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The *Cynotherium* from Corbeddu (Sardinia): comparative biometry with extant and fossil canids

Eisenmann, V. & Van der Geer, B., 1999 - The *Cynotherium* from Corbeddu (Sardinia): comparative biometry with extant and fossil canids - in: Reumer, J.W.F. & De Vos, J. (eds.) ELEPHANTS HAVE A SNORKEL! PAPERS IN HONOUR OF PAUL Y. SONDAAR - DEINSEA 7: 147-168 [ISSN 0923-9308].
Published 10 December 1999

A very well preserved canid skull from the Corbeddu Cave was compared to 80 skulls of *Vulpes vulpes* and *V. famelicus*, *Canis aureus*, *Cuon alpinus*, *Canis lupus*, and several fossil skulls of *Cynotherium* and *Cuon* using Simpson ratio diagrams for 11 measurements. The Corbeddu canid skull is very close to the Dragonara fossil and belongs to a *Cynotherium*. Craniological comparisons do not evidence a close relationship with any of the extant canids and support a full generic rank for the Sardinian canid. The most distinctive point of *Cynotherium* is the association of a wide muzzle with a small temporal fossa. Relatively wide muzzles characterise also Cuons, Wolves, and *Canis falconeri* in opposition to Jackals, *Canis etruscus*, and *C. arnensis*. The size of the temporal fossa is not known for *C. falconeri*. The small temporal fossa (found only in juvenile extant canids) could perhaps result from a neotenic evolution.

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Keywords: Sardinia, Corbeddu cave, *Cynotherium*, canids, Pleistocene

PREFACE

Publication aleas explain why this description of the skull of *Cynotherium* from Corbeddu will appear after the short note intended to complement it. In this previously published paper (Eisenmann 1990), a principal components analysis was run on 26 variables of 91 skulls (five Lycaons, 14 Wolves, 17 Foxes, 26 Cuons, 27 Jackals, one *Cynotherium*, and one *Nyctereutes*). Foxes, Jackals and Wolves appeared aligned according to size, and separated by their long faces and small tympanic bullae from Cuons and Lycaons, also aligned according to size. The *Cynotherium* was situated among the Jackals. The present paper, dealing with a slightly different sample studied in a different way, provides moreover illustrations of the *Cynotherium* skull, of the system of measurements, biometrical data on many modern canid skulls and comparisons with several skulls of *Canis etruscus*, *C. falconeri*, and *C. arnensis*.

INTRODUCTION

The skull of a canid (associated with a nearly complete skeleton) was found in Hall II of Corbeddu Cave (Sardinia), just at the top Level 1 of the layer 3, partly embedded in a breccia; it was dated at 11,350 +/- 100 years BP or 11,199 - 11,405 BC calibrated (Klein Hofmeijer 1996). Other skulls of canids have already been described from Sardinian deposits (Malatesta 1962 & 1970) and referred to *Cynotherium sardous* (MALATESTA 1970). Their exact age is not known; neither is the date of arrival known of *Cynotherium* or of its ancestor on Sardinia (Vigne 1983), even if a Middle Pleistocene age was suggested (Kotsakis 1980, Caloi et al. 1986). A fragmentary skull was described by M.-F. Bonifay (1994) from Corsica; it could be as old as the Würm I-Würm II Interstadial. Thus, the Corbeddu specimen is the only one dated. In addition, it is remarkably well preserved (Figures 1 and 2) and allows precise biometrical comparisons. Let us note immediately that, although obviously adult, the skull has a juvenile look. The impression is probably due to the round and smooth brain case, without marked crests (Figure 1). We will see that other features may also be considered as juvenile. In this paper we address several questions concerning the Corbeddu skull and, more generally, the canid craniology:

- does the Corbeddu skull belong to a *Cynotherium*?
- by what characters do the modern Eurasian canids differ?
- does the Corbeddu canid closely resemble one of the modern genera of Eurasian canids?
- can the observed differences be explained by sexual dimorphism or some other factor(s)?
- what can be said about some craniological proportions of fossil *Canis*?

MATERIAL COMPARED

A total of 80 skulls of modern canids is studied in the present paper: 17 *Vulpes vulpes* and *V. famelicus*; 24 *Canis aureus*; 25 *Cuon alpinus*; 14 *Canis lupus*. The skulls belong to the collections of the Muséum National d'Histoire Naturelle, in Paris (Laboratoire d'Anatomie comparée et Laboratoire des Mammifères et Oiseaux) and of the National Museum of Natural History (Naturalis), in Leiden. Fossil canids: *Canis etruscus* and *C. lupus lunellensis* (Bonifay 1971); *Cuon alpinus* var. *europea* (Boule 1927); *Canis arnensis* (Koufos 1987); *Cynotherium sardous* (Malatesta 1970); *Canis etruscus*, *C. falconeri*, and *C. arnensis* (Torre 1967); *C. etruscus* (Vekua 1995).

METHODS

More than 30 measurements were taken on each of the skulls of extant canids. Some of them are identical to the ones used by Clutton-Brock *et al.* (1976) and Radinsky (1981). Measurements for fossil skulls were taken from text descriptions and illustrations published by other authors. The system is illustrated here in Figure 3. In this paper we analyse the differences evidenced by ratio diagrams (Simpson 1941) on 11 variables:

- condylobasal length (1)
- post-palatal and palatal lengths (4 and 5)
- distance between the end of palatine fissures and Prosthion (6)
- length of P4, M1, and M2 (9)
- muzzle breadth at the 3rd incisors (10)
- palatal maximal breadth (13)
- cranial maximal breadth (20)
- bizygomatic breadth (21)
- breadth at the postorbital constriction (22);

the latter two variables are specially interesting because by substracting the second from the first, one can get the width of the temporal fossa (TFW), which is an estimator of the size of the temporal muscle.

- height of the face behind P4 (33).

The reference is the average Jackal skull. Each measure (or average) is converted in decimal logs. The difference with the Jackal corresponding log is plotted on one or the other side of the zero-reference line (corresponding to the average Jackal skull). When the dimensions are larger than in the Jackal, they are plotted above the zero line, when smaller – below. Appendici 1 to 5 give the statistics for these 34 measurements, i.e. the size of the sample (n), the average value (x), the observed range of variation (min and max), the standard deviation (s) and the coefficient of variation (v = 100s/x), respectively for the Jackals, Foxes, Cuons, Lycaons, and

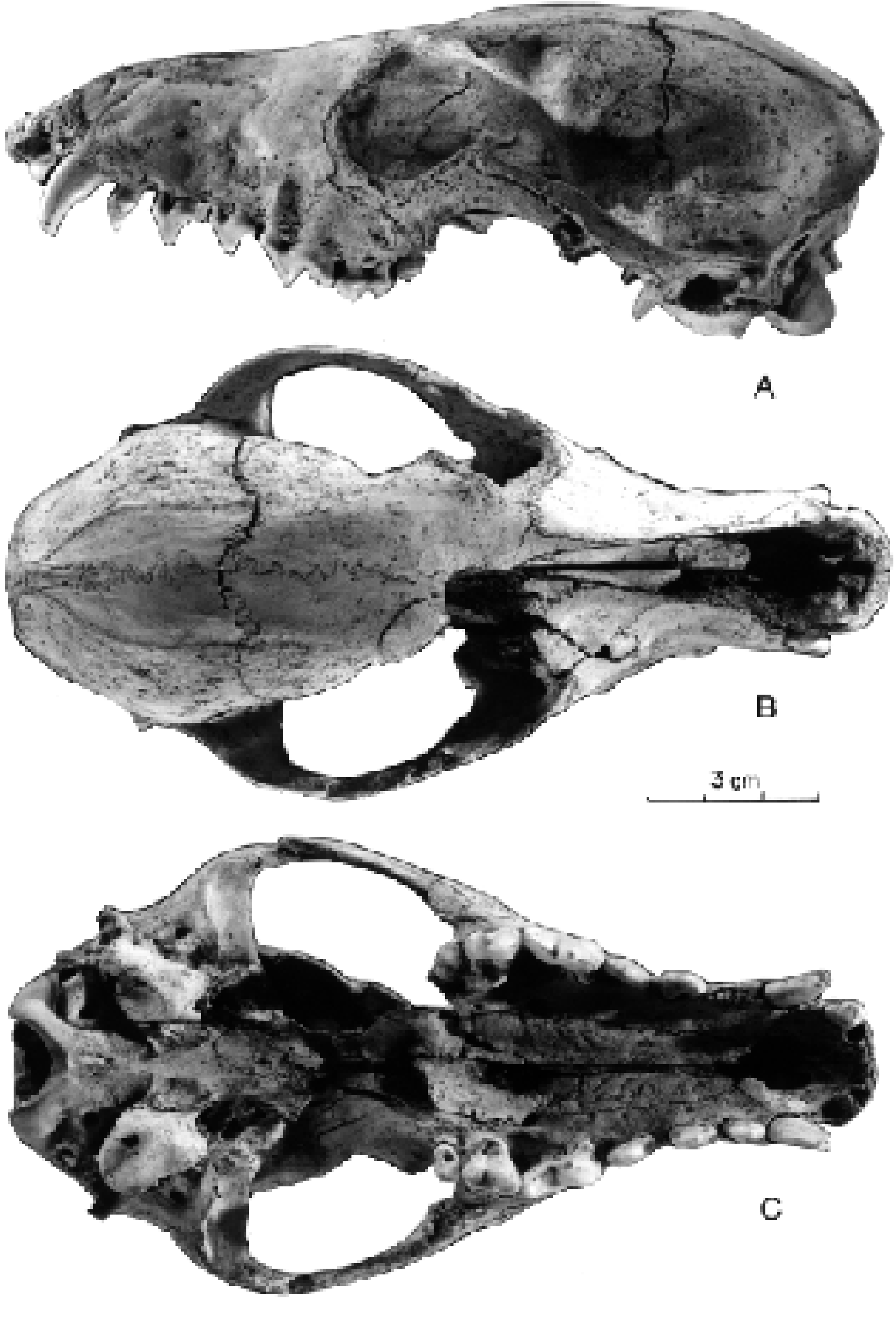

Figure 1 *Cynotherium* skull CB 1984-8022 from Corbeddu Cave. **A** profile; **B** dorsal view; **C** occlusal (ventral) view.

