Edited by / Sous la direction de

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Klimonas

An Early Pre-Pottery Neolithic Village in Cyprus
Un village néolithique pré-céramique ancien à Chypre

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Chap. 30

The extinct small Cypriot wild boar *(Sus scrofa circeus)*: osteological description, origins, and insular evolution

Jean-Denis Vigne, Thomas Cucchi, Auriale Domont, Hugo Harbers

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Abstract. *Thanks to a comprehensive morphometric study based on (i) the classical and multivariate analyses of 2640 new linear measurements, including log shape analyses for the humerus, talus and phalanges, and (ii) 2D and 3D geometric morphometrics on the lower cheek teeth and calcaneus, we reached three main conclusions regarding the origin and evolution of the wild boar of Klimonas.*

The Klimonas wild boar is the outcome of the insular evolution of the wild boar introduced to Cyprus during the 11th millennium and first described at Akrotiri-Aetokremnos. It displays at least three clear insularity syndromes: i) a 13% size reduction compared to the Near Eastern continental wild boar, ii) a significant reduction of the dewclaws which restricted its locomotive capability and iii) a molar form (size and shape) similar to that of the insular Corsico-Sardinian subspecies. We therefore propose that this small insular Cypriot wild boar should be considered as a new subspecies, Sus scrofa circeus.

Despite its moderate insular evolution, some of the morphological characteristics of this Cypriot wild boar suggest that they were introduced from Late Glacial wild boar populations of the north Levant plains and foothills, rather than from the south Levant and the southeast high plateaus.

The domestic pigs which were reared as early as the very end of the 9th millennium at Shillourokambos, which evolved towards a domestic form ca. 7500 BC and were also present during the 7th millennium at Khirokitia, were locally domesticated from the small endemic Cypriot wild boar. We could not detect any input of either wild or domestic suids from the continent. Both free ranging hunted and captive suids were consumed at Shillourokambos during the second half of the 8th millennium.

*Le petit sanglier chypriote éteint (*Sus scrofa *circeus, nov. ssp.) : description ostéologique, origines et évolution insulaire*

Résumé. *À travers l'analyse d'un large corpus de données ostéométriques, ce chapitre s'attache à trois questions : la caractérisation morphologique du petit sanglier de Klimonas et son degré d'endémisme insulaire, l'origine de cette lignée de suidés introduite sur l'île au 11e millénaire BC, et son rôle dans la naissance de l'élevage du porc observée précédemment à Shillourokambos dans le courant du 8e millénaire cal BC.*

En l'absence d'ADN préservé dans les vestiges de Klimonas et de Shillourokambos, trois approches méthodologiques sont développées conjointement et de façon complémentaire : l'analyse traditionnelle des mensurations linéaires issues de 918 restes de suinés de Klimonas totalisant 2814 mensurations, le traitement multivarié des séries les mieux documentées (humérus, talus, phalanges), notamment par la technique des Rapports de conformation logarithmiques (Log Shape Ratio, LSR) *et des tailles isométriques, et la morphométrie géométrique, en 2D pour les surfaces occlusale de 59 molaires inférieures et en 3D pour deux calcanéus de Klimonas et 9 calcanéus de Shillourokambos. Les sangliers de Klimonas présentent quatre caractéristiques majeures résultant d'une évolution insulaire de plus de 2 000 ans : i) une petite taille, de 13 % inférieure à la moyenne du Levant nord, qui s'inscrit dans le premier syndrome d'insularité des grands mammifères ; ii) une réduction allométrique des os des extrémités des membres, notamment les phalanges et plus particulièrement celles des doigts abaxiaux (2e et 5e doigts), témoignant d'une réduction des capacités locomotrices, surtout sur sols mous, en liaison avec l'absence de prédateur naturel sur l'île ; iii) une morphologie dentaire convergente avec celle de la sous-espèce corso-sarde* S. s. meridionalis, *témoignant d'une dérive génétique insulaire ; iv) quelques traits propres à la population chypriote, notamment des extrémités distales d'humérus plus trapues et des astragales plus élancés, ainsi qu'un dimorphisme sexuel sensiblement plus élevé que sur le continent. Ces traits témoignent d'un endémisme relativement marqué, justifiant l'appartenance de la population de Klimonas à une nouvelle sous-espèce de sanglier propre à Chypre,* Sus scrofa circeus. *Les sangliers du 11e millénaire (Akrotiri) sont déjà engagés sur cette voie évolutive, mais moins que ceux de Klimonas. La densification des populations humaines à la fin du 9e et au 8e millénaire modifie cette trajectoire en provoquant une légère augmentation de taille due à l'accroissement de la pression de prédation.*

La comparaison avec les données de nombreux sites du PPN du Sud-est anatolien, du Levant nord, de Damascène, de la côte libanaise et de la vallée du Jourdain (un seul site, cependant) suggère d'importantes similarités dans les conformations de l'humérus, du talus et des phalanges, et dans les formes (taille et conformation) des molaires inférieures avec le Levant nord, de la vallée du Tigre à celle de l'Euphrate et à la côte libanaise. Une origine à partir du Levant sud ou des hauts plateaux du Sud-est anatolien semble devoir être exclue, mais ce point reste à préciser à l'aide d'un corpus de référence plus large.

Les données surfaciques recueillies sur le calcanéus confirment que les sangliers de Klimonas étaient chassés, fait largement étayé par ailleurs (cf. chap. 29). Elles montrent aussi que, durant la seconde moitié du 8^e^ millénaire, les habitants de Shillourokambos continuaient à chasser des individus courant libres, tout en élevant d'autres individus en captivité. Les analyses de conformation de l'humérus, de l'astragale et des phalanges, tout comme les formes des molaires inférieures ne font apparaître aucune différence entre Klimonas et les différentes périodes d'occupation de Shillourokambos, si l'on excepte l'apparition d'un morphotype domestique aux alentours de 7500 cal BC, entièrement lié à la réduction de taille provoquée par la domestication. Aucune introduction de lignées exogènes n'a pu être détectée. Il apparaît donc que les villageois chypriotes du PPNB moyen ont initié l'élevage du porc à partir de la lignée locale de petit sanglier chypriote, S. s.circeus*, sans recours à des importations, tout comme ils l'ont fait un peu plus tard avec la chèvre marronne. Il apparaît que les espèces qui jouaient un rôle économique et symbolique important dans la vie des villageois PPNB ont été domestiquées localement, alors que les espèces absentes du bestiaire chypriote PPNB ont été introduites sous forme domestique à partir du continent.*

INTRODUCTION

A revision of the archaeozoological and chronological data from the Aetokremnos shelter (Akrotiri Peninsula, Simmons 1999) highlighted that shortly after the extinction of pigmy elephants and hippos, Epipalaeolithic people introduced wild boar *(Sus scrofa)* to Cyprus, between 10,500 and 9500 cal BC (Vigne *et al*. 2009, 2019b; Zazzo *et al*. 2015). The small size range of the 18 suid bones from Aetokremnos, similar to those of Klimonas (Vigne *et al*. 2012), suggested that at least the extremities of these wild boar were significantly reduced compared to the southwest Asian PPN wild boars, as a likely consequence of insularity. The overwhelming occurrence of this wild boar in the early 9th millennium PPNA faunal assemblages of Asprokremnos and Klimonas, as well as in the early PPNB phases of Shillourokambos (ca. 8500/7600 cal BC), suggests that this Cypriot suid population rapidly proliferated. Indeed, it was the only large ungulate species on the island from the Epipalaeolithic to the early PPNB, until the introduction of domestic goats and cattle ca. 8500 cal BC (Vigne *et al*. 2011c), i.e. during ca. two millennia.

This situation is highly remarkable. First, this overseas introduction of a large mammal is the earliest known in the Mediterranean Basin, possibly the world. Second, it predates by 2500 years the earliest evidence of ungulate domestication in southwest Asia and testifies that hunter-gatherers were manipulating or even managing wild ungulates before the beginning of the Holocene, probably even before the start of the Neolithic (Vigne *et al*. 2009, Vigne 2015). Third, there are no wild boars in Cyprus today, and neither are there any mentions of wild boars in Cyprus in the historical records (Hadjisterkotis 2000). Fourth, if one can consider it a now extinct new Mediterranean endemic insular taxon, it would be the only suid for the whole Quaternary after the Sardinian Middle-Late Pliocene *Sus sondaari* (Van der Made 1988, 1999).

The huge osteological documentation provided by the Klimonas excavations (4823 identified specimens) allows the documentation of this remarkable situation following three main questions:

– To what extent can we consider this suid as a new insular taxon; more precisely, in addition to the small size of the limb extremities, are there any other morphological manifestations of insularity syndrome, such as general size decrease, phenotypic idiosyncrasy or allometries between limbs and body.

– Despite these morphological changes, is there still a possibility to detect morphological traits enabling a discussion about the geographical origins of the first animals introduced during the Late Glacial?

– Starting from the middle PPNB of Shillourokambos (ca. 8000 cal BC), was this early population interbred with or entirely replaced by domestic suids introduced from the continent, as suggested earlier (Vigne *et al*. 2011c); or was it locally domesticated in Cyprus (as goats; Vigne *et al*. 2017d,e) and therefore consequently at the origin of all or part of the Neolithic Cypriot suids? Recent analyses of a large additional sample of bones from Shillourokambos shed new light on this question, making the local domestication hypothesis more probable (Vigne 2021b); however, it was not possible to fully answer this question due to the limited information at our disposal concerning the skeletal morphology of the small Cypriot suid represented at Klimonas.

This chapter aims to address these three questions by applying traditional, multivariate, and geometric morphometric (GMM) approaches to the now substantial Klimonas sample[1].

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[1] Despite many attempts, we never succeeded in extracting DNA from the Klimonas or Shillourokambos suid bones, aside from one poorly informative exception (G. Larson, pers. comm.).

1. MORPHOMETRIC APPROACHES BASED ON LINEAR MEASUREMENTS

1.1. MATERIAL AND METHODS

The measurements were recorded using a calliper with a precision of 1/10 mm, according to the standards of A. von den Driesch (1986), to which we added some measurements described in Vigne (2011c).

We scrutinized all the outlier dimensions to eliminate the possible (but very scarce) recording mistakes or pathologic anomalies. We controlled the measurements in terms of stratigraphic reliability and identified those which were likely to come from Neolithic (Sotira) pottery or historical deposits. These are presented separately from the PPNA measurements in the 13 appendices listed at the end of this chapter, together with the main statistic description of each dataset and some comparisons with Shillourokambos. Table 30-1 gives the number of measurements displayed in these appendices. The canine measurements are presented and processed separately in chap. 29 (appendix 29-2). In total, we took 2814 measurements from 918 specimens.

We only considered the PPNA specimens for statistical analyses, i.e. 2640 measurements from 863 specimens. Descriptive and comparative statistics, as well as mixture and factorial analyses, were processed with Past (ver. 4.04; Hammer *et al*. 2001). We based comparisons on both median (Kruskal-Wallis H test) and variances (ANOVA, Welch). Except where mentioned, Mann-Whitney pairwise comparisons were systematically used with Bonferroni correction (Rice 1988). Mostly, we used the Monte Carlo estimate of probability (permutation with 999 bootstraps). We had enough variables (4 to 5) to study the size and shape for the distal humeri, the talii and the phalanges separately: the isometric size was estimated by the logarithm means of all the measurements, according to Mosiman (1970), and the shape was quantified through the extraction residues of the isometric size for each osteometric variable (see Vigne 2015, 2021b). Differences in isometric size between the two samples, named x and y, were estimated by the formula:

Isometric size difference = [((10^LOG(x)) - (10^LOG(y)) / (((10^LOG(x)) + (10^LOG(y))/2)] 100.

Where x and y are the log means of the two samples.

As we did not find any essential differences in the cheek teeth measurements between the early and the late phases of the Shillourokambos occupation (8500–7000 cal BC; Vigne 2011, 2021), we grouped all of them for comparison with Klimonas. For Cyprus, comparisons were also processed with Akrotiri-Aetokremnos (ca. 10,000 cal BC; Vigne *et al*. 2009) and Khirokitia (6700–6000 cal BC; data from Davis 1984, 1994, and pers. comm.).

