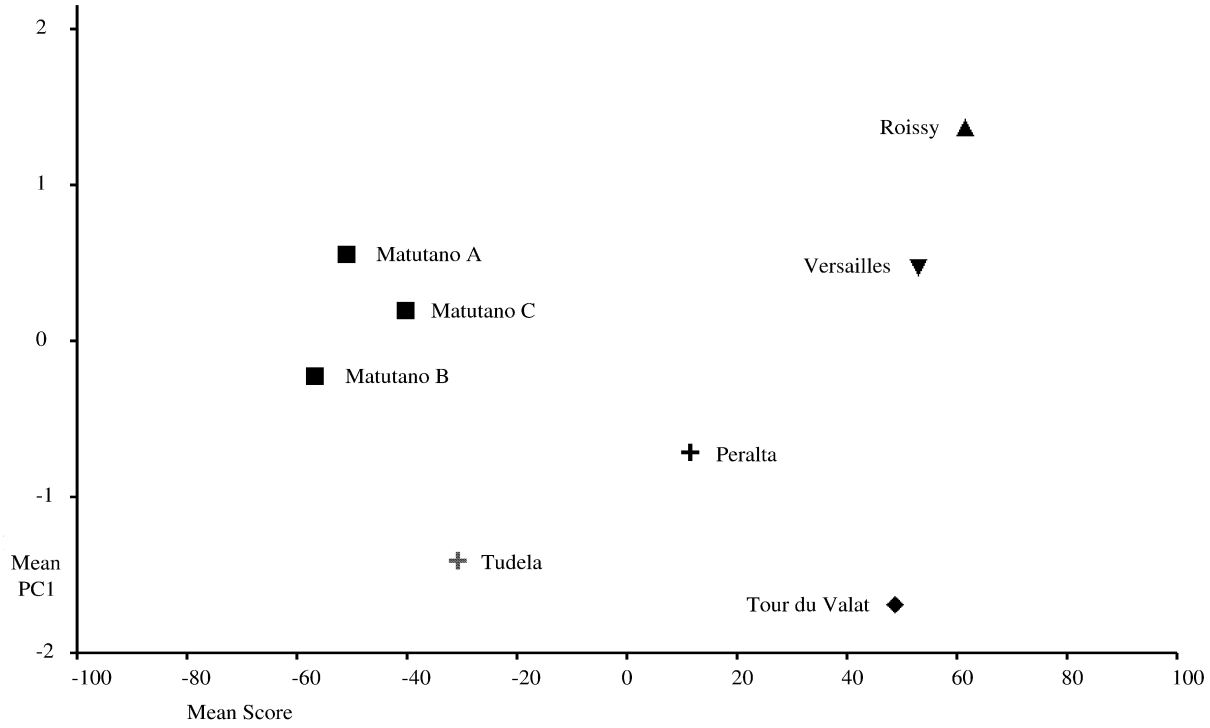

Figure 6. Plot of the mean first principal component against the mean discriminant score for various samples of modern rabbits and for three Magdalenian faunal phases at Cova Matutano. Only adult specimens are included, i.e. those in Stades 4 and 5 as defined by Gardeisen & Valenzuela Lamas (2004).