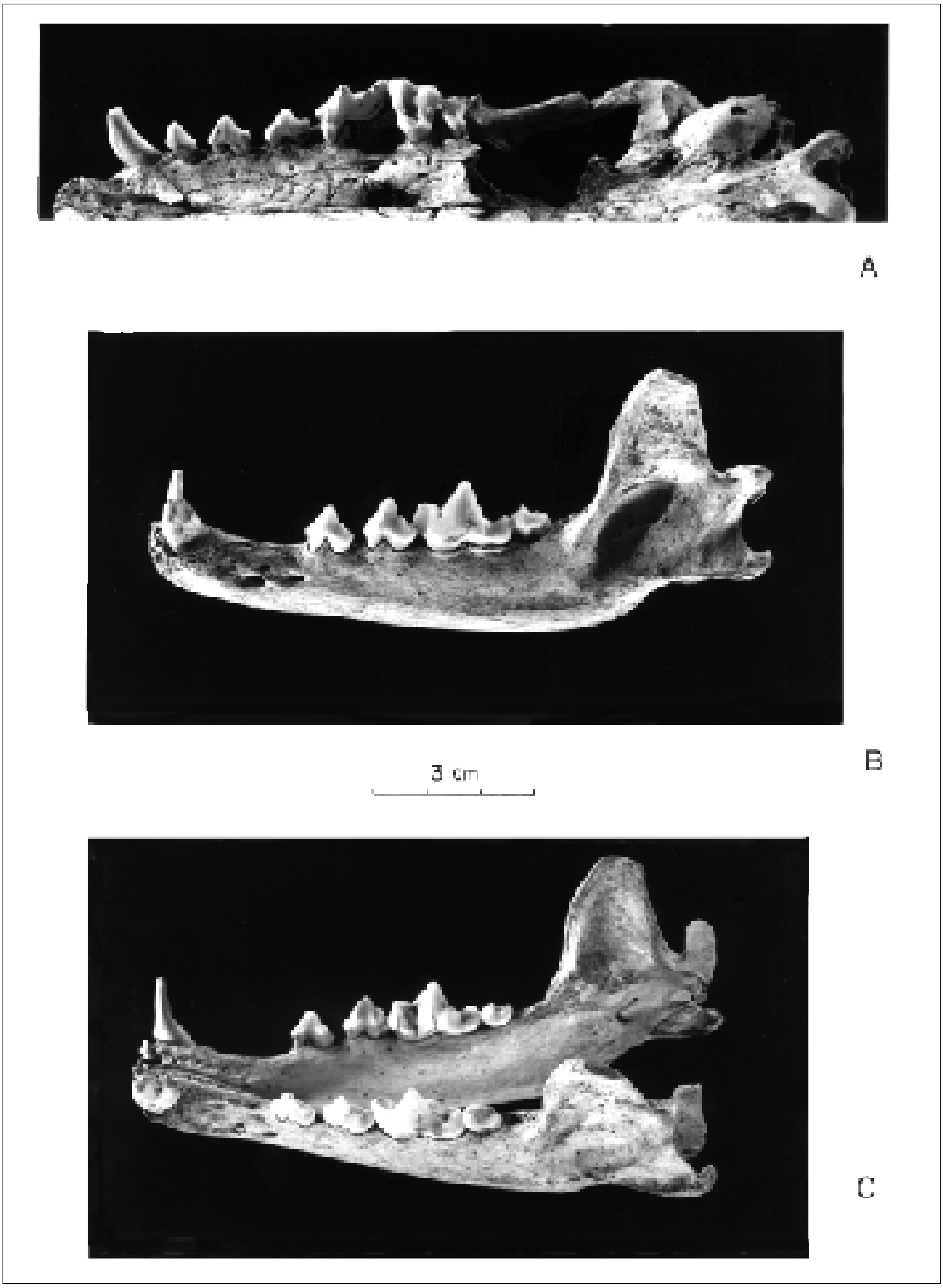

Figure 2 *Cynotherium* skull and mandible CB 1984-8022 from Corbeddu Cave. **A** upper dentition; **B** and **C** mandible and lower dentition.

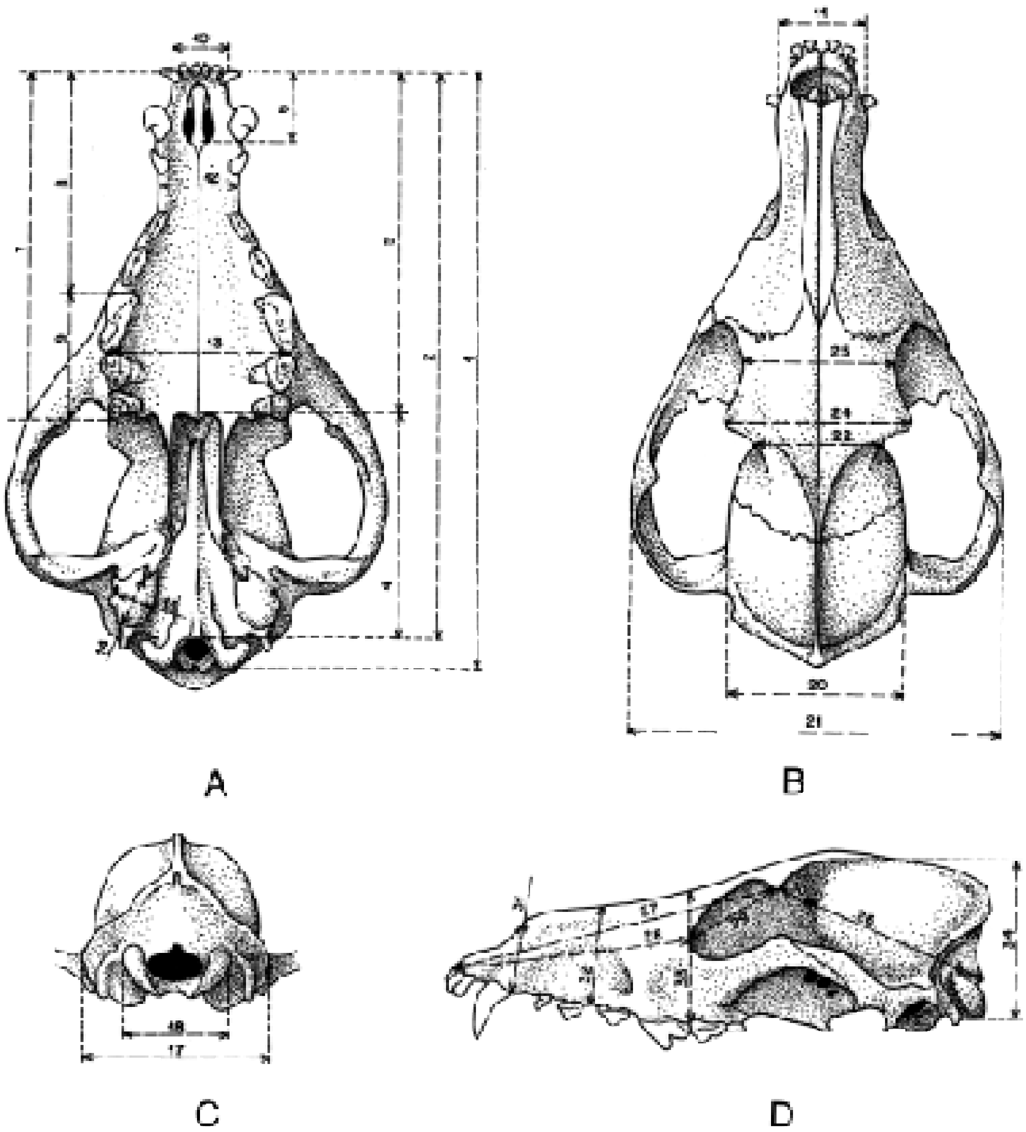

Figure 3 System of measurements for canid skulls. **A** occlusal (ventral) view; **B** dorsal view; **C** occipital view; **D** profile.