For the continental PPN sites we used the data from (fig. 30-1):

- Nemrik (Anatolia, 9500–8500 cal BC; measured by D. Helmer, pers. comm),
- Cafer Höyük (Anatolia, 8300–7500 cal BC; Helmer 2008 and pers. comm.),

	Specimens			Measurements		
	PPNA	Sotira /Hist.	Total	PPNA	Sotira /Hist.	Total
Skull	10	2	12	19	4	23
Upper cheek teeth	141	9	150	335	23	358
Upper canines	21	1	22	48	4	52
Lower cheek teeth	183	5	188	640	20	660
Lower canines	15		15	30		30
Vertebrae	12		12	57		57
Scapula	17	1	18	42	3	45
Humerus	29	5	34	82	20	102
Radius	34	1	35	48	1	49
Ulna	37		37	82		82
Carpal	15	1	16	49	4	53
Metacarpal	48	2	50	115	11	126
Pelvis	5	4	9	9	5	14
Femur	4	2	6	4	2	6
Patella	3		3	6		6
Tibia	30		30	85		85
Talus	27	2	29	110	10	120
Calcaneus	16	1	17	23	1	24
Other tarsal	10	2	12	11	2	13
Metatarsal	16	1	17	37	1	38
Phalanges 1 axial	49	8	57	200	25	225
Phalanges 1 abaxial	31	0	31	142	0	142
Phalanges 2 axial	39	4	43	182	20	202
Phalanges 2 abaxial	16	3	19	80	14	94
Phalanges 3 axial	29		29	101		101
Phalanges 3 abaxial	26	1	27	103	4	107
Total	**863**	**55**	**918**	**2640**	**174**	**2814**

Tab. 30-1 – *Number of* Sus scrofa *specimens and measurements collected at Klimonas.* • *Nombre de spécimens et de mensurations de* Sus scrofa *enregistrées à Klimonas.*

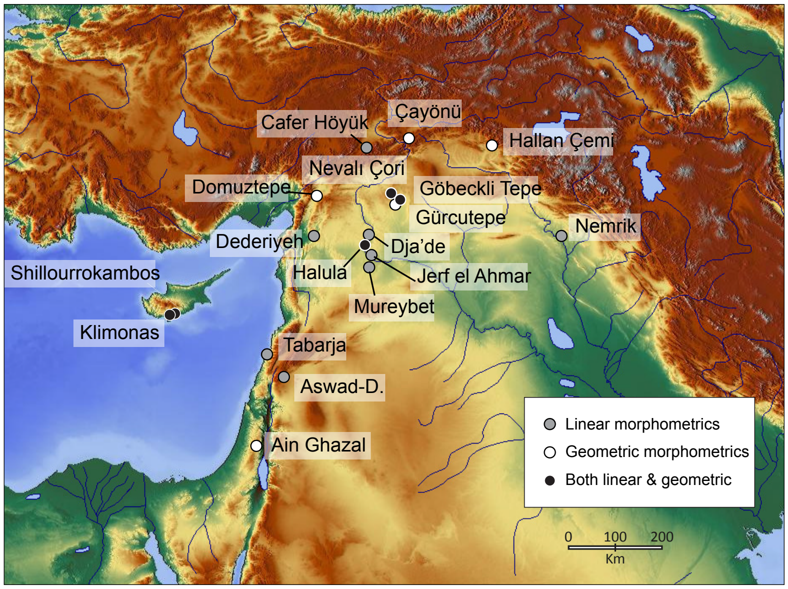


Fig. 30-1 – *Location of the PPN sites used in the morphometric comparisons of the Kilmonas suids. CAD T. Cucchi, CNRS, J.-D. Vigne, CNRS.* • *Localisation des sites pré-céramiques utilisés pour les comparaisons morphométriques des suinés de Klimonas. DAO T. Cucchi, CNRS, J.-D. Vigne, CNRS.*

- Göbekli and Nevalı Çori (Anatolia; J. Peters, pers. comm.),
- Dederiyeh (North Syria; Gourichon, pers. comm.),
- Dja'de and Jerf El Ahmar (Euphrates Valley, Syria; 9500–8500 cal BC; Gourichon, pers. comm.),
- Mureybet 1-3 (Euphrates Valley, Syria; 9000–8500 cal BC; Gourichon and Helmer 2008),
- Halula (Euphrates Valley, Syria; 7800–7000 cal BC; Saña-Segui 1999),
- Aswad-Damascus (Syria; Helmer and Gourichon 2008),
- Tabarja (Lebanon coast; 7800–7000 cal BC; Yazbeck 2020; measured by the author, courtesy of Jwana Chahoud and Corine Yazbeck).

1.2. CHEEK TEETH

1.2.1. Description and variability of the upper molars

The study concerned 180 PPNA molars or Dp4/ and their 335 measurements (appendix 30-2). The second molars were the most numerous (57); the third ones were the least numerous (35). The measurements were limited to length and width.

The frequency distribution of the upper cheek teeth measurements (fig. 30-2, A) did not differ from the normal distribution, except for the Dp4/ length (Shapiro-Wilk, p = .003). The coefficient of variation, comprised between 4.3 and 7.3, confirmed a good homogeneity for each of the eight measurements. However, nearly all of them showed a slightly bimodal kernel distribution (fig. 30-2, B), already mentioned for the Shillourokambos suids (Vigne 2011c). Mixture analyses indicated that for the M3/ and Dp4/lengths and the M1/width, the bimodal model fits better the kernel distribution than the unimodal one (Akaike information criterion; fig. 30-3) with differences of 11, 8 and 7% between the two groups.

None of the specimens that provided either of these two measurements was associated with a canine, which would have given information on sex, so it is impossible to verify whether these slight tendencies are the result of sexual dimorphism. If this interpretation could be verified, the sexual dimorphism may be estimated between zero (non-significant mixture analysis) and 10% for the M3/length. Although a bit higher, this value range would be compatible with those observed by Payne and Bull (1988) and Albarella *et al.* (2009) for sexual dimorphism using the cheek teeth of modern wild boars, including those from southwest Asia (0 to 4%).

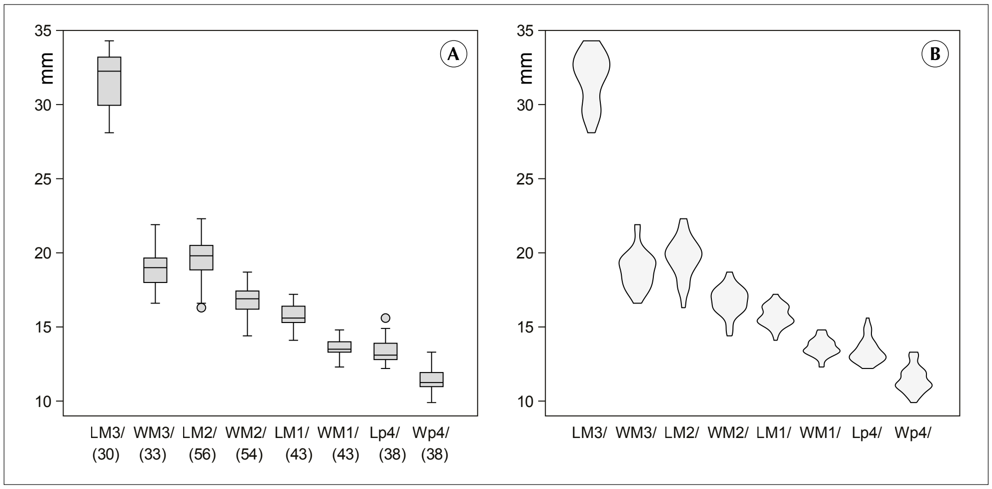


Fig. 30-2 – *Frequency distribution of the PPNA upper teeth measurements of Klimonas suids: A, boxplots with outliers; B, kernel densities ("violin") plots. CAD J.-D. Vigne, CNRS.* • *Distribution de fréquence des mensurations des dents supérieures PPNA de suidés de Klimonas; A, diagrammes en boîte et valeurs aberrantes; B, diagramme des densités de kernel (« en violon »). DAO J.-D. Vigne, CNRS.*

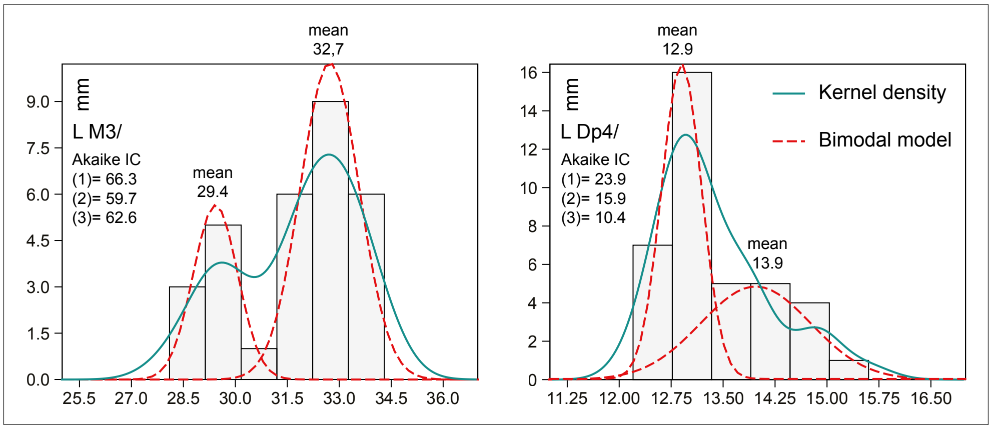
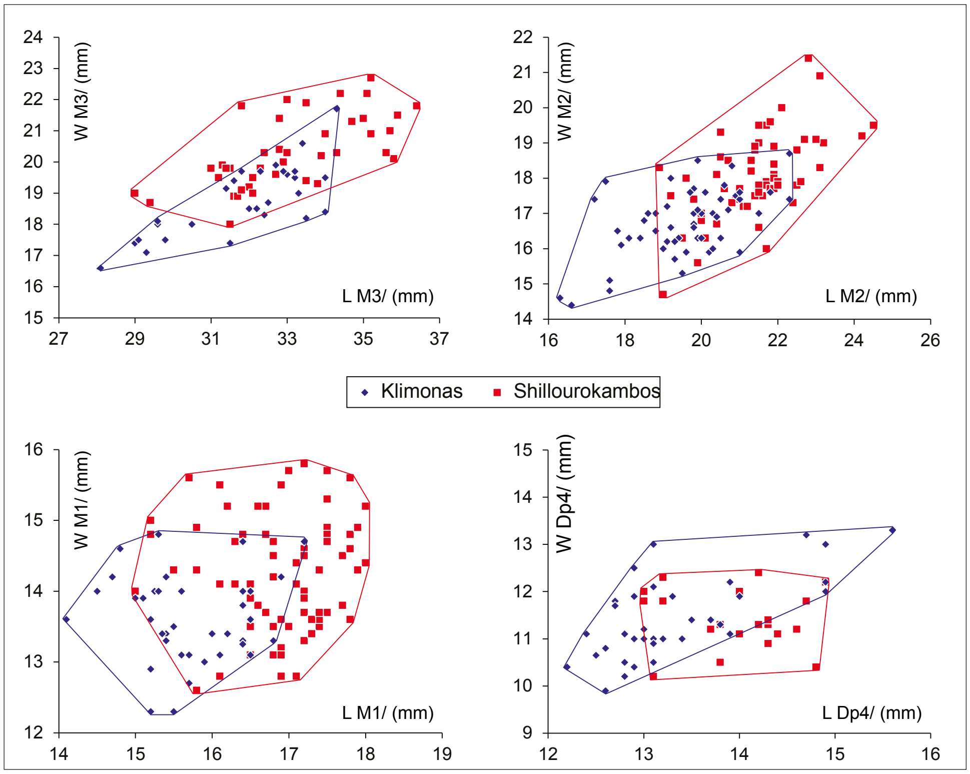
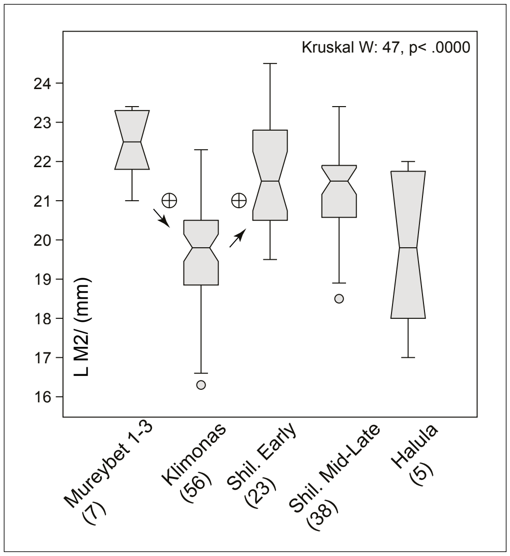


Fig. 30-3 – *Histogram (grey) and kernel distribution (green) of the M3/ and Dp4/ lengths and representation of the two putative groups modelled by mixture analyses (red) – Akaike criterion are given for 1 group (1), two groups (2) and three groups (3). CAD J.-D. Vigne, CNRS.* • *Histogramme (gris) et distribution de kernel (vert) des longueurs de M3/ et Dp4/, et représentation des deux groupes putatifs modélisés par les analyses de mélange (rouge). Les critères d'information d'Akaike sont donnés pour un groupe (1), deux groupes (2) et trois groupes (3). DAO J.-D. Vigne, CNRS.*



◂ Fig. 30-4 – *Biplot comparisons (length x width) of the upper cheek teeth from Klimonas and Shillourokambos. CAD J.-D. Vigne, CNRS.* • *Comparaisons bivariée (longueur x largeur) des dents jugales supérieures de Klimonas et de Shillourokambos. DAO J.-D. Vigne, CNRS.*

▾ Fig. 30-5 – *Notched boxplots of the second upper molar width from the Epipalaeolithic and PPN sites of Cyprus (Klimonas and Shillourokambos) and the Euphrates Valley (Mureybet and Halula). The plus sign (+) indicates highly significant differences (Mann-Whitney). CAD J.-D. Vigne, CNRS.* • *Diagrammes à encoches de la largeur de la deuxième molaire supérieure provenant des sites épipaléolithiques et PPN de Chypre (Klimonas et Shillourokambos) et de la vallée de l'Euphrate (Mureybet et Halula). Le signe « plus » indique des différences très significatives (Mann-Whitney). DAO J.-D. Vigne, CNRS.*



1.2.2. Upper molar comparisons with Shillourokambos and the near continent

Figure 30-4 shows that the upper cheek teeth measurements from Klimonas are systematically smaller than those from Shillourokambos, except for the fourth lacteal premolar. These differences are statistically highly significant (tab. 30-2). The difference between the means of the two sites fluctuates between 4 and 8.5%.