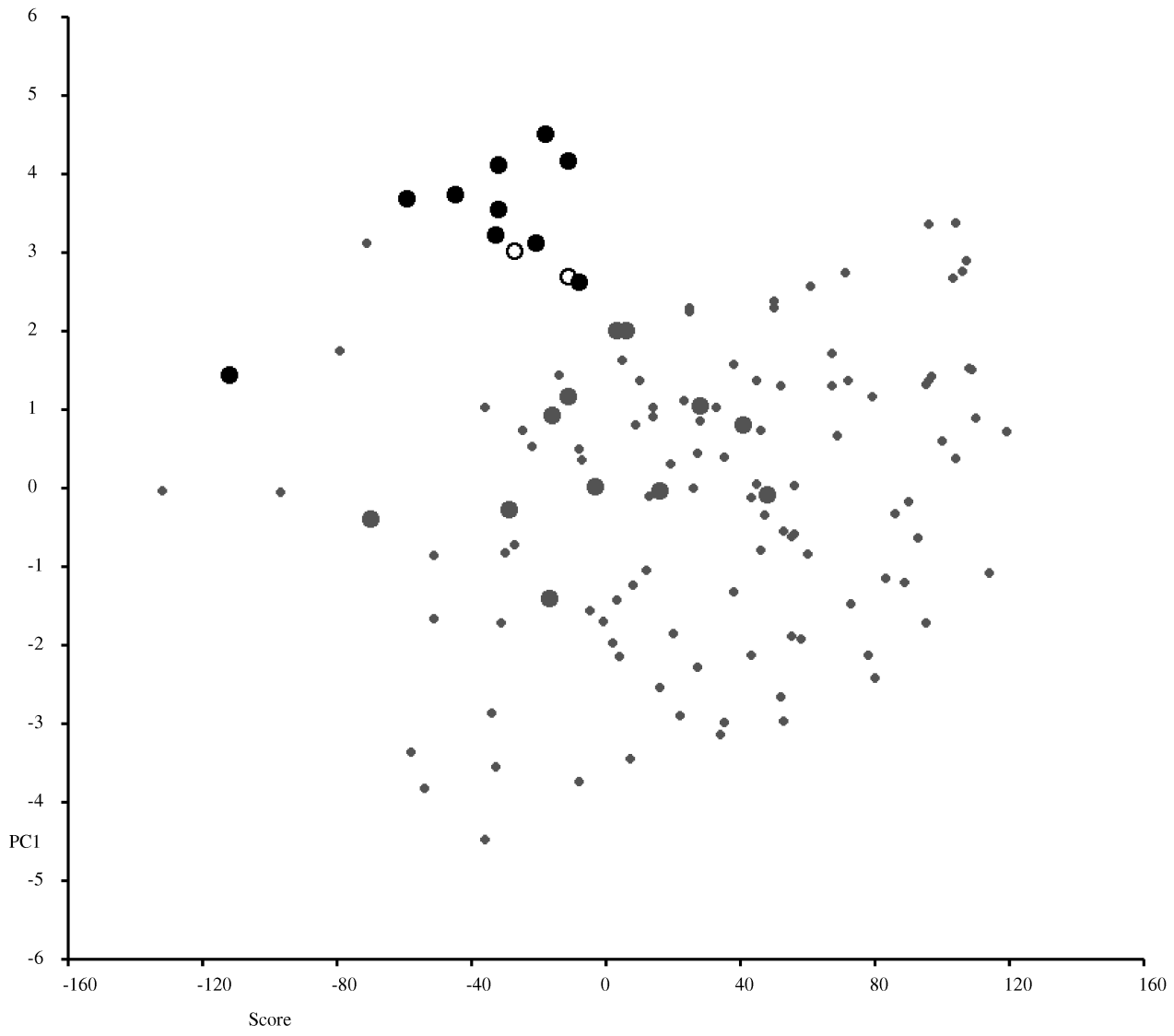

Figure 7. The individual values for the first principal component plotted against the individual discriminant scores for the adult Ambrussum specimens and for modern wild rabbits from Roissy, Versailles, Tour du Valat, Peralta and Tudela, i.e. those belonging to the subspecies *Oryctolagus cuniculus cuniculus*. The black filled circles are the Ambrussum specimens with a thick ischial shaft. The black open circles and the grey filled circles are the Ambrussum specimens with a slender ischial shaft. The small grey dots are the modern wild rabbits.

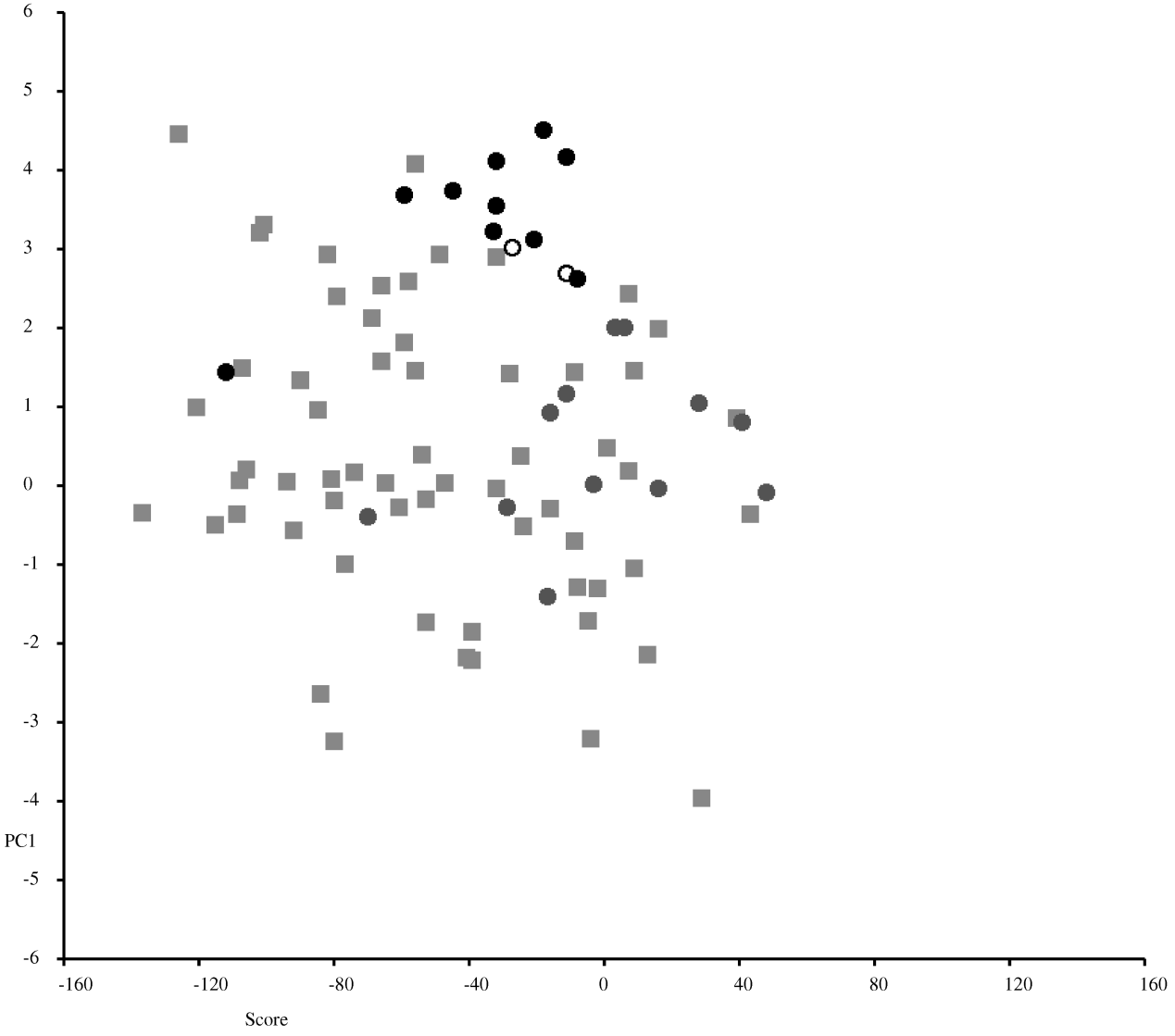

Figure 8. The individual values for the first principal component plotted against the individual discriminant scores for the adult Ambrussum specimens and for the Magdalenian specimens from the faunal phases A, B and C at Cova Matutano. The black filled circles and the black open circles are the "Large" Ambrussum specimens. The grey filled circles are the "Small" Ambrussum specimens. The paler grey squares are the Cova Matutano specimens.