Wolves. Appendix 6 gives the individual measurements used in ratio diagrams for fossil skulls of *Cynotherium* and *Cuon* and for two juvenile Jackals.

CYNOTHERIUM SARDOUS AND THE CORBEDDU SKULL

The ratio diagram (Fig. 4) shows clearly that the Corbeddu skull is smaller but has the same proportions as the Dragonara skull n^{0}1 which was referred to a female *Cynotherium sardous* (MALATESTA 1970). Some dimensions of the not so well preserved male skull from Dragonara (no.2) are impossible or difficult to estimate. However, the male skull seems to be slightly larger

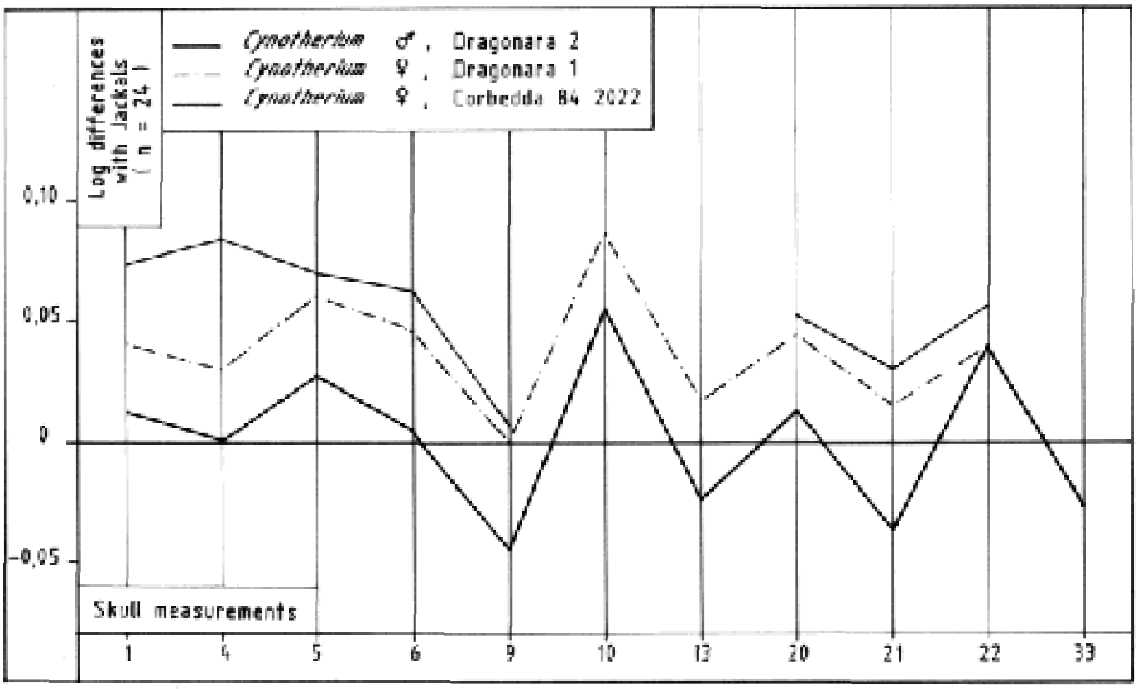

Figure 4 Ratio diagrams of *Cynotherium* skulls compared to the average *Canis aureus* skull (reference line). **1** = condylobasal length; **4** = post-palatal length; **5** = palatal length; **6** = distance between Prosthion and the end of palatine fissures; **9** = length of P4, M1 and M2; **10** = muzzle breadth at the 3rd incisors; **13** = palatal maximal breadth; **20** = cranial maximal breadth; **21** = bizygomatic breadth; **22** = breadth at the postorbital constriction; **33** = height of the face behind P4.

than the female. The diagram suggests that the Corbeddu skull belonged to a female, smaller than the Dragonara one, and differing from it by being relatively wider at the level of the postorbital constriction (measure 22).

CRANIAL DIFFERENCES BETWEEN MODERN GENERA (Fig. 5)

Foxes and Jackals

Average measurements in Fox skulls are smaller than in Jackals: the whole diagram for *Vulpes* is situated below the *Canis aureus* line (zero line); there is however an overlap for all measurements except the palatal breadth (13) and the breadth at the postorbital constriction (22) as can be seen in the Tables and by comparing Figures 6 and 8. Several measurements of the average Fox skull are not only smaller but relatively smaller when compared to its basicranial length (1): the distance between Prosthion and the posterior end of the palatine fissures (6), the length of P4M1M2 (9), most of widths: at the third incisors (10), maximal palatal (13), and at the postorbital constriction (22). One dimension is relatively larger: the cranial width.

Cuons and Jackals

Average dimensions are larger in Cuons but the overlap is very important for many measurements (Appendici and Figures 7-8). The *Cuon* average skull is relatively wider (measurements 10, 13, 20, 21, 22); it has a relatively shorter palate (5), a relatively longer distance between Prosthion and the posterior end of the palatine fissures (6), and a relatively higher face (33). The length of P4M1M2 (9) is relatively smaller. The tympanic bullae are larger.

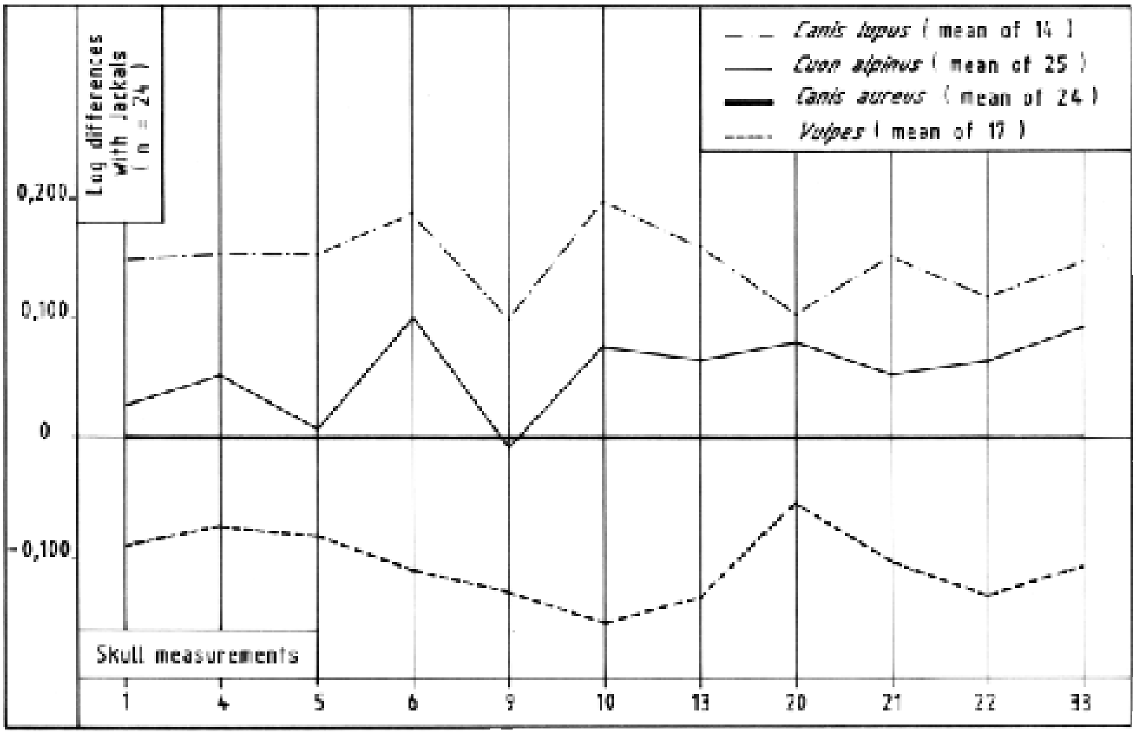

Figure 5 Ratio diagrams of ave rage skulls of Wolves, Cuons, Jackals, and Foxes. Same measurements as in Fig. 4.

Wolves and Jackals

Average measurements are larger in Wolves and there is no overlap (Appendici and Figures 6-8) except for the length of P4M1M2 (9). Moreover, the average Wolf skull differs by having a relatively longer distance between Prosthion and the posterior end of the palatine fissure (6), and by being relatively wider at the third incisors (10). Several dimensions are relatively smaller: length of P4M1M2 (9), cranial breadth (20), breadth at the postorbital constriction (22).