For all the available measurement series, especially L M2/ (fig. 30-5), the upper molars from Klimonas are significantly smaller than those from the Epipalaeolithic and early PPNA at Mureybet 1-3. The difference is estimated at 13% for the M2/ length. The measurements from Shillourokambos, either the early or late phase, are also smaller than those from Mureybet, but the difference is not significant, probably due to the small size of the Mureybet sample. The mean size of the Klimonas wild boars is approximately the same as that of the late PPNB domestic pigs from Halula.

Tab. 30-2 – *Descriptive statistics and parametric statistical comparisons between the upper cheek teeth measurements from Klimonas and Shillourokambos (all phases grouped together). Grey cells indicate significant differences.* • *Statistiques descriptives et comparaisons statistiques paramétriques entre les mesures des dents jugales supérieure de Klimonas et de Shillourokambos (toutes phases confondues). Les cellules grises indiquent les différences significatives.*

		M3/		M2/		M1/		Dp4/	
		L	W	L	W	L	W	L	W
Klimonas	N	30	33	56	54	43	43	38	38
	Mean	31,8	18,9	19,7	16,8	15,7	13,6	13,4	11,5
	Variance	2,99	1,48	1,83	0,88	0,47	0,35	0,63	0,71
Shillouro-kambos	N	40	44	61	60	70	71	21	21
	Mean	33,1	20,3	21,4	18,0	16,9	14,3	14,0	11,5
	Variance	3,22	1,33	1,55	1,40	0,51	0,66	0,37	0,43
Comparison	p Fisher	0,85	0,72	0,53	0,09	0,78	0,03	0,21	0,24
	p Student	0,0028	0,0000	0,0000	0,0000	0,0000	0,0000	0,0026	0,96
	p Mt Carlo	0,0038	0,0001	0,0001	0,0001	0,0001	0,0001	0,0027	0,0000
	p Man-W (Mt. C)	0,0157	0,0001	0,0001	0,0001	0,0001	0,0001	0,0009	0,6211
Morphological distance (%)		4,09	7,22	8,49	7,42	7,12	4,69	4,61	0,10

1.2.3. Description and variability of the lower molars

The study concerns 229 PPNA molars or Dp/4 and their 640 measurements (appendix 30-3). The first molars are the most numerous (69) and the Dp/4 the least (45). The measurements concern the total length and the width of each lobe.

The frequency distribution of the lower cheek teeth measurements did not differ from the normal distribution, except for the M/1 length (Shapiro-Wilk, p = .02) and the width of the Dp/4 first lobe (p = .015). The coefficient of variation, comprised between 3.8 and 6.2, confirms a good homogeneity for each of the 14 measurements. However, as with the upper molars, nearly all of them show a slight bimodal kernel distribution (fig. 30-6). The Akaike information criteria from the mixture analyses suggest that four measurements may fit better with a bimodal distribution than with the normal one: W2 of M/3, W2 of M/2, length of M/1 and W3 of P/4, three of them concerning the zone around the first molar. The differences between the two groups are 7, 10, 7 and 9%.

Using the group means modelled by mixture analyses, the dimorphism on the lower cheek teeth can be estimated between 0 and 10% (maximum for W2 of M/2). This range of values is

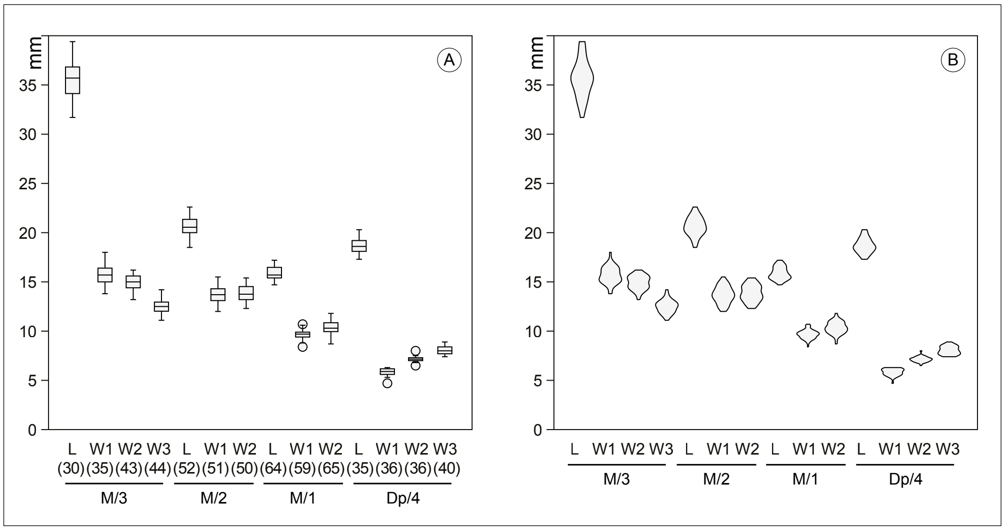


Fig. 30-6 – *Distribution of the PPNA lower suid teeth measurements from Klimonas: A, boxplots with outliers; B, kernel densities ("violin") plots. CAD J.-D. Vigne, CNRS.* • *Distribution des mensurations des dents inférieures PPNA des suidés de Klimonas : a, diagrammes en boite et valeurs aberrantes ; b, diagrammes de densités de kernel (« en violon »). DAO J.-D. Vigne, CNRS.*

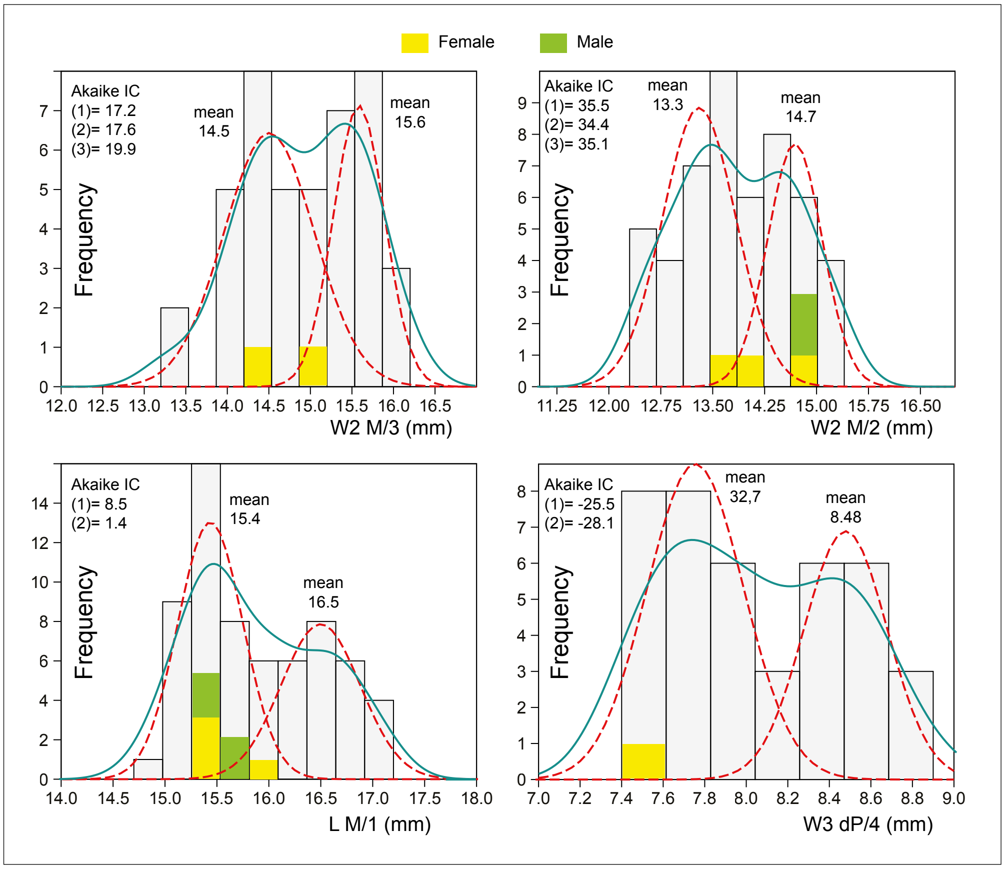


Fig. 30-7 – *Histogram and kernel distributions of the four lower cheek teeth measurements with putative bimodal distribution and representation of the two groups modelled by mixture analyses. Akaike criterion are given for one group (1), two groups (2) and, where possible, three groups (3). CAD J.-D. Vigne, CNRS.* • *Histogramme de distribution et densité de kernel de quatre mesures de dents jugales inférieure présentant une probable distribution bimodale, et représentation des deux groupes modélisés par les analyses de mélange. Les critères d'information d'Akaike sont donnés pour un groupe (1), deux groupes (2) et, lorsque cela était possible, trois groupes (3). DAO J.-D. Vigne, CNRS.*

the same for the upper teeth, compatible with a relatively high sexual dimorphism for the species. Unfortunately, most of the 16 cheek teeth measurements, associated with a canine and therefore attributable to a male or a female, plot in the extensive overlap zone of the two model profiles (fig. 30-7). Consequently, it was impossible to confirm the hypothesis that this dimorphism is due to sex, even though this explanation is still the most likely.

1.2.4. Comparisons of the lower molars with those from Shillourokambos and the near continent

Figure 30-8 shows that the Klimonas lower cheek teeth measurements are smaller than those of Shillourokambos, except for the third molar. The difference appears to be less than for the upper molars but, here again, they are statistically significant for M/2, M/1 and Dp/4 (tab. 30-3) and fluctuate within the same range of values (4.7 to 7.2%).

For all the measurements (fig. 30-9), the lower molars from Klimonas are significantly smaller than those of the Euphrates Valley wild boar (Epipalaeolithic and PPNA of Mureybet) and the Lebanese coast (PPNB Tabarja; only M/3). The mean differences of the latter are 8.3% for the M/3 length and 13.6 for the width. The first and second molars from Klimonas are also on average 13% smaller than those from Mureybet. Fig. 30-9 also shows that, here again, the length of the first and second lower molars from Shillourokambos are significantly larger than those from Klimonas yet remain substantially smaller than their wild counterparts on the continent. This confirms that, in Cyprus, there is no clear tendency of significant size variations between the 8^th^ and the 7^th^ millennia, represented by Shillourokambos and Khirokitia, aside from a slight increase in the M/1 size (Vigne 2011c, 2021b).