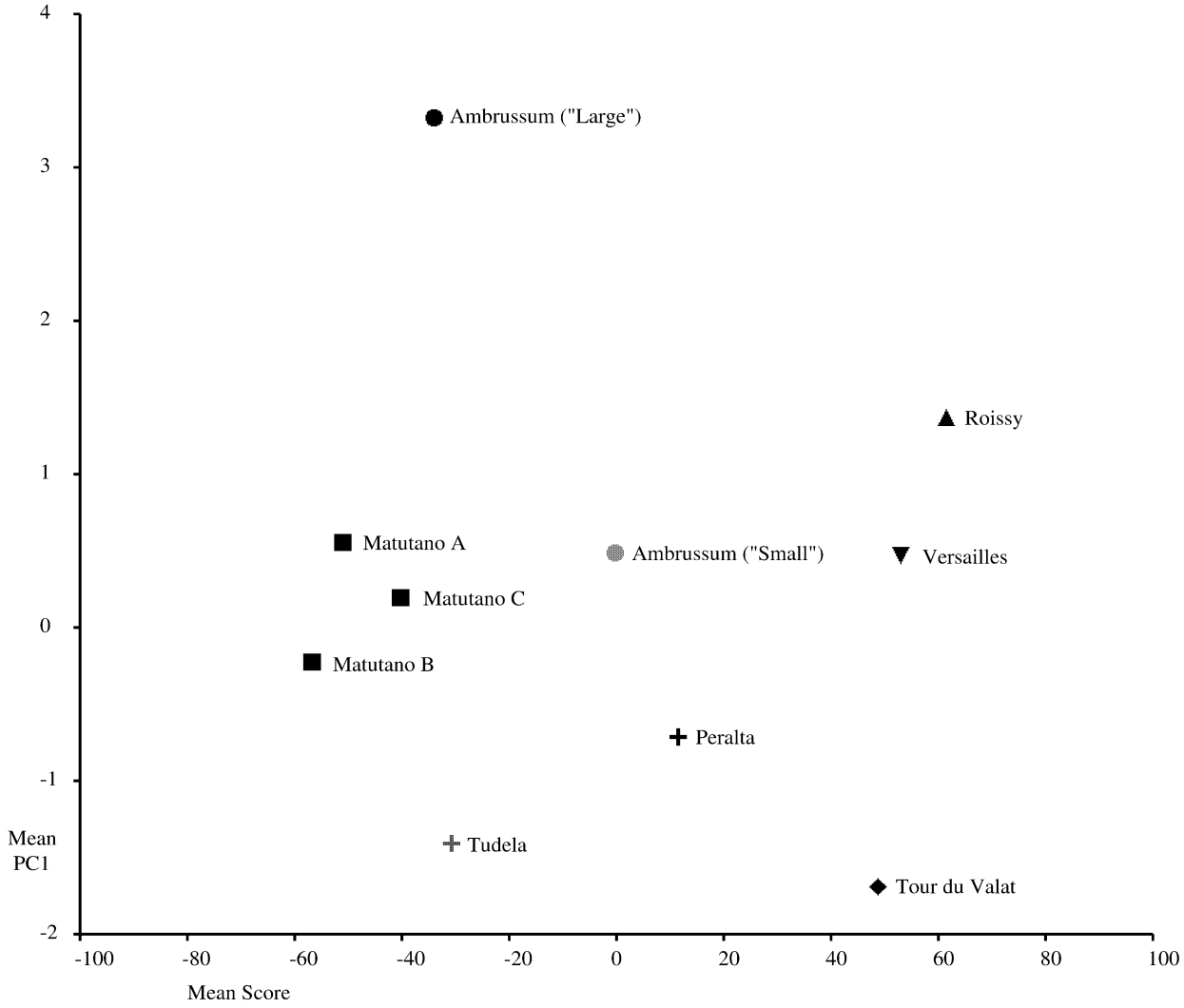

Figure 9. The same as Figure 6 but with the addition of the means for the "Large" and "Small" specimens from Ambrussum. It can be seen that the "Large" specimens not only are considerably larger than the wild rabbits, both modern and Magdalenian, but also have a shape that is at the opposite extreme to that of the French wild rabbits from Roissy, Versailles and Tour du Valat.