DIFFERENCES BEWEEN *CYNOTHERIUM* AND MODERN CANID SKULLS

Since *Cynotherium* has been considered in the past (Malatesta 1962) and is still considered by M.-F. Bonifay (1994) as a subgenus of *Cuon*, it is interesting to note that skull characters do not support such a close relationship. It has already been noted (Eisenmann 1990) that Lycaons and Cuons have much higher tympanic bullae (measurement 16) and shorter faces, in particular between Prosthion and P4 (measurement 8) than other extant Canids. Figure 7 shows the range of variation and average of some other measurements of *Cuons*, comparing them to the Corbeddu skull, to another fossil *Cynotherium*, and to the *Cuon* skull A described by Boule (1927) from the cave of l'Observatoire, at Monaco. Clearly the Monaco skull belongs to a large *Cuon* (we have probably underestimated the cranial width (20) when measuring it on the plate VIII of Boule). The Corbeddu skull is quite different by its relatively long palate (5) and short palatine fissures (6), as well as by its relatively larger breadth at the postorbital constriction (22), and its smaller height (33). Let us stress that Cuons have especially short palates and that no *Cuon* has such short palatine fissures as *Cynotherium*.

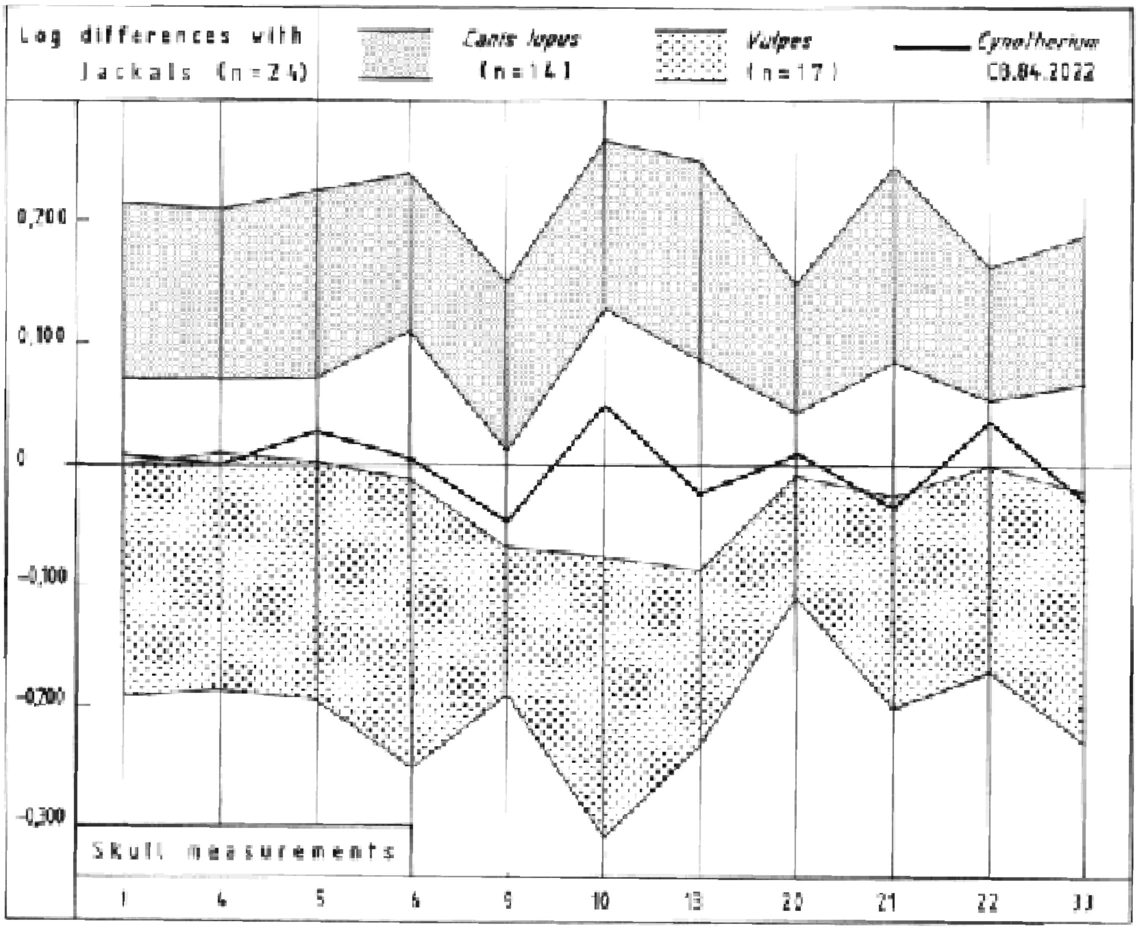

Figure 6 Ratio diagram of the CorbedduCynotherium skull compared to the ranges of variation of Wolves and Foxes. Same measurements as in Fig. 4.

A detailed comment of all distinctive characters evidenced by the ratio diagrams (Fig. 6 to 8) would be long and tiresome. In short, Foxes have smaller widths at the incisors; Wolves have smaller widths at the postorbital constriction, and correlatively more room for the temporal muscle. On the whole, size and proportions seem rather close to those of Jackals: at any rate, the major part of the Sardinian skull graph is included inside the range of variation of Jackals (Fig. 6) and the skull of *Cynotherium* plots near Jackal skulls on the multivariate analysis (Eisenmann 1 9 9 0). But the width of the temporal fossa (TFW = 21-22) is much larger in Jackals, and the muzzle is narrower.

SEXUAL DIMORPHISM IN *CANIS AUREUS* SKULLS

Since a sexual dimorphism is known to exist in Canids, one can wonder if the differences between the Corbeddu skull and the 'average skull' of Jackal, used as reference, are not sex related. In other terms, could the relatively small bizygomatic width of the Corbeddu specimen (or any other cranial character) be explained by the fact that the skull belonged to a female, whereas our reference sample of Jackal skulls could be composed mostly of males? To address this question, we have compared a sample of female Jackal skulls to a reference sample composed this time of only male skulls. Because the sex is known in only a few cases, both samples are small: 5 female skulls and 6 male skulls. The corres-

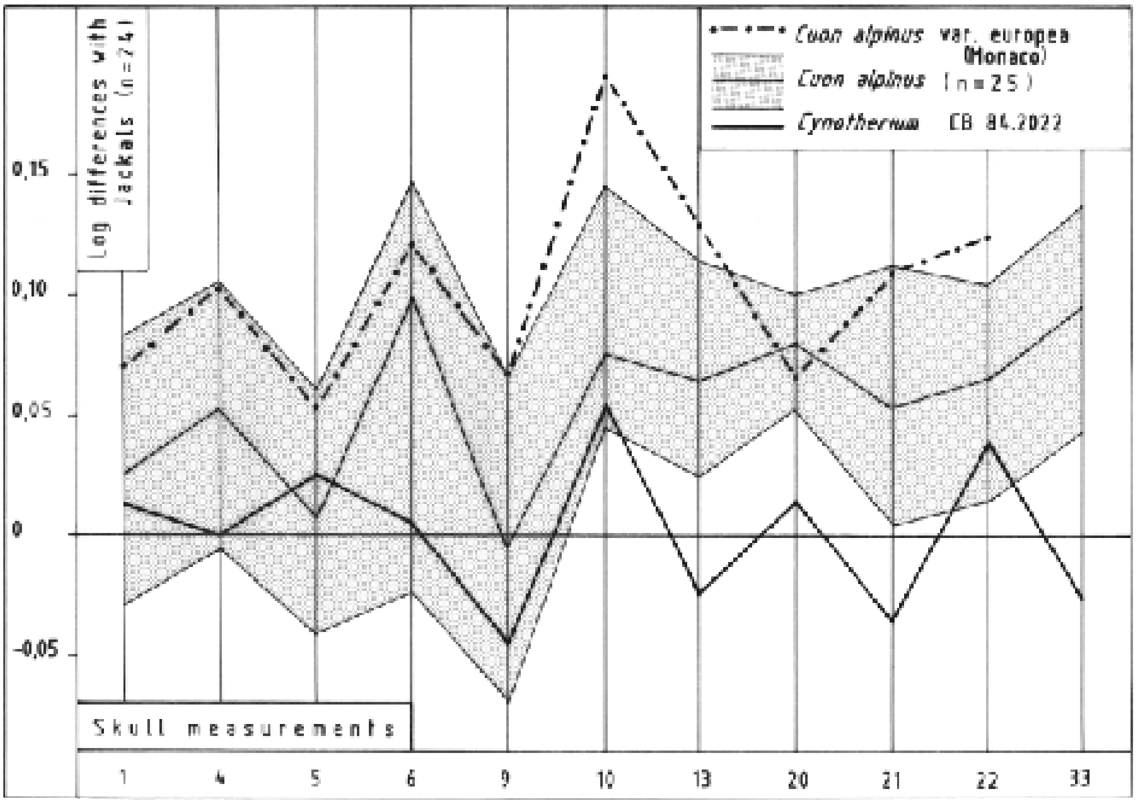

Figure 7 Ratio diagrams of the Corbeddu *Cynotherium* skull and the *Cuon alpinus* skull A from Monaco compared to the mean and range of variation of *Cuon* skulls. Same measurements as in Fig. 4.