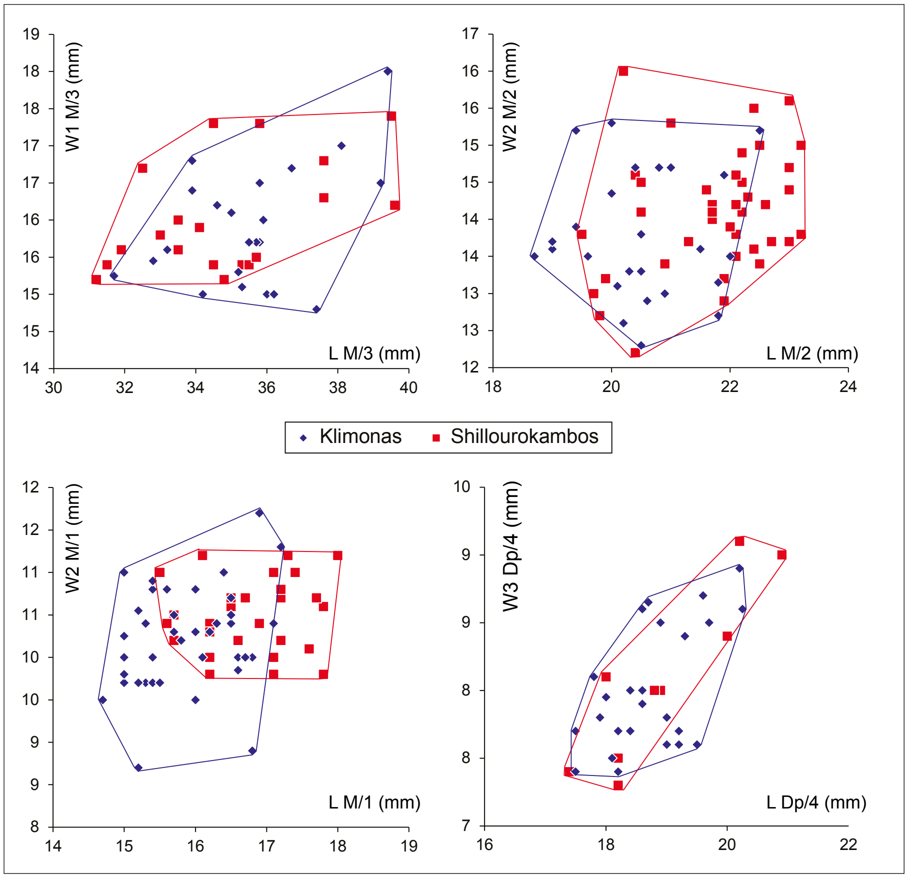


Fig. 30-8 – *Biplot comparisons (length x width) of the lower cheek teeth from Klimonas and Shillourokambos. CAD J.-D. Vigne, CNRS.*
• *Comparaisons bivariée (longueur x largeur) des dents jugales inférieures de Klimonas et de Shillourokambos. DAO J.-D. Vigne, CNRS.*

		M/3		M/2		M/1		Dp/4	
		L	W	L	W	L	W	L	W
Klimonas	N	30	35	52	36	50	37	35	40
	Mean	35,7	15,7	20,635	13,453	15,6	9,9216	18,68	8,0475
	Variance	3,66	0,77	0,90	0,37	0,20	0,15	0,59	0,18
Shillouro-kambos	N	20	21	39	39	28	29	9	9
	Mean	35,0	16,1	21,728	14,095	16,8	10,648	20,067	9,2
	Variance	6,14	0,52	1,12	0,66	0,52	0,58	10,59	13,82
Comparison	p Fisher	0,2	0,4	0,4650	0,0824	0,0000	0,0000	0,0000	0,0000
	p Student	0,3	0,1	0,0000	0,0000	0,0000	0,0000	0,2390	0,37998
	p Mt Carlo	0,3	0,1	0,0001	0,0003	0,0000	0,0001	0,0266	0,1268
	p Mann-W (Mt. C)	0,2	0,0841	0,0000	0,0004	0,0001	0,0000	0,249	0,9467
Morphological distance (%)				5,16	4,66	7,17	7,06		

Tab. 30-3 – *Descriptive statistics and comparisons between the lower cheek teeth measurements from Klimonas and Shillourokambos (all phases grouped together). Grey cells indicate the significant differences.*
• *Statistiques descriptives et comparaisons entre les mesures des dents jugales inférieures de Klimonas et de Shillourokambos (toutes phases confondues). Les cellules grisées indiquent les différences significatives.*

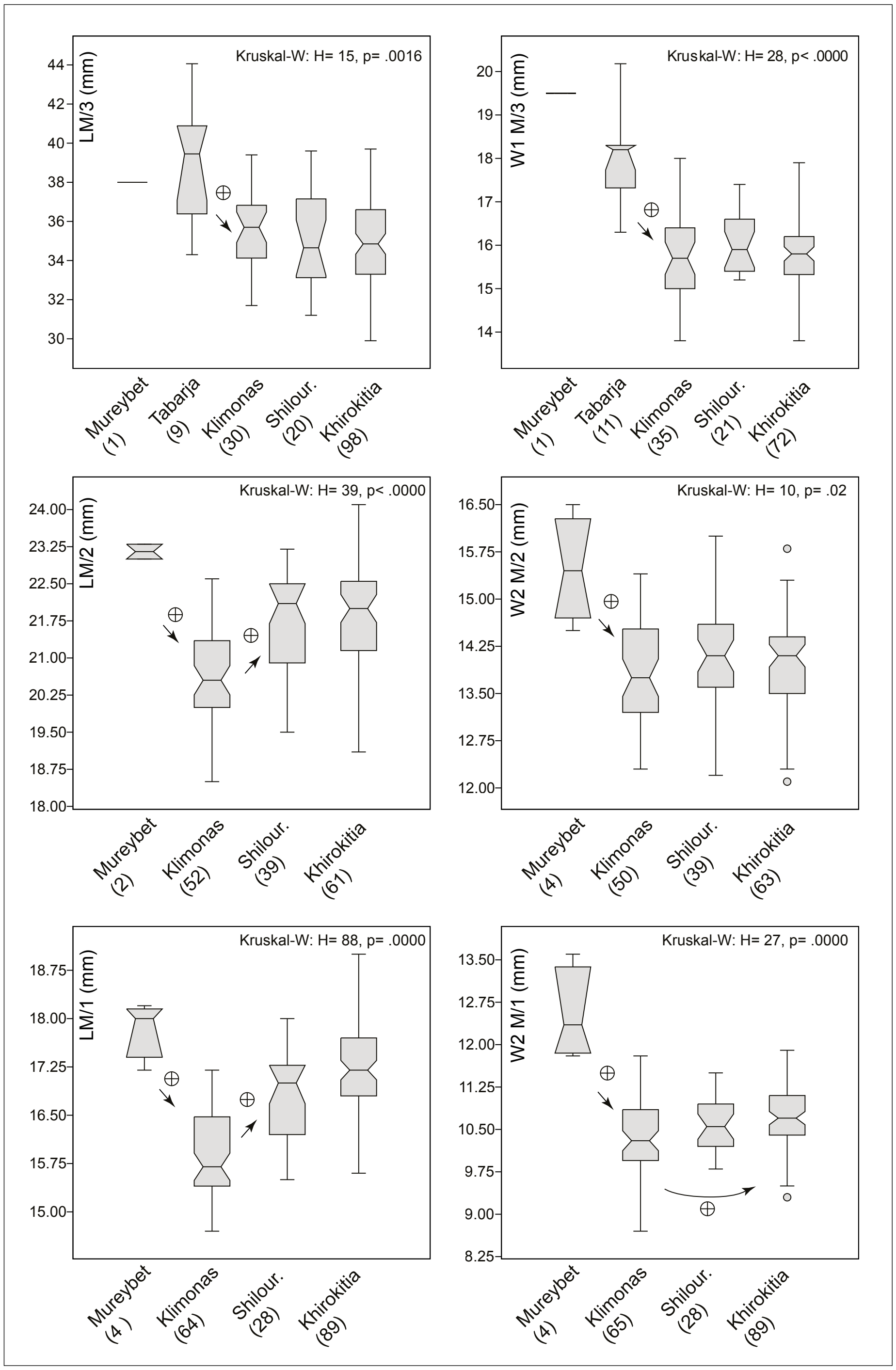


Fig. 30-9 – *Notched boxplots of the lower molar measurements from Klimonas compared with the early Holocene wild boars of the Euphrates Valley (Mureybet) and the Lebanon coast (Tabarja), with the Shillourambos PPNB and the Khirokitia aceramic Neolithic, for Cyprus. The plus sign (+) indicates highly significant differences (Mann-Whitney). CAD J.-D. Vigne, CNRS.*
• Boîtes à encoches des dimensions des molaires inférieures de Klimonas comparées à celles des sangliers de l'Holocène ancien de la vallée de l'Euphrate (Mureybet) et de la côte du Liban (Tabarja), au PPNB de Shillourombos et au Néolithique acéramique de Khirokitia, pour Chypre. Le signe «plus» indique des différences hautement significatives (Mann-Whitney). DAO J.-D. Vigne, CNRS.

1.2.5. Conclusion concerning the cheek teeth

Based on 975 length and width measurements of 409 upper and lower molars, the lacteal and final cheek teeth from Klimonas appear to be about 13% smaller than those of the north Levantine continental wild boar. Some of the measurements also show a tendency to bimodal distribution, which likely reflects a slightly higher (0 to 10%) sexual dimorphism than those of modern and early Holocene wild boars (0–4% according to Payne and Bull 1988). We also evidenced a 4 to 8% slight, but sometimes significant, increase of size between Klimonas and Shillourokambos.

Most of the differences between Klimonas and Shillourokambos are slightly more visible on the second and first molars than on the third, suggesting that they are connected to an allometric increase in the size of the rostrum regarding the rear part of the jaws. Unfortunately, because of the high level of bone fragmentation of the head, the measurements of the maxillae, mandibles and neuro-skulls are too scarce for any solid comparisons (appendix 30-1).

1.3. PROXIMAL ANTERIOR LIMB SKELETON

1.3.1. General overview

The measurements of the different anterior limb bones from Klimonas display a normal distribution (appendices 30-4, 30-5 and 30-6). However, some of them show a tendency to bimodal distribution (GLP scapula, KTO and LO ulna), which probably reflects a slight sexual dimorphism. When sufficiently numerous, they systematically appear slightly smaller than those of the early Holocene boar of the near continent. Still, the difference is never statistically significant because the sample size is usually too small. The comparison with the measurements of the early and middle-late phases of Shillourokambos suggests a slight tendency to size decrease (BG scapula, Bp radius). Only the distal part of the humerus brings more reliable and refined information.

1.3.2. Humerus

Appendix 30-4 provides 82 measurements collected from 29 PPNA specimens.

1.3.2.1. Sexual dimorphism

For the four dimensions of distal articulation (Bd, BT, H, HTC), the coefficient of variation is low (4 to 5.3%), and the values' distribution never differs from the normal model. However, for the height of the trochlea (H), the bimodal model fits better the kernel distribution than the unimodal one (fig. 30-10), with an 8.4% difference between the means of the two groups. This can be considered as an estimate of sexual dimorphism.

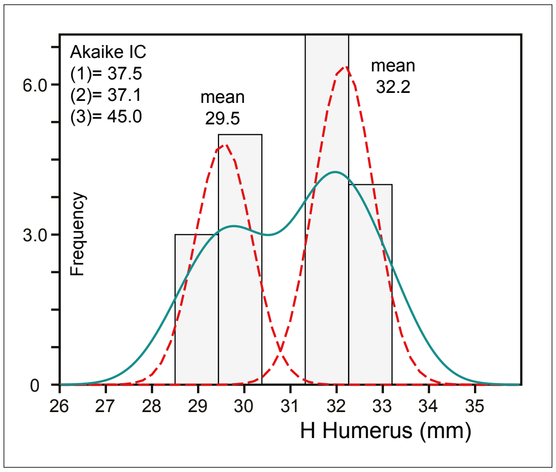


Fig. 30-10 – *Histogram and kernel distributions of the distal humeral trochlea height with putative bimodal form and representation of the two groups designed by mixture analyses. Akaike information criterion are given for one (1), two (2) and three groups (3). CAD J.-D. Vigne, CNRS.* • *Histogramme de distributions et densités de kernel de la hauteur de la trochlée distale de l'humérus présentant une forme bimodale et représentation des deux groupes modélisés par les analyses de mélange. Les critères d'information d'Akaike sont donnés pour un (1), deux (2) et trois groupes (3). DAO J.-D. Vigne, CNRS.*

1.3.2.2. Global size comparisons

Even though the difference is not statistically significant, because of the small size of the dataset for the continent, the humeral distal articulation measurements from Klimonas are noticeably smaller than those of the north Levant wild boar (fig. 30-11). The difference is more significant for the diameter of the trochlea for the ulna (HTC, ca. 10%) than for the width of the distal extremity (BT, ca. 4%).

As with the larger Klimonas sample (Vigne 2021b), we can confirm a complex evolution of size in Cyprus composed of four steps: stability along the 9th millennium (Klimonas and early phase A of Shillourokambos), significant decrease along the first half of the 8th millennium (early B to the middle A2 phases of Shillourokambos), slight recovery at the end of the same millennium (middle B and recent phases), then another decrease between the 8th and 7th millennia (Khirokitia).

1.3.2.3. Log shape ratio comparisons with the continent

Unfortunately, a complete set of the four distal articulation measurements of the humerus (Bd, BT, HTC, H) was scarce for the early Holocene Levantine wild boars (only one for Mureybet and three for Tabarja), which is why the smaller isometric size of Klimonas appears only slightly significant (t-test, p = 0.07; fig. 30-12, A). The difference in isometric size is only 4.8%.