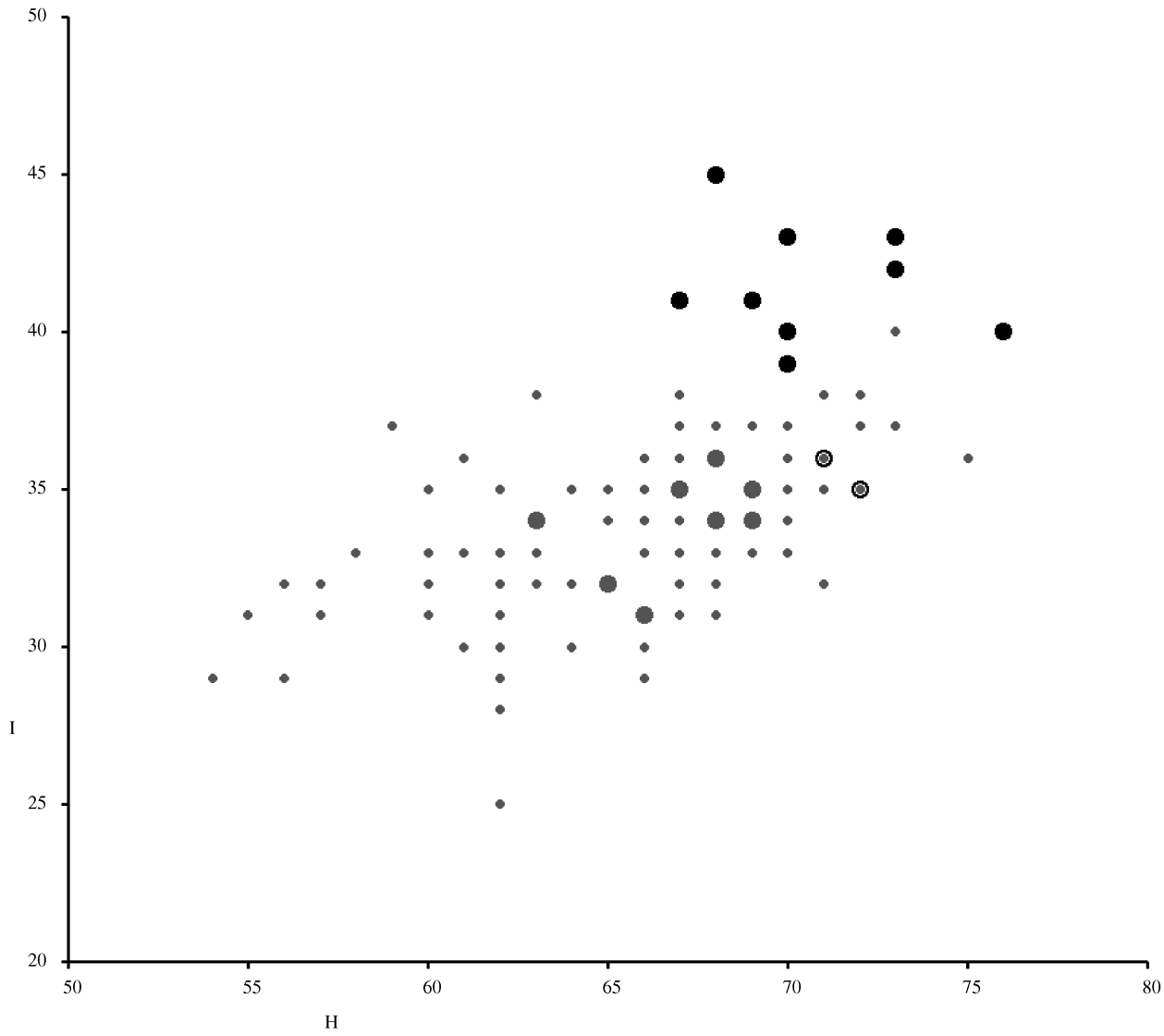

Figure 10. Measurement "I" plotted against measurement "H" for the modern wild specimens (small grey dots), the "Small" Ambrussum specimens (grey circles) and the "Large" Ambrussum specimens (black filled circles and black open circles). It can be seen that the "Small" specimens are indistinguishable from the wild ones but that most of the "Large" specimens stand apart from both, if the outlier from Roissy is excluded, with the exception of the two “Large” specimens with a slender ischial shaft. There are fewer "Small" Ambrussum specimens shown than in Figures 6 and 7 because in four cases circles are superimposed.