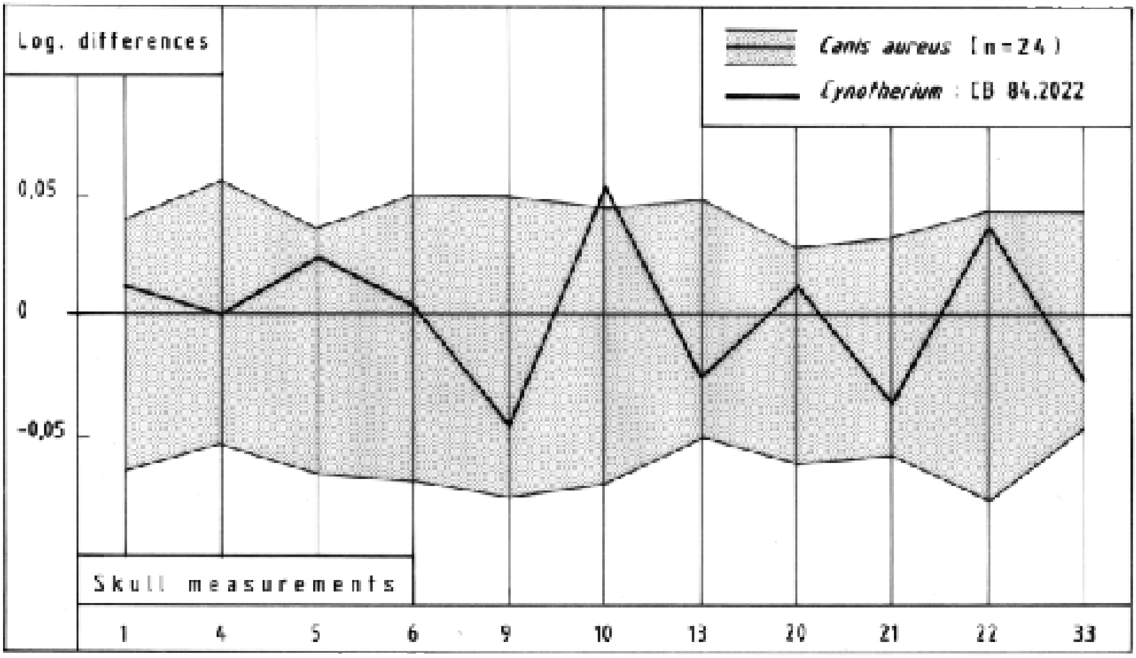

Figure 8 Ratio diagram of the CorbedduCynotherium skull compared to the range of variation for Jackal skulls. Same measurements as in Fig. 4.

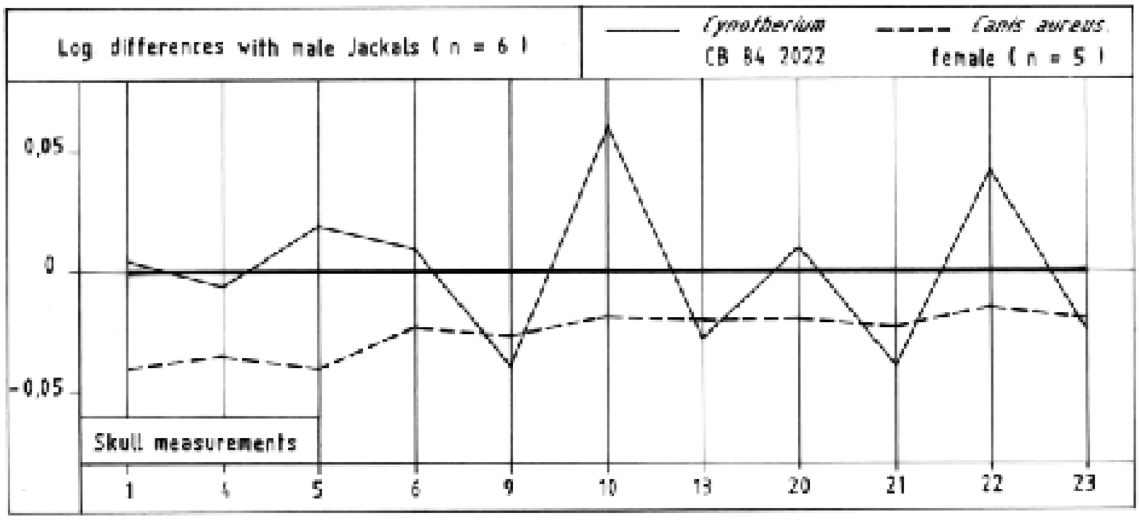

Figure 9 Ratio diagram of the Corbeddu *Cynotherium* skull compared to average female and male Jackal skulls. Same measurements as in Fig. 4.

ponding ratio diagram (Fig. 9) shows that indeed there is a sexual dimorphism, even if not very strong. Female skulls are smaller by all their measurements, especially the lengths (1, 4, 5), so that the female skull is relatively wider. But all the differences in proportions between male and female skulls are very slight when compared to the differences between the Corbeddu skull and the Jackal skulls, whether male or female. Obviously, the particularities of the Corbeddu skull cannot be explained by a sexual dimorphism.

OTHER POSSIBLE INTERPRETATIONS

Figure 10 compares the Corbeddu skull with the average diagram for two juvenile Jackals. The *Cynotherium* skull is clearly different by the shortness of the palatine fissures (6) and of the P4-M2 series (9), and by the width at the incisors (10). Other features are however surprisingly similar: relatively long palate (5), relatively small bizygomatic width (21), relatively wide postorbital constriction (22), and relatively small height behind the P4 (33). The regressions of the palatal length versus the condylobasal length or the postpalatal length show that juvenile Jackals and *Cynotherium* are not to be separated from our sample of adult Jackals. The same is true for the regression of the height of the skull versus the condylobasal length. But juvenile Jackals and the Corbeddu skull fall well outside the confidence interval of the regression line of the temporal fossa width (TFW) relatively to the basal length for 23 adult Jackals (Fig.11). The TFW (result of the substraction of the width at the postorbital constriction from the bizygomatic width) is related to the size of the temporal muscle.

In *Cynotherium* as well as in our juvenile Jackals the temporalis muscle was certainly less developed than in adult Jackals, which cannot but have a functional meaning. Radinsky (1981) found that among Carnivora, there is a positive allometry of the temporal fossa width (TFW = 21-22). In the intraspecific regressions that we have calculated for the logs (base 10) of TFW versus the basilar length (measurement 1), the slopes are indeed larger than 1, with the exception of Jackals (0,934). We have also calculated an interspecific regression using the average log values for Wolves, Cuons, Jackals, Foxes, and the logs for one single skull of *Nyctereutes procyonides*. The corresponding slope is of 1,136. For *Cynotherium* the slope is much larger: 1,504 if we use the 3 available specimens; 2,931 if we use only the two best preserved skulls (Corbeddu and Dragonara fema-

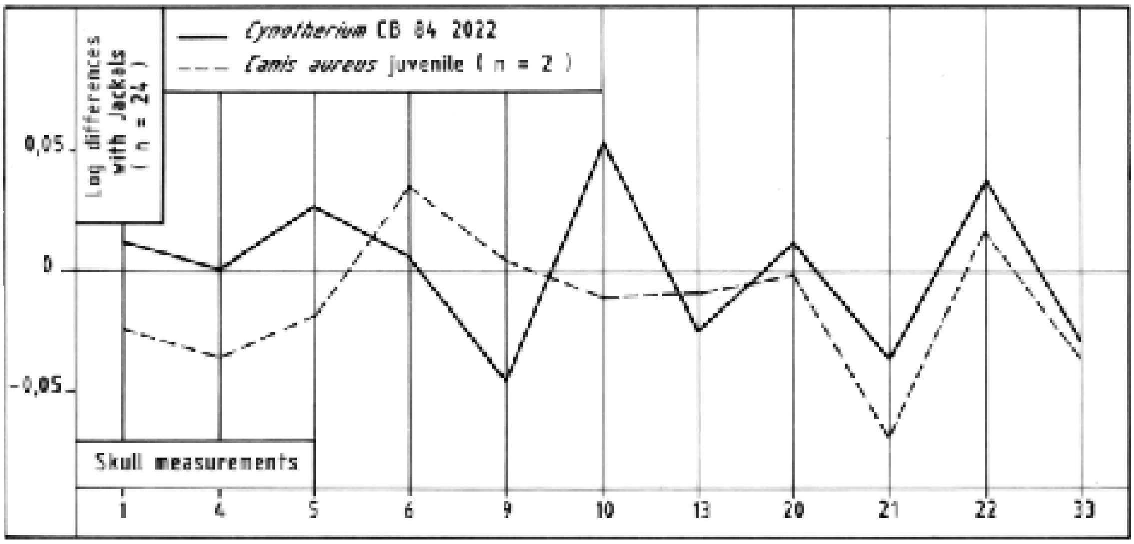

Figure 10 Ratio diagram of the CorbedduCynotherium skull compared to an average juvenile Jackal skull. Same measurements as in Fig. 4.

le). Large slopes seem characteristic for juvenile canids: 3,947 for two juvenile Jackals; 2,345 when a juvenile Wolf is added. Unfortunately, the specimens are few and we can only suggest that the relatively small TFW found in adult *Cynotherium* and its relatively large allometry may be neotenic characters (Dommergues *et al.* 1986).