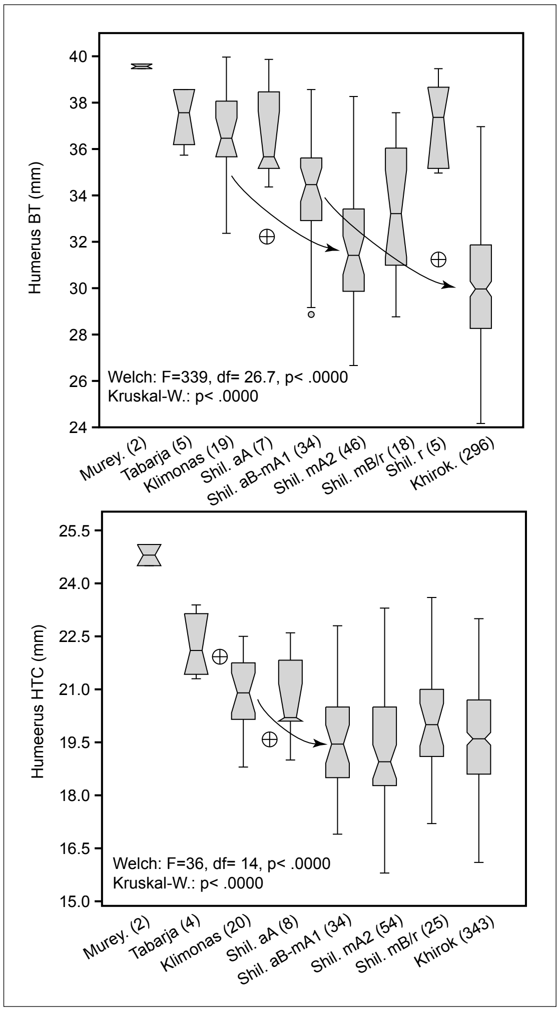


Fig. 30-11 – *Notched boxplots comparing suid distal humerus sizes from Klimonas with those of some PPN sites from the continent (Mureybet and Tabarja) and the different phases of Shillourokambos and Khirokitia. Shil, Shillourokambos, with phases aA (early A), aB (early B), m (middle), r (late). Khirok, Khirokitia. CAD J.-D. Vigne, CNRS.* • *Diagrammes a encoches pour comparer la taille de l'humérus distal des suidés de Klimonas avec ceux de certains sites PPN du continent (Mureybet et Tabarja) et des différentes phases de Shillourokambos et Khirokitia. Shil, Shillourokambos, avec les phases aA (ancienne A), aB (ancienne B), m (moyenne), r (récente). Khirok, Khirokitia. DAO J.-D. Vigne, CNRS.*

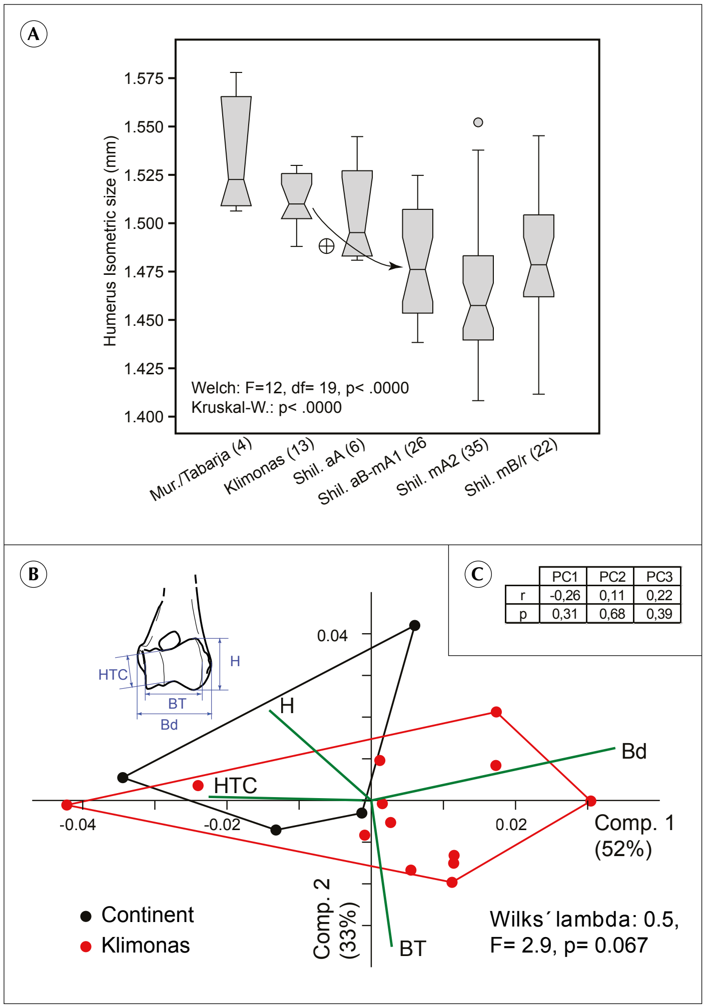


Fig. 30-12 – *Log shape ratio comparison (LSR) of the four osteometric distal humerus variables from Klimonas with those from the Levant: A, isometric size; B, projection of the first two axis of the PCA performed on the shape ratios; C, correlations between the PCA and the isometric size (Pearson's r, p = probability for a correlation). CAD J.-D. Vigne, CNRS.* • *Comparaison en Rapport logarithmique de conformation (LSR) des quatre variables ostéométriques des humérus distaux de Klimonas avec ceux du Levant : A, taille isométrique ; B, projection des deux premières composantes de l'ACP des variables de conformation ; C, corrélations entre les composantes de l'ACP et la taille isométrique (r de Pearson, p = probabilité d'une corrélation). DAO J.-D. Vigne, CNRS.*

The PCA performed on the Log Shape Ratio values evidenced some differences in the shape of the distal humerus articulation (fig. 30-12, B). Those from Klimonas plot on the right part of the projection, with high scores on the first component, mostly determined by the transversal thickness of the articular extremity (Bd and BT). Conversely, the continental wild boars plot on the left upper part of the diagram, with high scores on the first component, representing the large radius of the articular trochlea for the ulna. There was no significant correlation between any of the PCA axes and the isometric size (fig. 30-12, C), meaning that these shape differences are not correlated with size, i.e. they are not of allometric origin, and this is an actual shape difference.

This robustness of the humerus epicondyles, concerning the small size of the radius of the trochlea that we already pointed out in the previous paragraph, objectifies the a priori feeling that the distal humerus of the Klimonas wild boars were very "sturdy", especially the adult ones. This characterization can be considered as a specificity of the Cypriot wild boar.

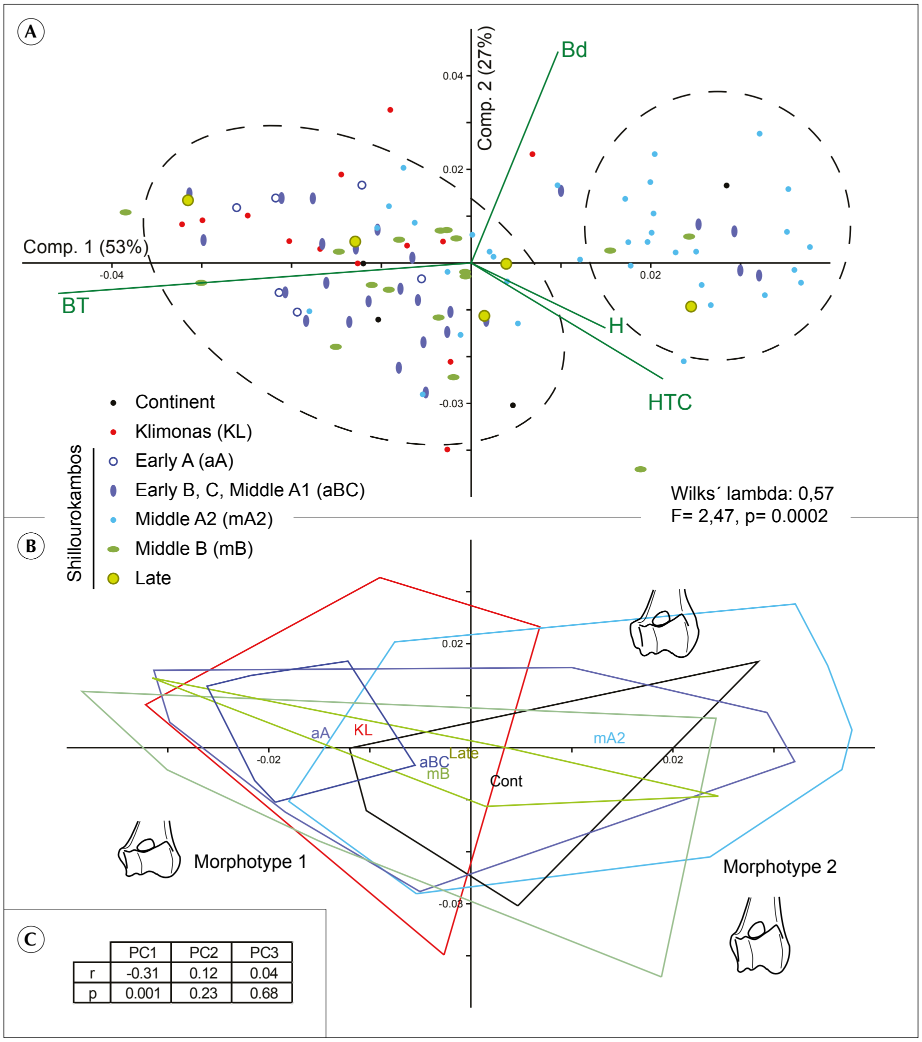
1.3.2.4. Isometric size and shape variations in Cyprus from the 9th to the 7th millennia BC

The evolution of the isometric size from Klimonas to the successive phases of Shillourokambos (fig. 30-12, A) confirms observations made on the global measurements: a relative stasis during the 9th millennium, then a significant decrease along the first half of the 8th millennium, and a clear (but not statistically significant) tendency to recovery at the end of the same millennium.

As already seen (Vigne 2021b), the PCA analyses of the shape ratios confirm the presence of significant differences, with the presence of two clusters. The first is in the left half of the diagram (fig. 30-13), showing a high correlation with the transversal breadth of the extremity (BT) regarding the three other measurements. The second clusters are in the right part of the diagram, with a proportionally smaller global breadth. Only the first morphotype is present in Cyprus during the 9th millennium (Klimonas and early phase A of Shillourokambos). The other phases of Shillourokambos (and the continent) display both morphotypes, the second being especially frequent in the middle phase A2 of Shillourokambos. The centre of gravity of the different periods shifts from the first to the second morphotype during the first half of the 8th millennium, then back towards the first morphotype during the second half; the most recent phase of Shillourokambos clustering in an intermediate position. The MANOVA is highly significant, as is the pairwise comparison with Bonferroni correction. It points out that the shape of the Klimonas humerus significantly differs from that of the middle phase A2 (p = 0.002), early phase B–C and middle phase A2 (p = 0.007) of Shillourokambos, and middle phase A2 and B (p = 0.03). Linear discriminant analyses (LDA) do not allow the groups to be separated clearly from each other (only 34% were correctly classified), however.

This pattern is similar to the one observed previously (Vigne 2021b), which we interpreted either as a consequence of the local domestication of the Klimonas morphotype or as a manifestation of the introduction of a different morphotype (from elsewhere in Cyprus or from the continent).

The study of the correlations between the isometric size and the Log Shape Ratio (fig. 30-13, C) demonstrates that the first component (53%) is highly correlated with size. This means that the shape differences that we observed between the two clusters reflects a difference of size, not a real difference in shape.



	PC1	PC2	PC3
r	-0.31	0.12	0.04
p	0.001	0.23	0.68

Fig. 30-13 – *Projection of the first two axis of the PCA performed on the log shape ratios (LSR) obtained from four measurements of the distal humerus for the continent, Klimonas and the different phases of Shillourokambos: A, with individual dots, shape variables and designation of the two groups by ellipses; B, with convex hulls and the gravity centres of the different groups; C, correlations between the PCA and the isometric size (Pearson's r, p = probability for correlation). CAD J.-D. Vigne, CNRS.* • *Projection des deux premières composantes de l'ACP des rapports logarithmiques de conformation (LSR) obtenus à partir des quatre mesures de l'humérus distal pour le continent, Klimonas et les différentes phases de Shillourokambos : A, avec les points individuels, les variables de forme et la désignation des deux groupes (ellipses) ; B, avec les contours convexes et les centres de gravité des différents groupes ; C, corrélations entre les composantes de l'ACP et la taille isométrique (r de Pearson, p = probabilité de corrélation). DAO J.-D. Vigne, CNRS.*

1.3.2.5. Interpretation

The last observation suggests that contrary to what we observed earlier between the continent and Klimonas, there is no difference in shape between Klimonas and the different phases at Shillourokambos. This fact tends to exclude the hypothesis of the introduction of a new lineage coming from the continent. It indicates that, as already suggested (Vigne 2015), this is the small Cypriot wild boar that was locally domesticated during the 8th millennium. The size decrease during the first half of the 8th millennium, as well as its allometric consequences on shape, should therefore be interpreted as the consequence of the beginning of suid herding around 8000 cal BC. The fluctuations in size (and allometric shape) during the second half of the 8th millennium (middle phase B, late phase of Shillourokambos) can therefore be interpreted as the presence of both domestic and wild suids, acquired by either herding or hunting. This is coherent with the observation that pig husbandry developed significantly during the middle phase A2 of Shillourokambos, then decreased in favour of sheep and goat herding during the middle B and late phases (Vigne and Carrère 2021). This should be confirmed later in this chapter by the GMM approach, which is better adapted to these issues.