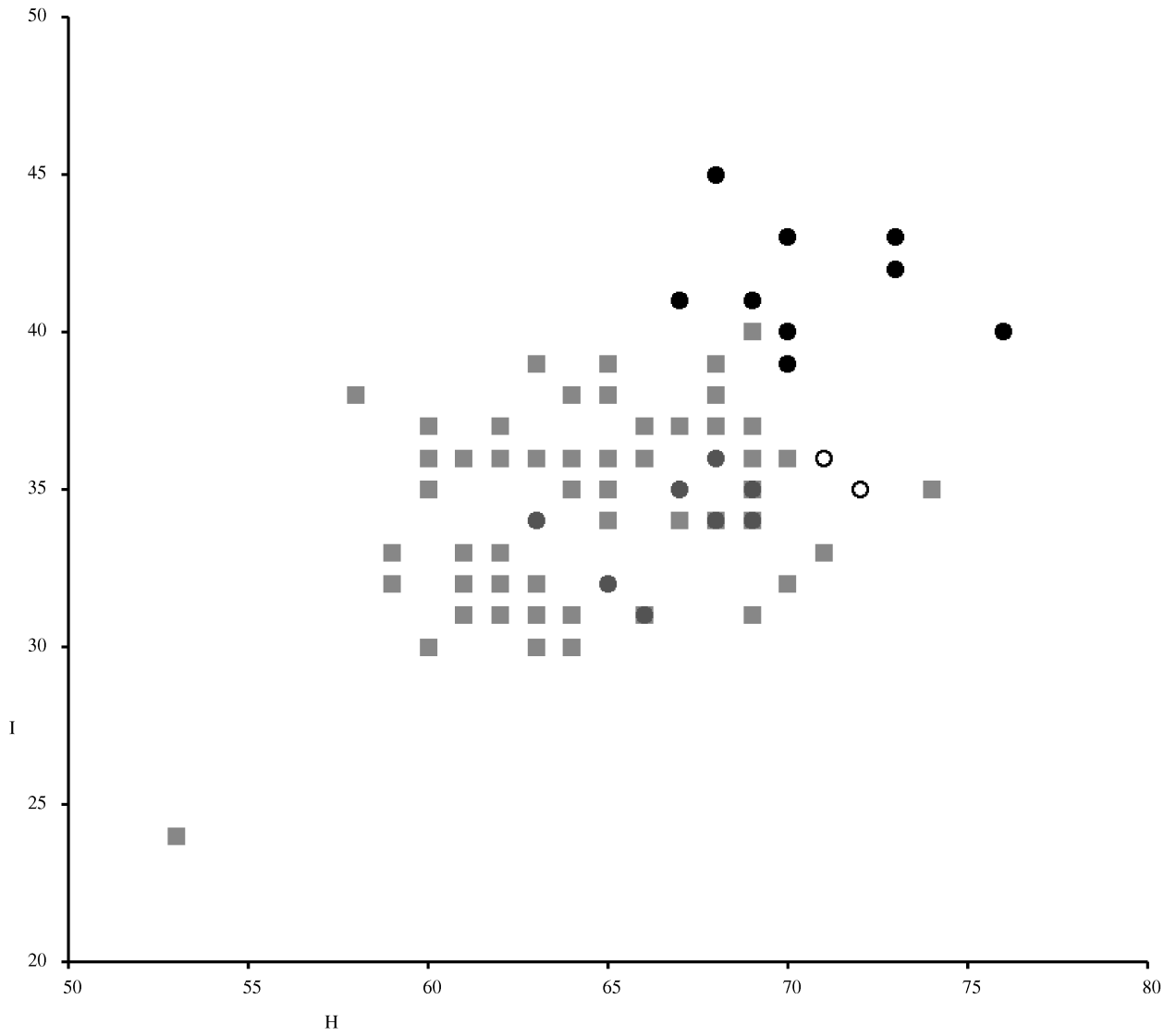

Figure 11. Measurement "I" plotted against measurement "H" for the Magdalenian specimens from Cova Matutano (grey squares), the "Small" Ambrussum specimens (grey circles) and the "Large" Ambrussum specimens (black filled circles and black open circles). It can be seen that the "Small" specimens are indistinguishable from the Matutano ones but that in the "Large" specimens measurement "I" is greater in the majority of cases although there is considerable overlap,

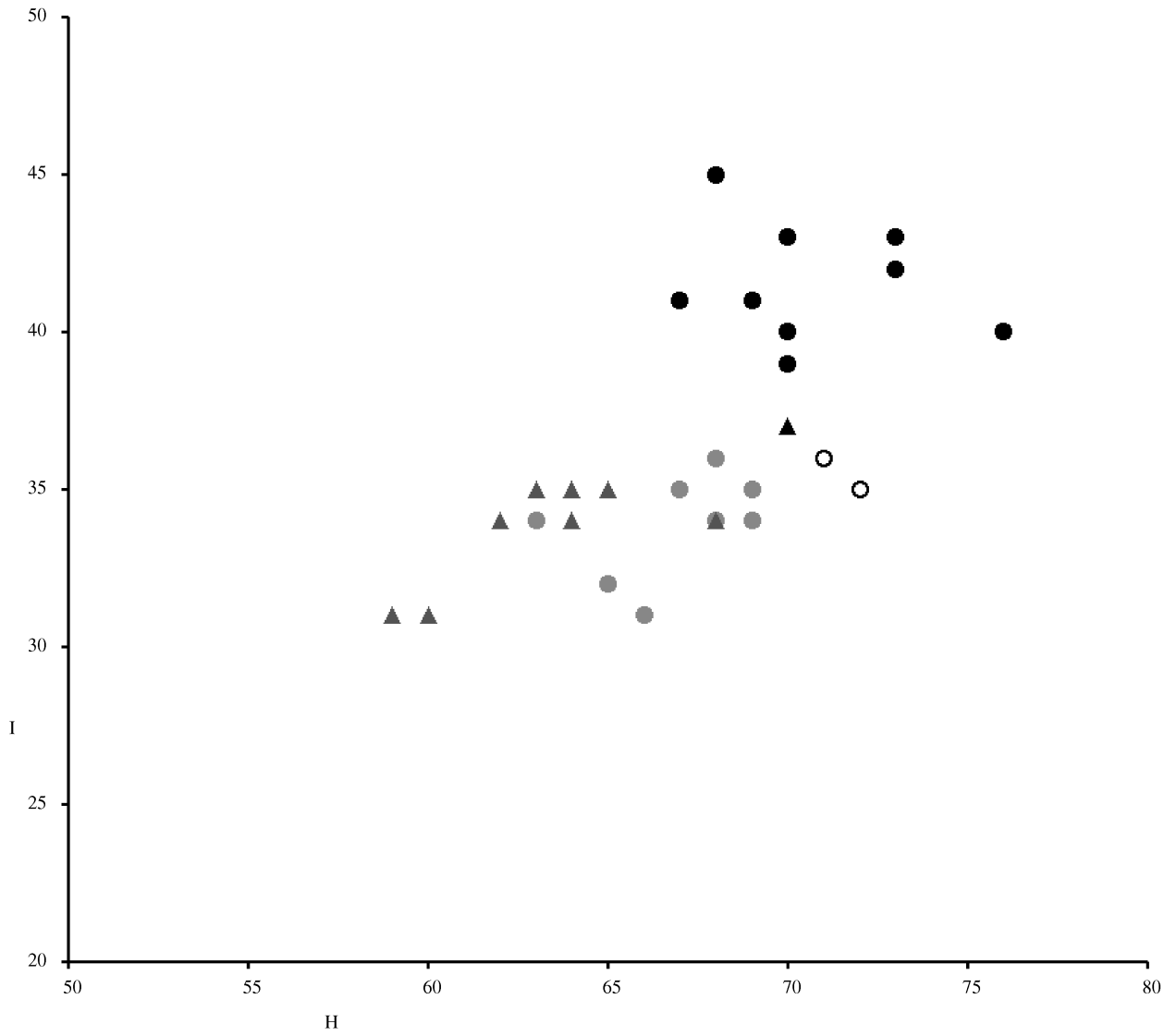

Figure 12. Measurement "I" plotted against measurement "H" for the three growth stages recorded in the Ambrussum specimens (Gardeisen 2012). The triangles indicate specimens in Stade 3 (juveniles), the circles those in Stade 4 (sub-adults) and Stade 5 (adults). The "Small" specimens are in grey and the "Large" ones in black.