Canis arnensis, *Canis etruscus*, and *Canis falconeri*

In the first paper on *Cynotherium* (Eisenmann 1990), no clear affinities were evidenced between modern Jackals or Wolves and fossil *Canis falconeri*, *C. etruscus*, and *C. arnensis*, partly because of preservation problems. We believe now that two parameters usually measurable in fossil skulls may throw some light on these affinities. A scatter diagram of decimal logarithms of the muzzle widths at the third incisors versus the lengths of P4M1M2 separates quite well Cuons and Wolves (because of their relatively wider muzzle) from Jackals (Fig. 12). In his revision of Villafranchian canids, Torre (1967) recognised three species: the very large *Canis falconeri*, the middle-sized *C. etruscus*, and the small *C. arnensis*. On our scatter diagram, the three species plot quite apart. *C. etruscus* and *C. arnensis* differ by size but plot along the line of modern Jackals. *C. falconeri* is the only one to plot along the line of modern Wolves though its dimensions are larger. Stehlin (quoted by Torre) believed that *C. falconeri* could be the ancestor of Wolves but Torre disagrees with Stehlin because of the brachyodonty of *C. falconeri*. Torre finds great similarities between *C. falconeri* and *C. antonii*, a Chinese Villafranchian species (and indeed both are very large and have wide muzzles). Concerning the ancestors of Wolves, Torre's opinion is that they may more probably be found among *C. etruscus* while *C. arnensis* is more like a large Jackal. Vekua (1995) referred to *C. etruscus* a beautifully preserved skull from the Middle or Late Villafranchian of Dmanisi (Georgia). This skull is quite larger than the other *C. etruscus* skulls but plots along their line. Another Villafranchian skull was described by Koufos (1987) from Gerakarou (Greece) and referred to *C. arnensis*. Although slightly smaller than *C. etruscus*, it plots quite near to them. M.-F. Bonifay (1971) described several skulls from the French Grottes de l'Escale (Early Middle Pleistocene) and Lunel Viel (Middle Pleistocene). The first ones were referred to *Canis etruscus* (which, in her opinion, inclu-

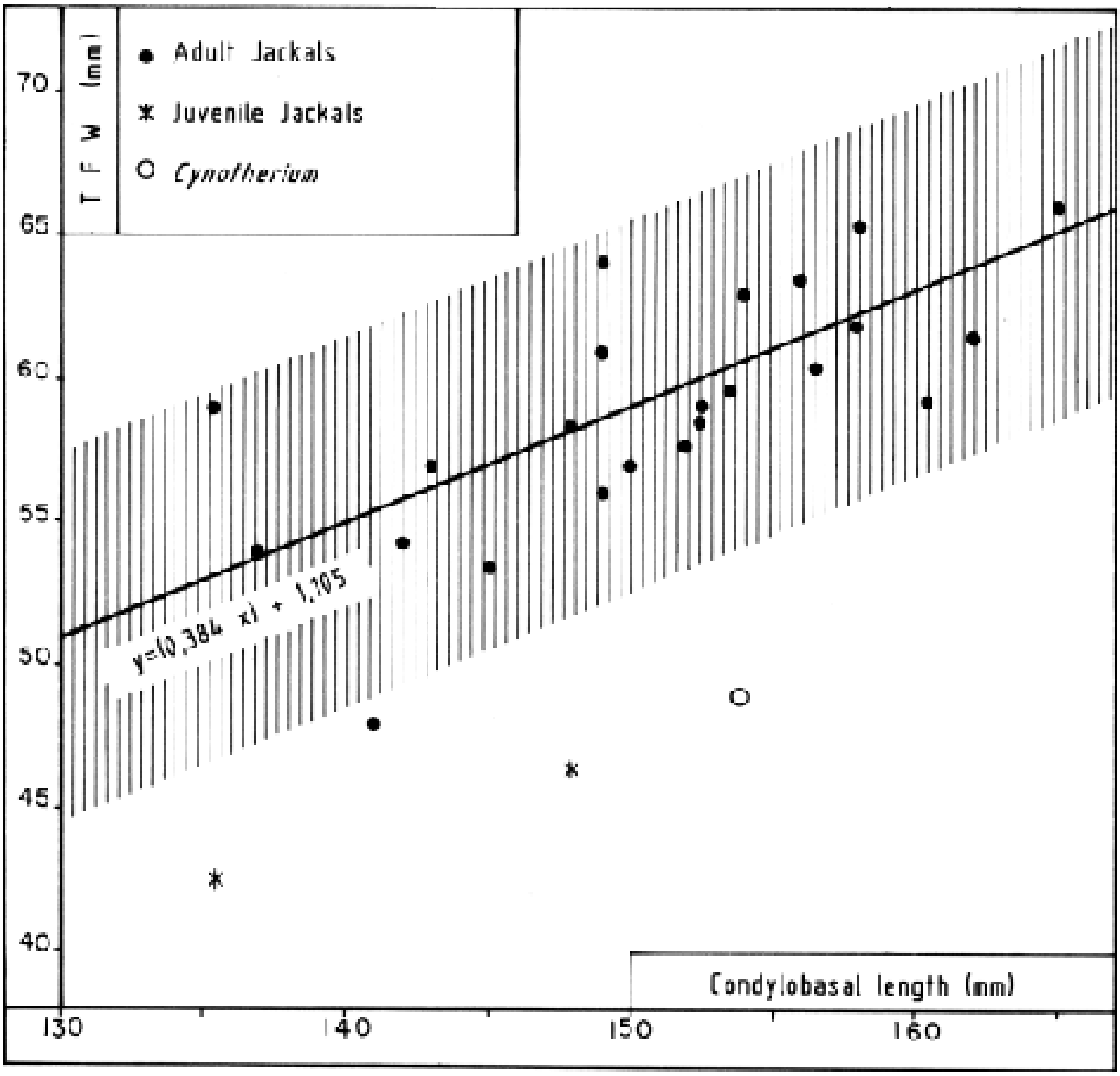

Figure 11 Scatter diagram, regression line, and confidence interval of Temporal Fossa Width (TFW) versus condylobasal length for Jackals and the Corbeddu *Cynotherium*.

des *C. arnensis*). The skulls of Lunel Viel were referred to *C. lupus lunellensis*. None of them plots along the Wolf line; the skull D8 of Escale plots near *C. etruscus*, the other three near *C. arnensis*. As could be expected because of its wide muzzle, *Cynotherium* plots along the Cuon-Wolf line.

CONCLUSIONS

Biometrical comparisons show that the Corbeddu canid is very close to the Dragonara canid ascribed to *Cynotherium sardous* by Malatesta (1970). The size is about that of a Jackal skull but there are at least two important cranial differences: *Cynotherium* has a much larger width at the incisors and much smaller temporal fossae. Although some dental and cranial characters may have suggested an affinity with *Cuon*, this affinity is not supported by craniometry: *Cynotherium* has smaller tympanic bullae, a longer face, a shorter postpalatal length and