1.4. POSTERIOR LIMB SKELETON

1.4.1. General overview

The pelvis, femurs, patellae, calcanei and naviculars measurements from Klimonas each represent a small dataset, from which emerge no remarkable character and no clear tendency when compared with the Shillourokambos series (appendices 30-7 and 30-8). Only the tibia and, moreover, the talus provide interesting information.

1.4.2. Tibia

The 78 measurements recorded from the 26 distal tibia extremities correspond to four variables: KD, Bd, Bdart, Td. Only Td showed non-normal distribution frequencies. Mixture analyses indicate that the bimodal model fits better to this distribution than the unimodal one (Akaike: 60 contra 63). The morphological distance between the two groups modelled by mixture analyses rises to 17%, suggesting a high (sexual?) dimorphism on this specific anatomic variable.

Comparison of the tibia measurements did not show any significant difference with the various phases of Shillourokambos or with Khirokitia (ANOVA, Welch: F = 1,53, df = 42,8, p = 0,22).

1.4.3. Talus

1.4.3.1. Presentation and distribution of the (sexual?) dimorphism data

Appendix 30-8 displays the 110 measurements made on the 27 talus specimens, as well as their pattern of frequency distribution for the five variables proposed by A. von den Driech (1976): GLl, GLm, Tm, Tl and Bd. None were significantly different from the normal distribution, and there was no tendency to any bimodality, except maybe for GLm (not significant). Maybe the (sexual?) dimorphism is masked by the presence of some young male talii.

1.4.3.2. Global size comparisons

Whatever variables one considers, the size of the Klimonas astragalus is significantly smaller when compared to the PPNA or early PPNB wild boar of the North Levant (e.g. GLl, fig. 30-14, A). The pairwise Mann-Whitney test is highly significant between Klimonas and all continental sites considered. Since there is no significant pairwise difference within the continental sites or between the Lebanon site (Tabarja) and all the other sites when they are grouped together (pMC = 0.23), we can consider that our different continent samples, admittedly small, constitute a relatively homogeneous meta-sample. Its mean GLl is 14% larger than that of Klimonas (44.3 contra 51 mm).

Comparisons of the GLl measurements between Klimonas and the different phases of Shillourokambos and Khirokitia (fig. 30-14, B) evidence relative stability from the beginning of the 9th to the end of the 7th millennium. There is, however, a slight but significant size decrease ca. 7400 cal BC, between the middle phases A2 and B of Shillourokambos, the latter being the same size as in Khirokitia.

1.4.3.3. Log shape ratio comparisons with the continent

The Mureybet dataset is the only continental one with more than three talii measurements. It can be compared with the four Klimonas variables (GLl, GLm, Tl and Bd), relying on a reasonable number of specimens for the latter (15) and the former (10).

A significant 15.1% size reduction can be observed for Klimonas (fig. 30-15, A).

PCA analyses of the shape ratios highlights significant shape differences (Wilks = 0.52, p = 0.009), consisting of three points: i) a much more important shape variability for Klimonas than for Mureybet (fig. 30-15, B, C); ii) a greater thickness of the Klimonas talus, expressed by the extension of the convex hull towards the negative values of the second component (fig. 30-15, B), determined by the lateral depth (Tl); iii) secondarily, larger developments of the talii lengths (GLl and GLm) regarding their depth and distal breadth are visible in the numerous specimens plotting towards the high or low values of the third component (fig. 30-15, C).

These shape differences are partly due to an allometric effect, since the first and the third PCA components (54% and 12% of the variance, respectively) are correlated to the isometric size (Pearson's r = 0.41 and 0.58, p = 0.04 and 0.002, respectively). Only a minimum of 34% of the differences are actual differences in shape unrelated to an allometric effect.

LDA confirms the significant shape differences between Klimonas and Mureybet, with a relatively high rate of correct classification (88%, fig. 30-15, D).

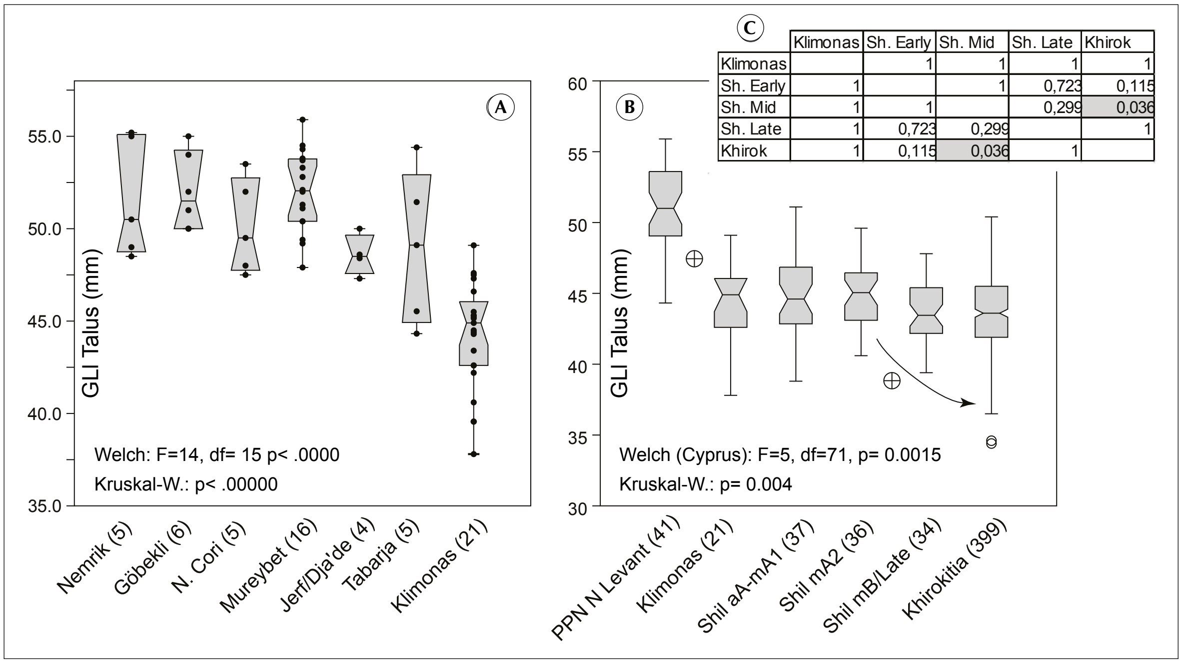
The Klimonas talii are thus 15% smaller than those of the Euphrates Valley PPNA. Their shape is more diverse and slightly different from the latter; however, a large part of these differences is due to size.

1.4.3.4. Isometric size and shape variations inside Cyprus from the 9th to the 7th millennia

The dataset of measurements for the Klimonas talii and for the different phases of Shillourokambos are composed of five variables: GLl, GLm, Tm, Tl, Bd. The Log Shape Ratio analyses rests on 104 specimens, including 14 from Klimonas.

There were very few or no variations in the isometric size (fig. 30-16, A). It appears, however, that Klimonas does not differ from the early phases of Shillourokambos, though the size did slightly but clearly decrease (a difference of only 3.9%) between the middle A1 and middle B phases, i.e. between 7600 and 7400 cal BC. The only slightly significant Mann-Whitney p value was found between the early phases and middle phase B (p = 0.08). In addition, the isometric size of middle phase A1 and, and to a lesser extent A2, are very variable, suggesting the presence of both large (hunted) and smaller (domesticated?) suids.

PCA analyses of the 520 shape indexes (fig. 30-16, B) indicate no difference during the chronological sequences, from the early 9th (Klimonas) to the late 8th millennia (Shillourokambos late phase). More than 90% of the total shape variance (PC1xPC2) are significantly correlated with the isometric size (PC1, Pearson's r = 0.3, p = 0.002; PC2, Pearson's r = 0.92, p < 0.0000), indicating a strong allometric effect. The total absence of non-allometric shape differences between the different chronological groups, whereas there are sensitive non-allometric shape discrepancies between Klimonas and Mureybet, suggests that no continental suids were introduced into the Cyprus populations within these two millennia (Vigne 2015). The only significant change in the shape of talii is a slight decrease in size at the end of the first half of the 8th millennium, probably resulting from the effects of an intensification of suid management.



	Klimonas	Sh. Early	Sh. Mid	Sh. Late	Khirok
Klimonas		1	1	1	1
Sh. Early	1		1	0,723	0,115
Sh. Mid	1	1		0,299	0,036
Sh. Late	1	0,723	0,299		1
Khirok	1	0,115	0,036	1	

Fig. 30-14 – *Boxplot comparison of the Klimonas suid talii GLl: A, with several PPNA or early PPNB sites from South East Anatolia (Nemrik, Göbekli, Nevalı Çori), the Middle Euphrates Valley (Mureybet, Jerf El Ahmar, Dja'de) and the Lebanon coast (Tabarja); B, with the different phases of Shillourokambos and Khirokitia. C, pairwise Mann-Whitney probabilities for the Cyprus sites, with Bonferroni correction (the significant differences are in grey). CAD J.-D. Vigne, CNRS. • Diagrammes à encoches de la GLl de l'astragale des suidés de Klimonas : A, avec plusieurs sites PPNA ou PPNB anciens du sud-est de l'Anatolie (Nemrik, Göbekli, Nevalı Çori), de la moyenne vallée de l'Euphrate (Mureybet, Jerf El Ahmar, Dja'de) et du littoral libanais (Tabarja) ; B, avec les différentes phases de Shillourokambos et avec Khirokitia. C, probabilités deux à deux de Mann-Whitney pour les sites de Chypre, après correction de Bonferroni (les différences significatives sont en grisé). DAO J.-D. Vigne, CNRS.*

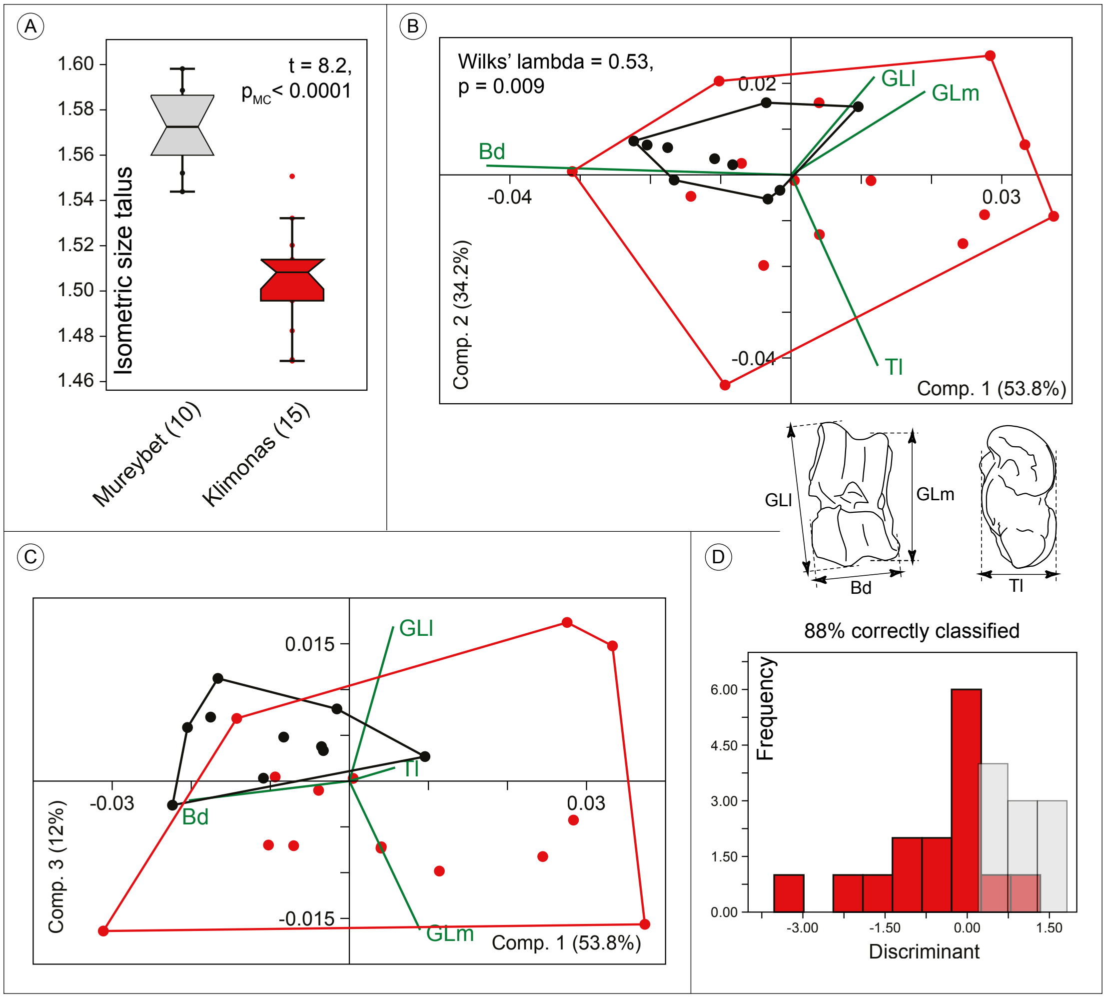


Fig. 30-15 – *Size (A) and shape (B,C,D) comparisons between the astragalus from Klimonas (red) and Mureybet, based on the log shape ratio (LSR) analyses of four osteometric variables. B and C, scatter diagrams of the PCA analyses according to the first and second components (88% of the variance), and the first and third components (66% of the variance). D, distribution histogram of the talus shape indexes on the discriminant axe obtained from linear discriminant analyses (LDA). CAD J.-D. Vigne, CNRS.* • *Comparaisons de la taille (A) et de la conformation (B,C,D) des astragales de Klimonas (en rouge) et de Mureybet, sur la base des analyses en Log shape ratio de quatre variables ostéométriques. B et C, diagrammes de dispersion des analyses PCA en fonction, respectivement, des première et deuxième composantes (88 % de la variance), et des première et troisième composantes (66 % de la variance). D, histogramme de distribution des indices de forme de l'astragale sur l'axe issu de l'analyse linéaire discriminante. DAO J.-D. Vigne, CNRS.*