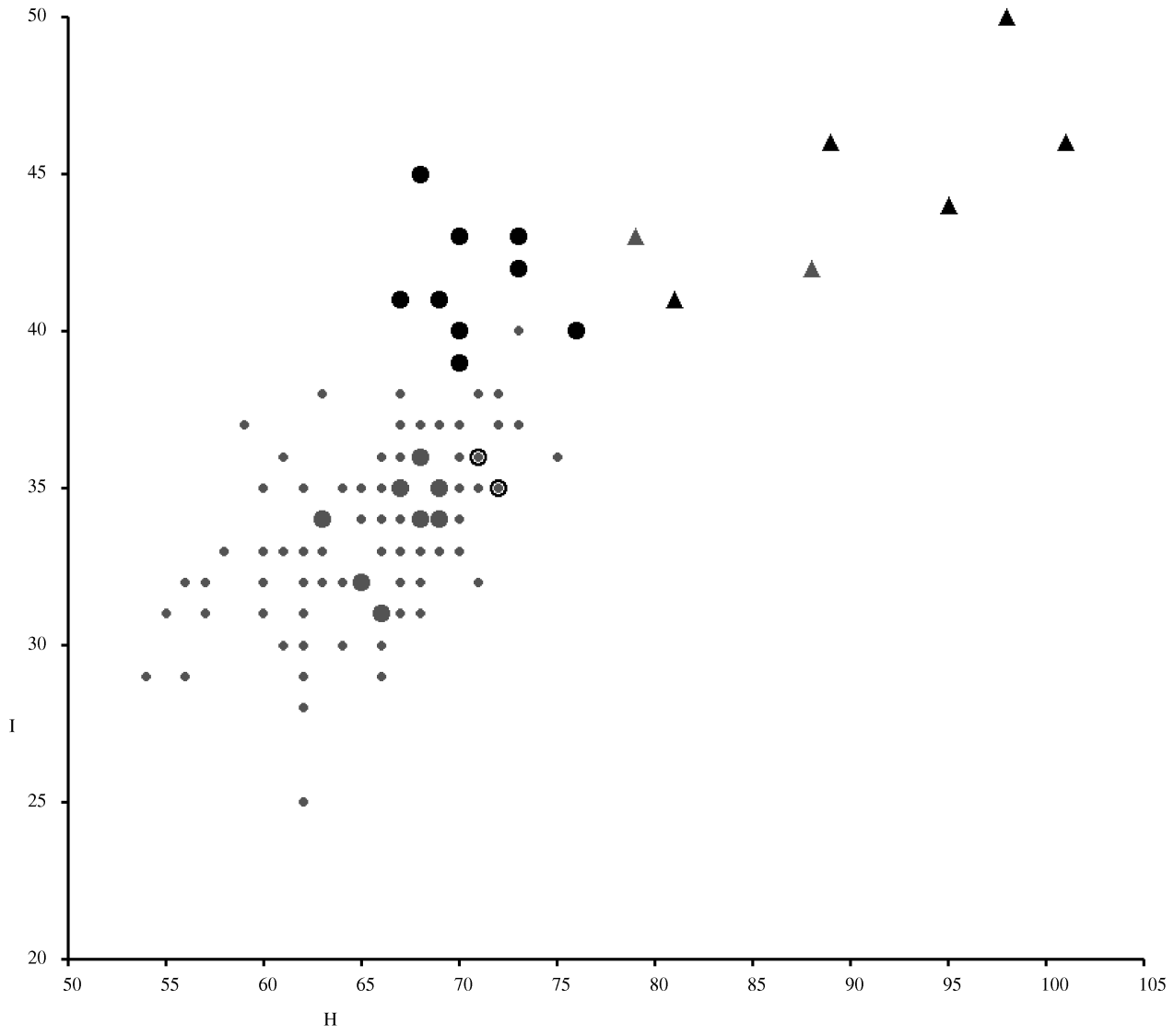

Figure 13. Measurement "I" plotted against measurement "H" for the modern wild specimens (small grey dots), the "Small" Ambrussum specimens (grey circles), the "Large" Ambrussum specimens (black circles), specimens of the Gris de Vienne breed (black triangles) and specimens of the Papillon breed (grey triangles).