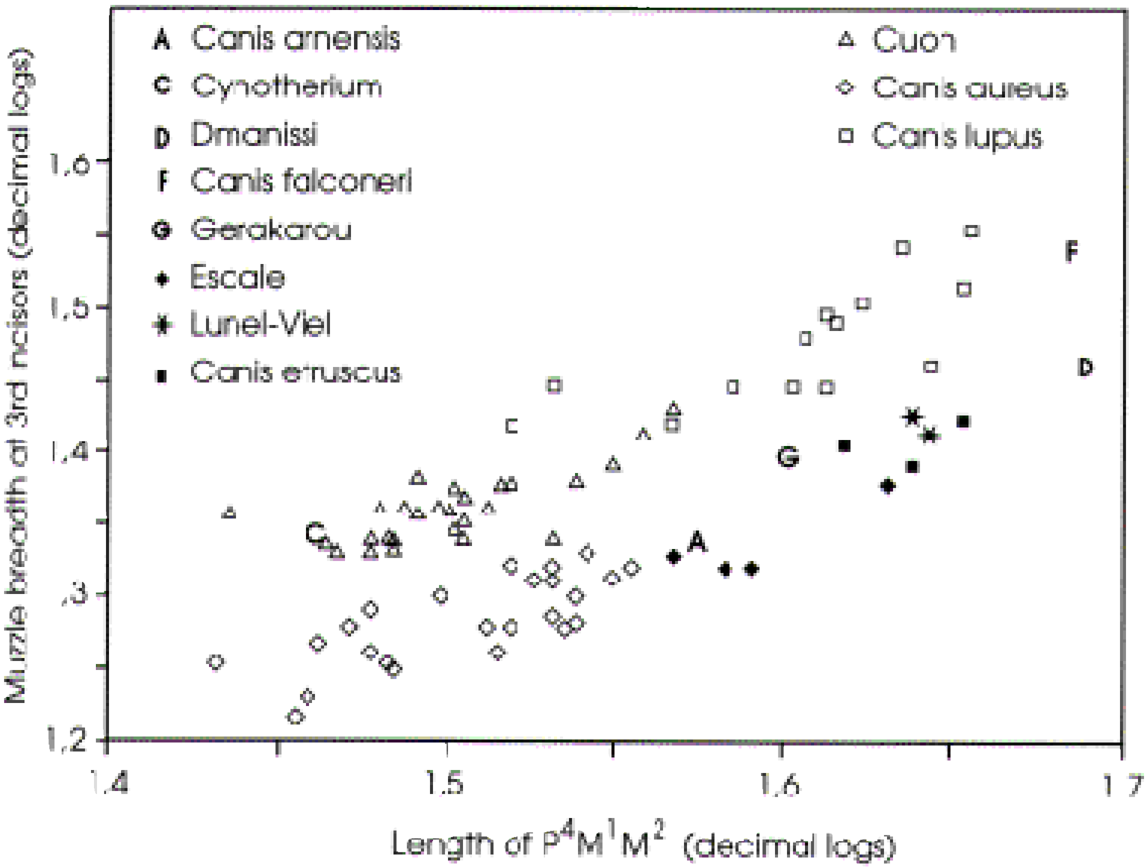

Figure 12 Scatter diagram of decimal logarithms of the muzzle width versus the length of P4, M1 and M2 in some extant and fossil canids.

shorter palatine fissures. The *Cynotherium* skull proportions are on the whole not very different from those of Foxes but the width at the third incisors is much larger in the Sardinian canid. Wolves are naturally much larger and, moreover, they have large temporal fossae. Thus it seems difficult to place *Cynotherium* in any of the studied modern genera and we agree with Malatesta who proposes to give it a full generic rank. The question of the taxonomic affinities of *Cynotherium* is very hard to address on the restricted basis of our craniological study. The peculiar proportions of *Cynotherium* can be interpreted as the result of the insular evolution of a continental form (Sondaar 1977). If we suppose that the ancestor was a kind of Jackal like *Canis arnensis*, it is interesting to note that juvenile Jackals have, like *Cynotherium*, relatively small temporal fossae. This character could therefore be ascribed to a neotenic evolution. A large width at the third incisors, however, is not a juvenile character for Jackals. It would point to affinities with Wolf-like species like *C. lupus* or *C. falconeri* but these are especially large forms which makes them rather unprobable ancestors for the small *Cynotherium*. The development of the temporal fossa is unknown both in *Canis falconeri* and *C. antonii*. We have already noted why *Cuons* were probably not the ancestors of *Cynotherium*. Other forms like *Xenocyon* (SCHÜTT 1974) could qualify for this position; unfortunately their skull characters are not known.

The width of the muzzle has certainly functional implications. But Radinsky (1981) did not include it in his study of Carnivora skulls and we have till now not found any discussion of this character. According to our data, there is a very good interspecific correlation between width of the muzzle and size of the temporal fossa for Lycaons, Wolves, Cuons, Jackals and Foxes. *Cynotherium* does not fit on this interspecific regression line, the width at the incisors being larger than what the size of the temporal fossa would warrant for the other Canids. At the moment, this original association between small temporal fossa and wide muzzle seems very characteristic of *Cynotherium*. If this genus did evolve from a kind of Fox or Jackal, it must have acquired a wide muzzle; if the ancestor was a kind of Wolf, *Lycaon*, or *Cuon*, it must have reduced the temporal fossa. Original associations of characters define species or genera; for instance *C. falconeri* and *C. antonii* seem characterised by the association of Wolf-like features and brachyodont teeth. But original associations are rarely found in recent fossils. Insular evolution may probably be held responsible for the originality of *Cynotherium*.

ACKNOWLEDGEMENTS

Our first thanks are to Paul Sondaar for teaching us a lot, and particularly equids to one of us. He allowed us to study the Corbeddu canid, and we were helped by all our friends and colleagues excavators at the site. We are very grateful to the curators of osteological collections at the MNHN, Paris, and NNM, Leiden. We thank also Germaine Petter and Jean-Denis Vigne for helping us with the bibliography, and for many interesting comments, suggestions and discussions. Photographs were made by L. Merlette, drawings by Ch. Durand, H. Lavina, and F. Pilard.

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received 7 August 1998

APPENDIX I

Measures	n	x	min	max	s	v
1	26	140,3	129,4	166,0	8 85	5,93
2	26	141,3	123,0	156,0	8.11	5,74
3	26	8,0	5,0	1 0	1 33	16,63
4	25	63,9	56,0	73,4	4.09	6,40
5	25	77 1	66,5	84,6	4.58	5,94
6	25	20,2	17 1	22,5	1 59	7 87
7	26	79,1	68,0	85,	5.03	6,36
8	26	47 8	40,8	54,0	3.41	7 13
8 6	25	27,6	22,3	34,0	2 86	10,36
9	26	32,1	27,0	35,9	2.50	7 79
10	26	19,3	16,5	21 5	1 30	6,74
11	26	27 0	23,4	31 0	2 36	8,74
12	26	24,5	21,3	27 6	1 88	7 67
3	25	50,7	45,3	57 0	3,18	6,27
4	26	21,6	19,0	23,7	1 28	5,93
5	26	15,7	14,0	7 5	1 00	6,37
6	24	8,6	7,5	0,0	0.68	7 91
7	26	53,3	47,5	58,	2 56	4,80
8	26	29,9	25,0	33,6	1 86	6 22
9	26	23,5	19,6	26,6	1 70	7 23
20	26	52,1	45,5	56,0	2 87	5 51
21	26	87 5	74,7	95,5	5 71	6 53
22	26	29,9	25,0	33,5	2 14	7 16
23	26	57 6	42,7	66,0	5 73	9 95
24	26	42,8	32,5	48,9	3.59	8 39
25	26	28,0	21,0	32 2	2 76	9 86
26	26	62,5	56,0	69,0	3,07	4 91
27	26	99,9	83,0	114,0	7,22	7,23
28	26	66,4	54,0	73,6	4,96	7,47
29	26	29,4	26,0	35 2	2 17	7 38
30	26	10,9	6,5	5 2	2 31	21 19
31	25	22,1	18,0	26 0	2,49	1,27
32	26	27 7	24,0	33,0	2,45	8,84
33	26	45,7	39,0	51 0	3,28	7 8
34	26	44,9	40,5	48 0	1,89	4,21

APPENDIX 1 (caption)

Adult *Canis aureus*, skull measurements in millimetres. Measures are: **1**= condylobasal length; **2** = basicranial length; **3** = difference between 1 and 2; **4** = post-palatal length; **5** = palatal length; **6** = distance between Prosthion and the end of palatine fissures; **7** = from Prosthion to the last molar; **8** = from Prosthion to the P4; **9** = length of P4, M1 and M2; **10** = muzzle width at the 3rd incisors; **11** = maximal muzzle width at the canines; **12** = width at the diastema; **13** = palatal maximal width; **14** = length of tympanic bulla; **15** = width of tympanic bulla; **16** = height of tympanic bulla; **17** = maximal occipital width; **18** = width at the occipital condyles; **19** = difference between 17 and 18; **20** = cranial maximal width; **21** = bizygomatic width; **22** = width at the postorbital constriction; **23** = temporal fossa width (21-22); **24** = maximal frontal width; **25** = minimal frontal width; **26** = cranial length; **27** = facial length; **28** = from Prosthion to orbit; **29** = orbital length; **30** = length of the post-orbital constriction; **31** = height of the muzzle behind canines; **32** = height of the muzzle between P2 and P3; **33** = height of the face behind P4; **34** = height of the cranium. Other abbreviations: n = number of observations; x = ave rage value; min = minimal observed value; max = maximal observed value; s = standard deviation; v = coefficient of variation (v = 100s/x).

APPENDIX 2 Adult *Vulpes vulpes* and *Vulpes famelicus*, skull measurements in mm. Legend: see Appendix 1.