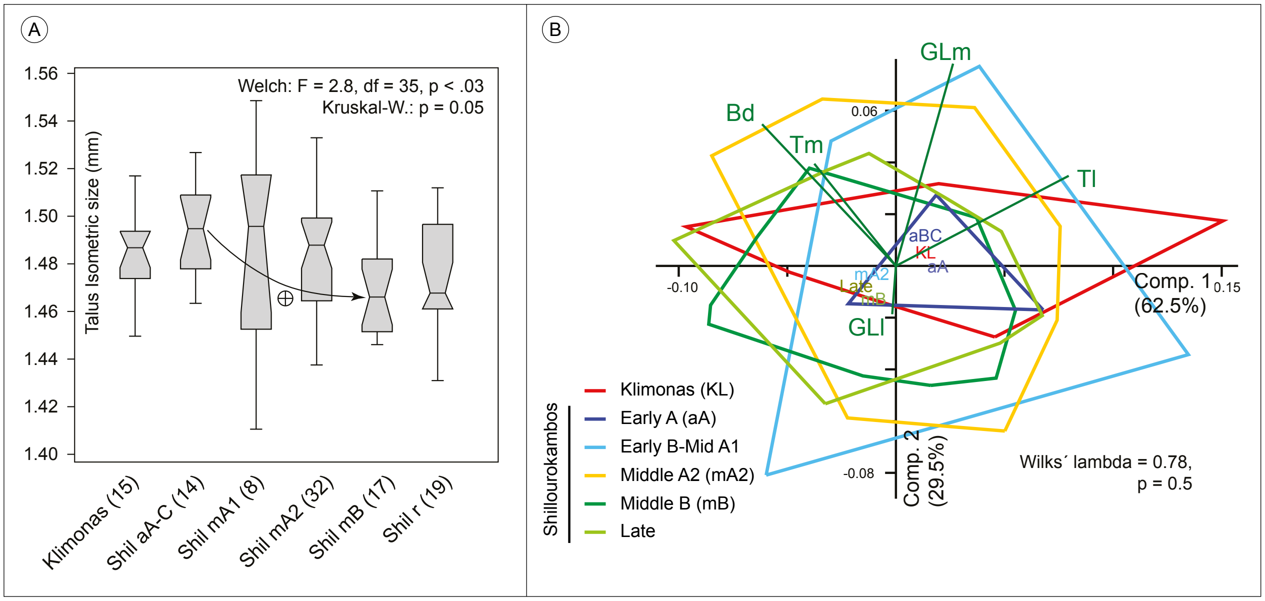


Fig. 30-16 – *Comparisons of the isometric size (A) and shape (B) between the talii from Klimonas and those of the different Shillourokambos phases, based on the log shape ratio (LSR) analyses of five osteometric variables (GLl, GLm, Tl, Tm, Bd). B, scatter diagrams of the PCA analyses according to the first and second components (92% of the variance). CAD J.-D. Vigne, CNRS.* • *Comparaisons de la taille isométrique (A) et de la conformation (B) des astragales de Klimonas et de ceux des différentes phases de Shillourokambos, en se basant sur les analyses en Rapports logarithmique de conformation (LSR) de cinq variables ostéométriques (GLl, GLm, Tl, Tm, Bd). B, diagrammes de dispersion des analyses PCA en fonction des première et deuxième composantes (92 % de la variance). DAO J.-D. Vigne, CNRS.*

1.5. EXTREMITIES

1.5.1. Metapodials

Only the metacarpal dataset was large enough for analyses and comparisons (appendix 30-9). The distribution of the measurements was normal. There was a clear tendency in size reduction between Klimonas and Shillourokambos, the latter considered as a whole, but the samples are too small to test the statistical significance.

1.5.2. First and second axial phalanges

A good number of PPNA first (49) and second (39) axial phalanges could be measured (appendices 30-10 and 30-11). The distribution of the measurements was normal except for the diaphysis diameters, which better fit the bimodal than the normal distribution model for both first and second phalanges. The difference between the two groups is, respectively, 12% and 17%, due to different causes (sex, mixture of anterior and posterior, mixture of III and IV fingers).

Bivariate comparison with some PPN datasets from the continent (Mureybet, Dja'de, Cafer, Aswad-Damascus) and between Akrotiri (only one first axial phalanx), Klimonas, and the different phases of Shillourokambos evidence a strong and significant global size difference between Cyprus, on the one hand, and the middle and north Levant, on the other (fig. 30-17, appendices 30-10 and 30-11; t-test: p_{MC} <0.0001 for both phalanges). However, the Anatolian site of Cafer plots closer to the Cypriot sites, with a slightly larger size. The difference between the means of the Levant and Cyprus is, respectively, 9.3 and 12% for GL, 15 and 11% for Bp, and 11 and 13% for Bd.

To compare Klimonas with the PPN continental and Cypriot sites, Log Shape Ratio analyses with 4 and 5 variables (GL, Bp, SD, Bd + Dp) recorded 140 and 110 data for the first phalanges and 155 and 200 for the second ones.

Several observations emerged:

- The isometric size is rather homogeneous on the continent (fig. 30-18, A, C), especially between distant sites such as Cafer (southeast Anatolia), Mureybet and Dederiyeh (Middle Euphrates) and Aswad (Damascus region).

- This is also the case for the Cyprus sites, with no significant size variation during the 9th and 8th millennium phases of Klimonas and Shillourokambos occupation.

- The isometric sizes from the continent are higher than those of Cyprus, between 13.4 to 15.5% on average; the pairwise difference between the continental and Cyprus datasets was always highly significant (Mann-Whitney, $p < 0.001$ for both the first and the second phalanges).

- There are clear and significant shape differences between Anatolia (Cafer) and the north Levant (Mureybet, Dja'de, Dederiyeh and Aswad); for the first phalanges, this consists of a strong allometric decrease in the diaphysis breadth (KD) with reference to the length and distal width (GL and Bd; correlation between the isometric size and the first component, $p < 0.0000$; fig. 30-18, B); it is more or less the same for the second phalanges, with a strong correlation of the second component at Cafer, highly correlated with GL and Bd and negatively correlated with KD (fig. 30-18, D); here again, these differences are very allometric.

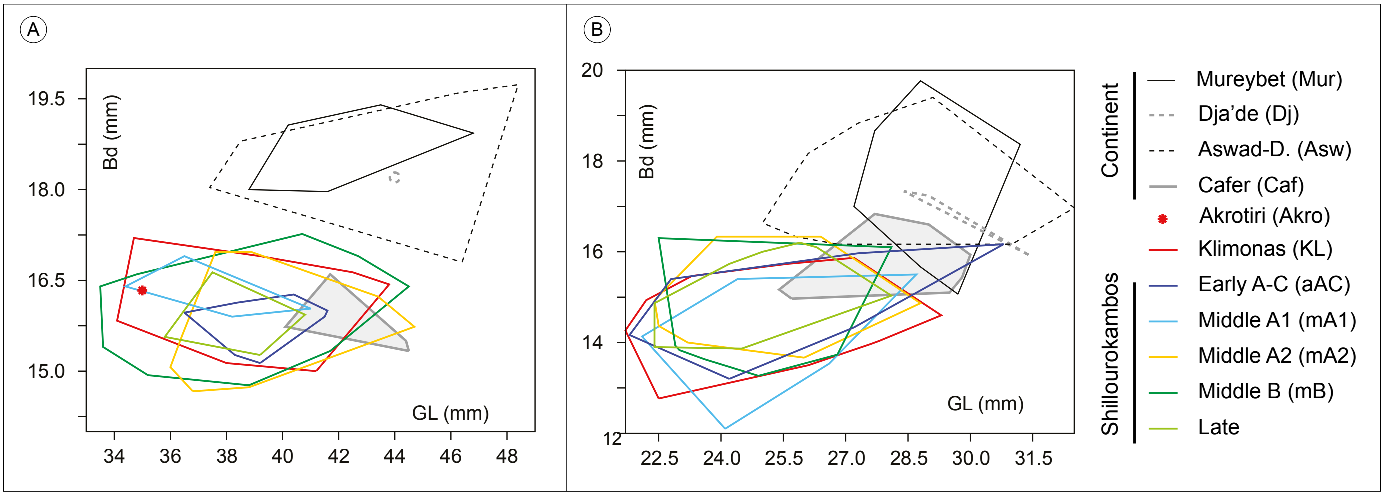


Fig. 30-17 – *Biplot of the length (GL) and distal breadth (Bd) of the first (A) and second (B) axial phalanges from four PPN sites in South East Asia (Cafer, Mureybet, Dja'de, Aswad) and three Cypriot sites (Akrotiri, Klimonas and the different phases of Shillourokambos). The curves are smoothed by a 3-point moving average. CAD J.-D. Vigne, CNRS.* • *Comparaison bivariée de la longueur (GL) et de la largeur distale (Bd) des première (A) et deuxième (B) phalanges axiales de quatre sites PPN d'Asie du Sud-Est (Cafer, Mureybet, Dja'de, Aswad) et de trois sites de Chypre (Akrotiri, Klimonas et les différentes phases de Shillourokambos). Les courbes sont lissées par une moyenne mobile de 3 points. DAO J.-D. Vigne, CNRS.*

- There is no significant shape difference between the north Levant and Cyprus, nor between the different Cypriot datasets; the MANOVA without Cafer was not significant for the first phalanges; and even though it is significant for the second phalanges (p = 0.003), none of the pairwise p values, which indicate significant differences between Aswad and all the Cyprus series, are any more significant after the Bonferroni correction.

- The single first phalanx from Akrotiri plots far outside the convex hulls of the other Cypriot sites.

These observations confirm the diminutive size of the Cyprus wild boar and the stability of its morphology during the 9th–8th millennia. It suggests better similarities with the PPN wild boars of the Levantine plains and valleys than with those of high plateaus of southeast Anatolia. The difference between the single Akrotiri phalanx and the rest of the Cyprus bones is enigmatical.

1.5.3. First and second abaxial phalanges

The first abaxial phalanges provide interesting information (appendix 30-12). The dataset is rich with a total of 142 measurements from 31 specimens. The distribution is normal for all the measurements except for Bp, for which the bimodal distribution model fits better. Here again, comparison with the data from Cafer and Aswad-Damascus indicates a significantly smaller size for the Cyprus wild boar (-22% for GL, -16% for Bp), and a very good homogeneity for all the Cyprus measurements, including the single Akrotiri phalanx.

The dataset for the second abaxial phalanges (appendix 30-12) is smaller and there are few comparative measurements available in the literature. The only noticeable observation is a strong and repeated tendency to bimodality for all the Klimonas measurements, except GL, with 18 to 31% differences between the two groups (anterior-posterior? II/Vth finger?).

1.5.4. Third phalanges

The third axial phalanges also provide a good dataset (101 measurements; appendix 30-13), and again display a recurrent tendency to bimodality; the distance between the two groups reaching 15% for height (H).

The third axial phalanges of Klimonas are significantly smaller than those of Aswad (minus 12% for DLS) but, here again, about the same size as in Cafer (only three specimens; fig. 30-19, A).

The most surprising pattern is that the two third phalanges from Akrotiri are admittedly smaller than those from Aswad, as previously mentioned (Vigne *et al*. 2009), but they plot in an intermediate position between the Damascus site and Klimonas. This trend is even more visible with the four third abaxial phalanges from Akrotiri (fig. 30-19, B), which do not differ in size from the (currently only) two phalanges from Cafer, but which are significantly larger than those from Klimonas (23.6% for Ld, 21.6% for DLS).

This suggests two interesting hypotheses:

- The size reduction of the extremities was ongoing ca. 10,000 cal BC; it had reached its minimum before the occupation of Klimonas, ca. 8800 cal BC and did not change throughout the following two millennia.

- The size reduction of the Cypriot wild boar limb extremities seems to have been stronger than the other parts of the skeleton, as a possible expression of the second insularity syndrome, i.e. a size reduction in some of the extremity bones.