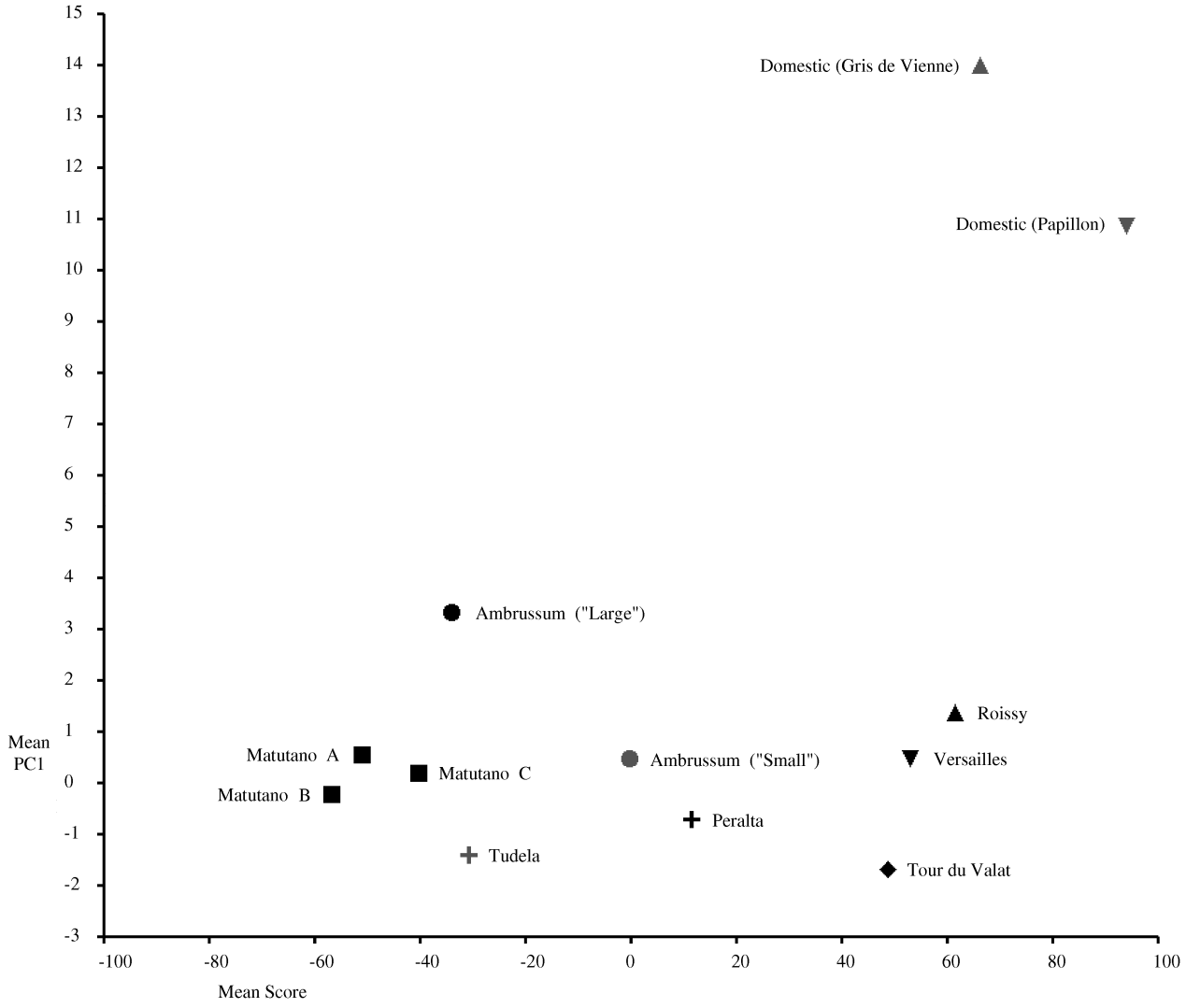

Figure 14. The mean first principal component plotted against the mean discriminant score, as in Figure 9, with the addition of the specimens of the Gris de Vienne and Papillon breeds.

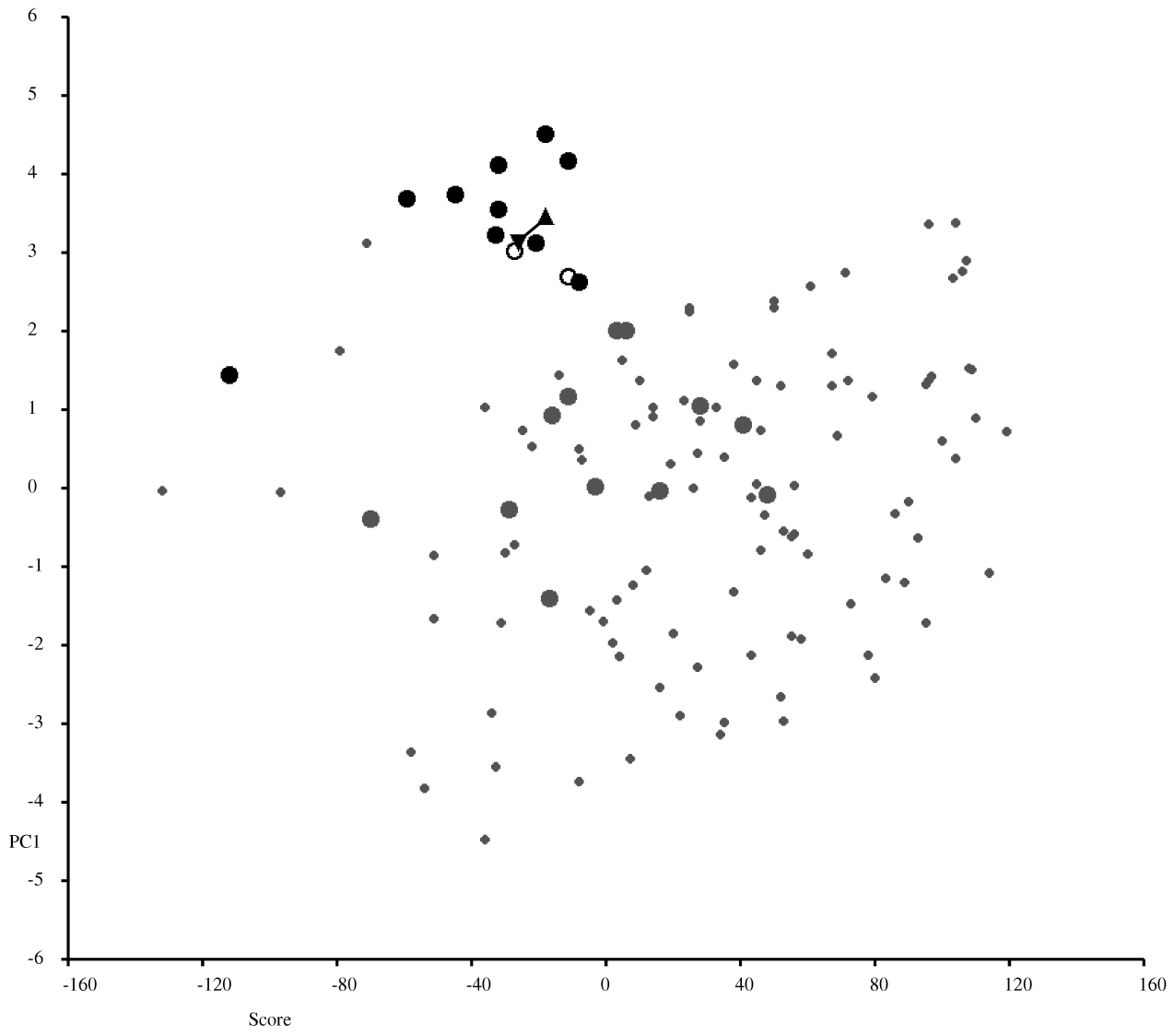

Figure 15. The same as Figure 7 but with the specimen from Lunel Viel added (black triangles). The two triangles close together joined by a line are the maximum and minimum estimates.