Measures	n	x	min	max	s	v
1	16	122,6	95,6	150,0	17.86	14.57
2	16	116,9	91 5	143,0	16,97	14,52
3	16	5,8	3 5	7,0	1,09	18,79
4	15	53,9	42 0	66,0	7,26	13,47
5	16	64.2	49.3	78.0	10.91	16.99
6	15	15,6	1 2	19,5	2,48	15,90
7	16	67,3	53,2	80,2	9,47	14.07
8	17	43,3	33,0	53,7	6,94	16,03
8 5	17	29.6	22.8	35.7	4.12	13.92
9	16	24,1	20,6	27,5	2,24	9,29
10	17	13,6	9 5	16,2	2,10	15,44
11	17	20,9	14,5	26,0	3,63	17,37
12	17	18.4	14.0	22.3	2.84	15.43
13	17	37,3	30,0	42,0	4,36	11,69
14	16	20,2	17 0	22,2	1,51	7,48
15	16	13,6	11 2	16,5	1,56	11,47
16	14	8.2	6 5	10.2	1 11	13.54
17	16	43,7	36,3	50,7	4,59	10,50
18	16	23,5	19 5	27,0	2,44	10,38
19	16	20,2	15 0	23,0	2,55	12,62
20	15	44.7	39 3	50.0	3.55	7.94
21	17	70,2	55 7	84,0	9,40	13,39
22	17	22,2	20,0	24,5	1,65	7,43
23	17	48,0	32 7	63,0	9,24	19.25
24	17	33,5	25,3	42,8	4,80	14,33
25	7	25,6	19,2	32,2	4,06	15,86
26	15	54,9	47,0	62,5	5,87	10.69
27	7	79,3	60,0	97,6	12,97	16,36
28	7	54,4	38,5	69,0	10,44	19,19
29	7	23,6	19,3	28,0	2,90	12,29
30	7	6,8	2 5	10,7	2,52	37,06
31	7	17,3	12,2	22,5	3,15	18,21
32	7	21,5	15,9	27,2	3,40	15,81
33	7	36,4	27	44,0	5,19	14,26
34	6	36,8	29,0	45,7	4,73	12,85

APPENDIX 3 Adult *Cuon alpinus javanicus*, skull measurements in millimetres. Legend: see Appendix 1.

Measures	n	x	min	max	s	v
1	25	159,8	140,0	182,0	9,42	5 89
2	24	151 1	134,0	171,0	8,87	5 87
3	24	8 7	5,0	1 5	1,42	16,32
4	24	72,6	63,6	82 3	4,30	5 92
5	27	79,2	70,5	89,0	4 9	5 29
6	27	25,3	19,0	28 2	2,02	7 98
7	27	80 1	71,0	9 2	4,68	5 84
8	27	49,6	44,3	57 0	2,91	5 87
8 6	27	24,3	20,0	32,5	2,49	10,25
9	27	31,8	27,2	37 0	2,20	6 92
10	27	23 1	21,5	27 0	1,35	5 84
11	27	35 7	32,2	40,0	1 76	4 93
12	27	35,3	33,0	38,0	1 52	4 31
13	27	59,0	53,8	66,0	3,00	5 08
14	26	24 2	20,1	27 0	1 76	7,27
15	26	16 2	14,0	18,9	0 96	5 93
16	25	11 2	9,5	13,2	0 94	8 39
17	26	61,8	55,6	67 0	3 07	4 97
18	26	32,9	30,3	39,0	1 93	5,87
19	26	28,9	24 1	33,0	2. 3	7,37
20	26	63,1	59,0	66 0	1 87	2 96
21	26	100,6	89,5	114,5	5,38	5 35
22	26	34,5	30,8	38 0	1 84	5,33
23	26	66,1	54,5	76 5	5,02	7,59
24	26	46,8	40,7	51 5	2 74	5,85
25	27	34,2	30 1	42,2	2 97	8,68
26	26	74,3	69 0	79 0	2 41	3,24
27	27	104,2	89 6	117 5	6 47	6,21
28	27	67 7	57 5	76 0	4.22	6.23
29	26	31 9	28,8	35,2	1 69	5,30
30	27	2,1	7 0	21,0	2 76	22 73
31	27	30,7	27 0	34,0	1 93	6,29
32	27	36,6	32,5	42,2	2 28	6 23
33	27	57 7	51 0	64,0	3 38	5 86
34	25	53,9	50,0	59,0	2 11	3,91

APPENDIX 4 Adult *Lycaon pictus*, skull measurements in millimetres. Legend: see Appendix 1.

Measures	n	x	min	max	s	v
1	5	185,9	175,0	200,0	9,26	4,98
2	5	176,1	165,0	191,0	9,65	5,48
3	5	9,8	9,0	10,0	0,45	4,59
4	5	83,3	78,0	89,3	4,38	5,26
5	5	93,6	88,0	101,6	5,08	5,43
6	5	30,7	27,5	34,0	2,61	8,50
7	5	92,4	86,0	99,5	4,99	5,40
8	5	56,7	51,0	62,0	4,30	7,58
8 6	5	26,0	23,5	29,6	2,85	10,96
9	5	36,3	34,0	40,5	2,47	6,80
0	5	30,3	26,0	32,2	2,56	8,45
1	5	45,5	41,0	48,0	2,80	6,15
2	5	45,5	39,0	47,8	3,72	8,18
3	5	72,4	64,0	76,4	4,85	6,70
4	5	27,4	24,0	30,2	2,26	8,25
5	5	18,9	16,0	20,3	1,77	9,37
6	5	13,2	12,0	14,4	0,88	6,67
7	5	72,6	67,0	76,8	3,66	5,03
8	5	39,2	35,0	42,0	2,65	6,76
9	5	33,4	32,0	35,1	1,42	4,25
20	5	69,9	65,0	73,5	3,25	4,65
21	5	126,4	115,0	133,0	7,19	5,69
22	5	39,6	37,7	41,3	1,40	3,54
23	5	86,7	77,3	93,1	6,31	7,28
24	5	54,0	50,0	59,0	3,32	6,15
25	5	39,7	36,0	46,0	4,03	10,15
26	5	80,0	77,0	84,0	3,06	3,83
27	5	124,7	110,0	137,0	10,20	8,18
28	5	81,5	75,0	91,5	5,38	7,83
29	5	38,0	29,0	42,0	5,23	13,76
30	5	16,6	9,0	22,0	4,93	29,70
31	5	37,2	32,0	41,0	3,31	8,90
32	5	41,5	36,8	45,0	3,29	7,93
33	5	65,2	60,0	68,5	3,70	5,67
34	5	60,8	59,0	62,3	1,29	2,12

APPENDIX 5 Adult *Canis lupus*, skull measurements in millimetres. Legend: see Appendix 1.

Measures	n	x	min	max	s	v
1	13	211,9	177,5	248,5	19,53	9,22
2	13	200,5	168,0	235,7	18,60	9,28
3	13	11,4	9,0	13,5	1,26	11 05
4	13	91 1	76,0	105,5	9,48	10,41
5	14	109,6	92,0	131 0	9,88	9,01
6	14	30,5	26,0	34,8	2,65	8,69
7	14	110,6	90,5	131 0	10,14	9 17
8	14	71,6	57,5	88,0	7,38	10,31
8 - 6	14	41 1	31,5	53,2	5,32	12 94
9	14	40,3	33,0	45 2	3,81	9,45
10	13	30,3	26,3	36 0	3,07	10,13
11	13	43,5	37,5	54,5	4,47	10,28
12	14	39,3	33,0	48 0	4,07	10,36
13	14	73,6	62,5	91 0	7,05	9 58
14	13	25,1	21,2	27 5	1,90	7 57
15	13	19.8	17.0	21 5	1.31	6.62
16	13	10,1	7 5	12 0	1,53	15,15
17	14	74,8	63,9	84 5	6,07	8 11
18	13	43,7	37,3	50,6	4 11	9,41
19	13	30,7	25,4	39 7	4,06	3,22
20	14	66,5	57 7	74,5	5,20	7,82
21	14	124,7	107,0	157,0	14,43	11,57
22	13	39,3	33 7	43,5	2,83	7,20
23	13	86,2	67,0	113,5	13,76	15 96
24	14	57,5	47 0	71,5	6,24	10,85
25	14	41,4	33,0	52,0	4,79	11,57
26	12	80,6	66,0	89,0	6,67	8,28
27	14	146,9	120,0	169,0	12,94	8,81
28	14	99,4	79,5	119,0	10 13	10 19
29	14	37,0	33,5	44,0	3,34	9,03
30	14	23,1	12,5	30,0	5,32	23,03
31	12	35,0	30,5	42 7	3,48	9,94
32	14	41,3	36,0	47,5	3,63	8,79
33	14	64,4	54,5	72,5	5,33	8,28
34	14	59,8	53,3	67,0	4,04	6,76

APPENDIX 6 Adult *Cynotherium sardous* from Corbeddu and Dragonara; adult *Cuon alpinus* from Monaco; juvenile *Canis aureus*, skull measurements in millimetres. Legend: see Appendix 1.

Measures	Cynotherium CB 84-2022	Cynotherium Dragonara 1	Cynotherium Dragonara 2	Cuon alpinus Monacao A	Jackal juv 1876-208	Jackal juv 1920-123
1	154,0	165,0	78,0	176,0	135,5	146,0
4	64,3	69,0	78,0	81,6	56,0	62,0
5	82,6	89,0	9 ,0	87,6	70,8	77,5
6	20,3	22,3	23,1	26,4	21,5	22,0
9	29,0	32,0	32,5	37,2	30,5	34,5
10	22,0	23,5	2 ,0	30,0	17,8	20,0
13	48,2	53,0	58,0	68,4	49,5	50 0
20	54,0	58,0	59,0	62,4	52,5	49 5
21	81,6	92,0	95,0	114,0	76,2	83,2
22	32,6	32,5	34,0	39,6	33,5	29,0
23	49,0	59,5	6 ,0	74,4	42,7	54,2
33	43,3				45,5	45,0