Appendix 1:

Definitions of the measurements taken.

Figures 1 and 2 show the approximate positions in which the measurements are taken. All the measurements are taken with a vernier gauge with "knife-edge" blades (i.e. they should have reasonably narrow edges, although that is only really important for F1).

The formal definitions are as follows:

H = minimax diameter of ischial shaft, between the acetabulum and the *spina ischiadica*.

I = absolute minimum diameter of ischial shaft (usually in the same place as H, but sometimes much more caudal).

J = minimum height of the lateral side of the acetabulum, i.e. the minimax. This is only just possible in lagomorphs, one of the blades of the vernier gauge lying almost flat against the back of the acetabulum (i.e. the medial side). It also needs a certain delicacy of touch because the edge of the acetabulum is easily damaged. In addition the acetabulum needs to be fully fused.

E = absolute minimum diameter of the shaft of the ilium. This is very oblique in rabbits, at about 45 degrees to the axis of the ilium. It should not enter the area of fusion with the sacrum (which it very occasionally tends to do).

F = minimax diameter of the shaft of the ilium, usually the absolute minimax but sometimes a local minimax. The measurement is near to or equivalent to the dorso-ventral height in most cases, but taken as a minimax. However, in some cases, when the *spina iliaca dorsalis caudalis* extends a long way caudally, this is only a local minimax and the absolute minimax is further round, more or less parallel to F1. Sometimes it is difficult to take because the depression on the ventral side of the *spina iliaca ventralis caudalis* is very shallow and the bone then has to be placed right between the tips of the blades of the vernier gauge in order to find the minimax.

F1 = minimax diameter of the shaft of the ilium with one blade of the vernier gauge placed between the edge of the acetabulum and the *spina iliaca ventralis caudalis*. One needs to be careful to avoid damaging the *spina*.

For detailed drawings and nomenclature see Barone et al. (1973, 24).

Appendix 2:

List of measurements.

Column 1 shows JPNW's reference number.
Column 2 shows the side; l = left; r = right.
Column 3 shows the age-group according to AG's Stades.
Column 4 shows the group the specimen has been assigned to : L = "Large"; S = "Small".
Columns 5 to 10 show the measurements in millimetres.

Ambrussum:

No.	Side	Stade	Group	F1	F	E	J	H	I
1	r	5	S	8.5	7.7	4.7	8.0	6.7	3.5
2	r	5	L	8.8	7.7	4.9	8.4	7.3	4.3
3	r	5	L	8.8	7.5	4.5	8.4	7.2	3.5
4	r	5	S	8.2	7.5	4.1	8.3	6.8	3.4
5	r	5	S	8.5	6.8	4.0	8.0	6.5	3.2
6	r	5	S	7.9	7.1	4.5	8.2	6.8	3.4
7	r	4	L	8.4	7.5	4.9	8.4	6.8	4.5
8	r	4	S	8.0	7.2	3.9	7.7	6.9	3.4
9	r	4	L	8.5	7.5	4.6	8.6	7.0	4.0
10	r	4	L	9.0	7.5	4.5	8.6	7.6	4.0
11	r	4	L	5.8	7.0	4.0	8.2	6.7	4.1
12	r	3	S	7.8	6.9	3.9	7.7	6.5	3.5
13	r	3	S	7.5	6.4	4.5	6.7	6.4	3.5
14	r	3	S	7.6	6.8	4.3	8.1	7.0	3.7
15	r	3	S	8.1	6.7	4.3	7.7	6.8	3.4
16	r	3	S	7.6	6.1	3.8	7.5	6.3	3.5
17	r	3	L	7.2	6.4	3.8	7.0	5.9	3.1
18	l	5	S	8.4	6.8	4.2	8.0	6.6	3.1
19	l	5	S	8.5	7.6	4.7	8.3	7.0	4.3
20	l	5	S	7.9	7.2	4.3	8.3	6.9	3.5
21	l	5	S	8.5	7.5	4.7	8.0	6.8	3.6
22	l	5	L	8.8	7.6	4.9	8.3	7.3	4.2
23	l	4	S	7.8	7.1	4.1	7.7	6.9	3.4
24	l	4	S	8.2	6.7	4.4	7.7	6.7	3.5
25	l	4	L	8.5	6.9	5.1	8.1	6.9	4.1
26	l	4	S	8.3	7.4	4.1	8.1	6.8	3.4
27	l	4	L	8.8	7.5	4.6	8.6	7.1	3.6
28	l	4	L	8.4	7.5	4.6	8.7	7.0	3.9
29	l	4	S	7.7	7.0	3.8	7.5	6.3	3.4
30	l	4	L	8.9	7.4	4.5	8.4	7.3	4.2
31	l	3	S	7.5	6.7	4.4	8.1	7.0	3.7
32	l	3	S	7.2	6.4	3.9	7.1	6.0	3.1
33	l	3	S	7.7	6.6	4.6	7.1	6.4	3.4
34	l	3	S	7.6	6.2	3.6	7.4	6.2	3.4

Lunel Viel:

No.	Side	Stade	Group	F1	F	E	J	H	I
8	l	-	L	8.5	7.7-8.0	4.5	8.5	7.0	3.9

To calculate the first principal component and the discriminant score for a specimen directly from the raw measurements in millimetres, the following formulae can be used:

$$PC1 = 0.753F1 + 1.150F + 1.080E + 0.974J + 1.022H + 1.327I - 37.6209$$

$$Score = - 95.75F1 + 25.65F + 75.64E - 36.61J + 94.27H - 64.97I + 155.109$$