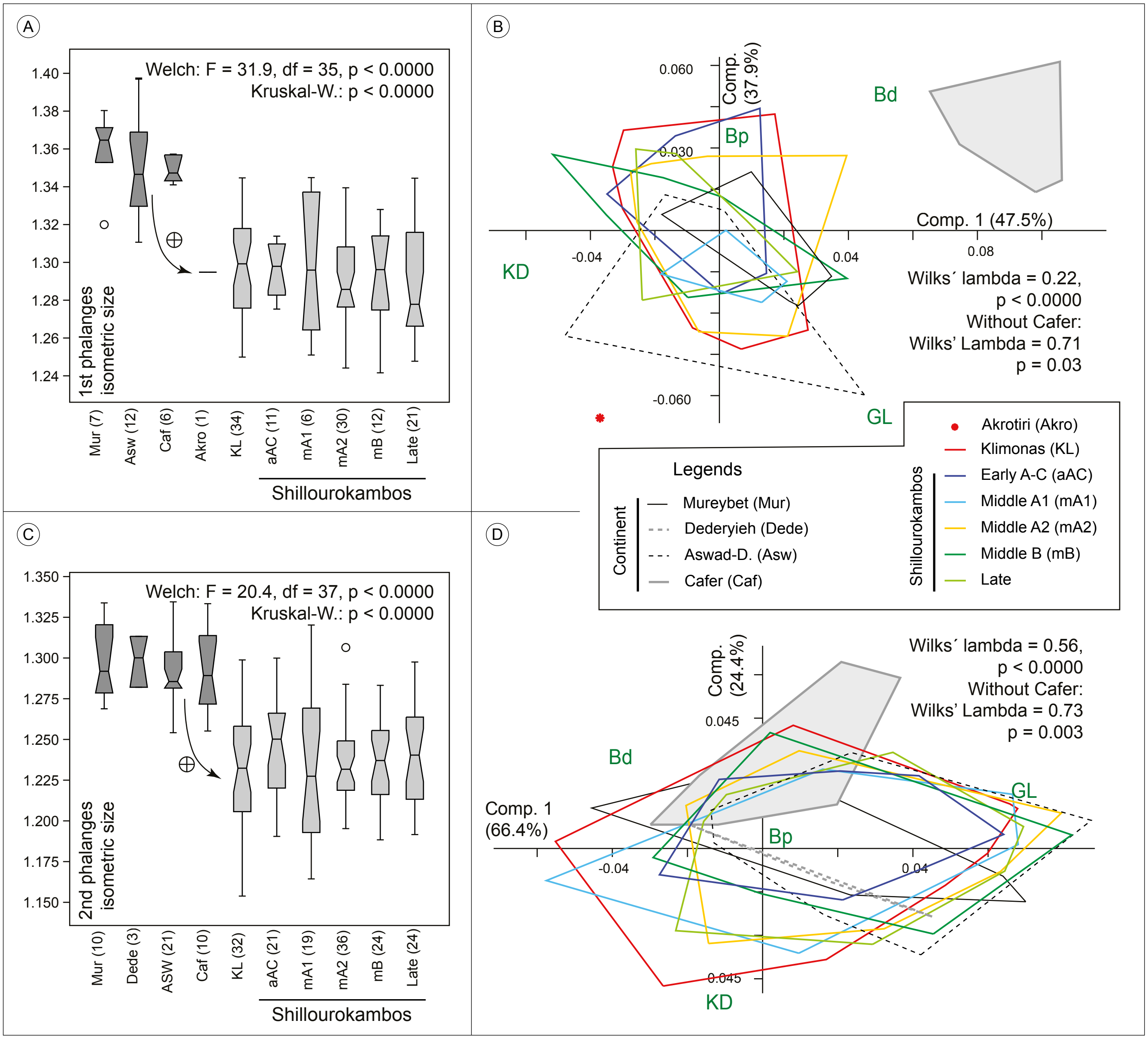


Fig. 30-18 – *Comparisons of the isometric sizes (A,C) and shapes (B,D) between the first (A,B) and second (C,D) axial phalanges from four PPN sites in South East Asia (Mureybet, Aswad, Dederyieh, Cafer) and three sites in Cyprus (Akrotiri, Klimonas and the different phases of Shillourokambos), based on the log shape ratio (LSR) analyses of four osteometric variables (GL, Bp, KD, Bd). B and D, scatter diagrams of the PCA analyses according to the first and second components (75% and 71% of the variance, respectively). CAD J.-D. Vigne, CNRS.* • *Comparaisons des tailles (A, C) et des formes (B, D) isométriques entre les première (A, B) et deuxième (C, D) phalanges axiales de quatre sites PPN d'Asie du Sud-Est (Mureybet, Aswad, Dederyieh, Cafer) et de trois sites de Chypre (Akrotiri, Klimonas et les différentes phases de Shillourokambos), en se basant sur les Rapports logarithmiques de conformation établis sur quatre variables ostéométriques (GL, Bp, KD, Bd). B et D, diagrammes de dispersion des analyses en composantes principales selon la première et la deuxième composante (75 % et 71 % de la variance, respectivement). DAO J.-D. Vigne, CNRS.*

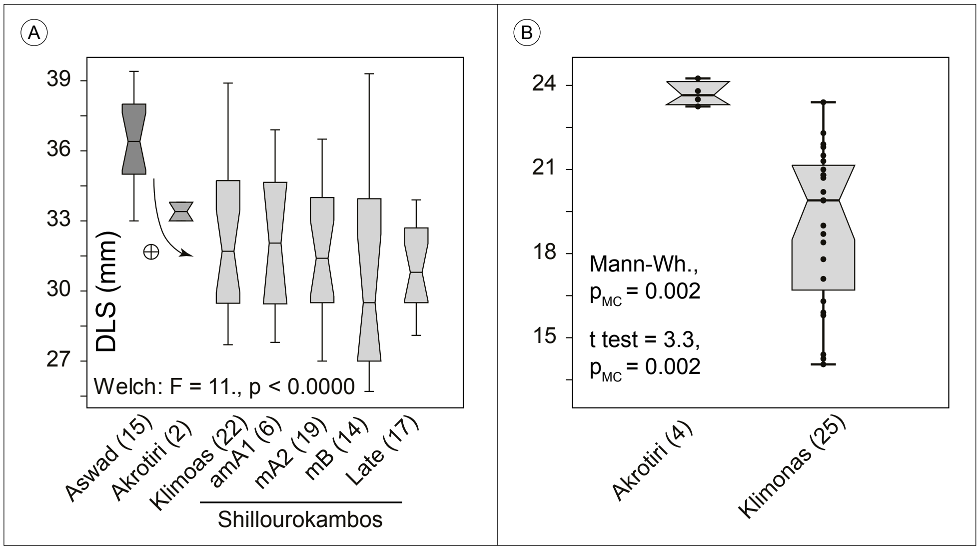


Fig. 30-19 – *Third phalanges: A, comparison of the axial phalange lengths from Klimonas with those of Aswad-Damascus and two other Cypriot sites, Akrotiri and Shillourokambos; B, comparison of the abaxial phalange lengths from Klimonas with those of Akrotiri-Aetokremnos. CAD J.-D. Vigne, CNRS.* • *Troisième phalange: A, comparaison de la longueur des phalanges axiales de Klimonas avec celles d'Aswad-Damas et de deux autres sites chypriotes, Akrotiri et Shillourokambos; B, comparaison de la longueur des phalanges abaxiales de Klimonas avec celles d'Akrotiri-Aetokremnos. DAO J.-D. Vigne, CNRS.*

1.6. DISCUSSION OF THE RESULTS OBTAINED FROM TRADITIONAL MEASUREMENTS

1.6.1. Osteometric characterisation of the small PPN Cypriot wild boar

The more than 2600 osteometric data recorded from Klimonas provide the first opportunity to describe and compare the skeletal morphology of the small PPN Cypriot wild boar. It not only differs from the continental wild boars due to its small size, as previously mentioned (Vigne *et al*. 2009, Vigne 2015, 2021b), but also by its slightly more significant sexual dimorphism, evidenced through a series of minor shape differences, some of them not connected with the smaller size, and putatively by some slight modifications in the boars' locomotor apparatus. Furthermore, these observations allow us to start a discussion about the geographical origin of this Cyprus lineage.

1.6.1.1. Sexual dimorphism

If we exclude the phalanges, for which the polymorphism can result from several different reasons (anterior/posterior, 3rd/4th finger, sex) and the limited datasets, we notice the bimodal tendency of the kernel distribution at 55.6% for the 45 osteometric variables (tab. 30-4). The Gaussian mixture analyses of one-third of these bimodal distributions (20% of the variables) provided a minimal value of the Akaike criterion for two groups, making the presence of two groups more probable than that of a unique one.

For these nine variables displaying a significant bimodal distribution, the estimate of the size distances between the two groups scored within the range observed by Payne and Bull (1986) for the forelimb (only one measurement: humerus). It seems, however, that the Klimonas dimorphism is higher for some teeth measurements (up to 11% contra 4% for Anatolia) and that it can reach very high values for some hindlimb measurements, such as the depth of the tibia distal extremity (17%), which seems to be particularly affected by dimorphism, part of the variation being admittedly due to allometries.

Of course, we could not demonstrate that these dimorphisms resulted from sexual dimorphism, but the repetition of similar patterns and the variation range of the differences between the mean or modes of the two groups, compatible with that of the modern Anatolian wild boar described by Payne and Bull (1986), make it much more probable. In addition, the distances between the two groups are estimated based on models that are sensitive to the stochastic effects on the composition of the relatively small samples of data. However, although it is not massive, it seems that the Klimonas wild boar displays a higher sexual dimorphism than the already described populations of the continent, either archaeological or extant (see also Albarella *et al*. 2009).

Accentuation of sexual dimorphism has never been mentioned as a component of insularity syndrome in mammals. Conversely, insularity is reputed to provoke a reduction of the sexual dimorphism in lizards, birds, and small mammals (Shuster and Wade 2003). It has been observed, however, that for some small island lizard populations in southern Italy, the size and the colouration pattern tend to evolve towards starker contrasts between males and females as an adaptation to unpredictable nutritional resources ("reverse island syndrome", Raia *et al*. 2010). As they are very different in size, the male and female lizards exploit different ranges of prey, subsequently reducing intersexual competition and increasing their population fitness. The high density of wild boars in Cyprus, due to limited predation pressure and no competition with other ungulates, generated a particular ecological situation, which may have fostered a unique evolutionary trajectory (Raia and Meiri 2006). This could have entailed a strong intraspecific competition liable to increase the fitness of larger males and smaller females and to contrast the sexual dimorphism for some skeletal parts.

Skeleton part	Nb of measured speciments	Nb of well documented variables datasets (NIsp>15)	Nb of bimodal kernel distributions	Nb of var. with minimum Akaike criterion for 2 groups	Estimation of the morphol. distance	Continent reference % (Payne & Bull 1986)
Upper teeth	141	8	7	3	L M3/= 11% W M1/=7% L dp4/= 8%	0-4%
Lower teeth	183	14	9	4	W2 M/3= 7% W2 M/2= 10% L M/1= 7% W3 dp/4= 9%	
Scapula	17	3	2			Forelimb 8-12%
Humerus	29	4	1	1	H= 8,4%	
Radius	34	2	0			
Ulna	37	3	2			
Tibia	30	4	2	1	Td= 17%	Hind-limb 7%
Calcaneus	16	2	1			
Talus	27	5	1			
Total	**514**	**45**	**25**	**9**		
%			**55,6**	**20,0**		

Tab. 30-4 – *Recapitulation of the frequency distributions likely to be considered as bimodal and interpreted as an expression of sexual dimorphism. For each, estimation of the distance (%) between the two sexes based on the outputs of Gaussian mixture analyses.* • *Récapitulation des distributions de fréquences susceptibles d'être considérées comme bimodales et interprétées comme l'expression du dimorphisme sexuel. Pour chacune d'elles, estimation de la distance (%) entre les deux sexes sur la base des résultats des analyses de mélange gaussiens.*

1.6.1.2. Global and isometric size reduction

Appendix 30-14 exhibits the 29 size difference estimations, either global or isometric, for the skeletal parts for which the sample sizes of both Klimonas and the continent were large enough (fig. 30-20, A). The six isometric size estimates fluctuate between 4.8 and 16.9%, in the same range as the other 20 values (between 4 and 22.6%; fig. 30-20, B). The distribution of the 29 estimates (Cafer was excluded) does not differ from the normal distribution and indicates that the size of the Klimonas wild boar was on average 13.3% smaller than that of his contemporaneous continental counterparts of the north and middle Levant, as previously mentioned (Vigne *et al*. 2012).

Where available, comparisons with the PPN sites from the Anatolian plateau (Cafer Höyük), indicate a lesser size difference with Klimonas, estimated at 8.2%, on average (N = 3).

1.6.1.3. Reduction of the locomotor apparatus

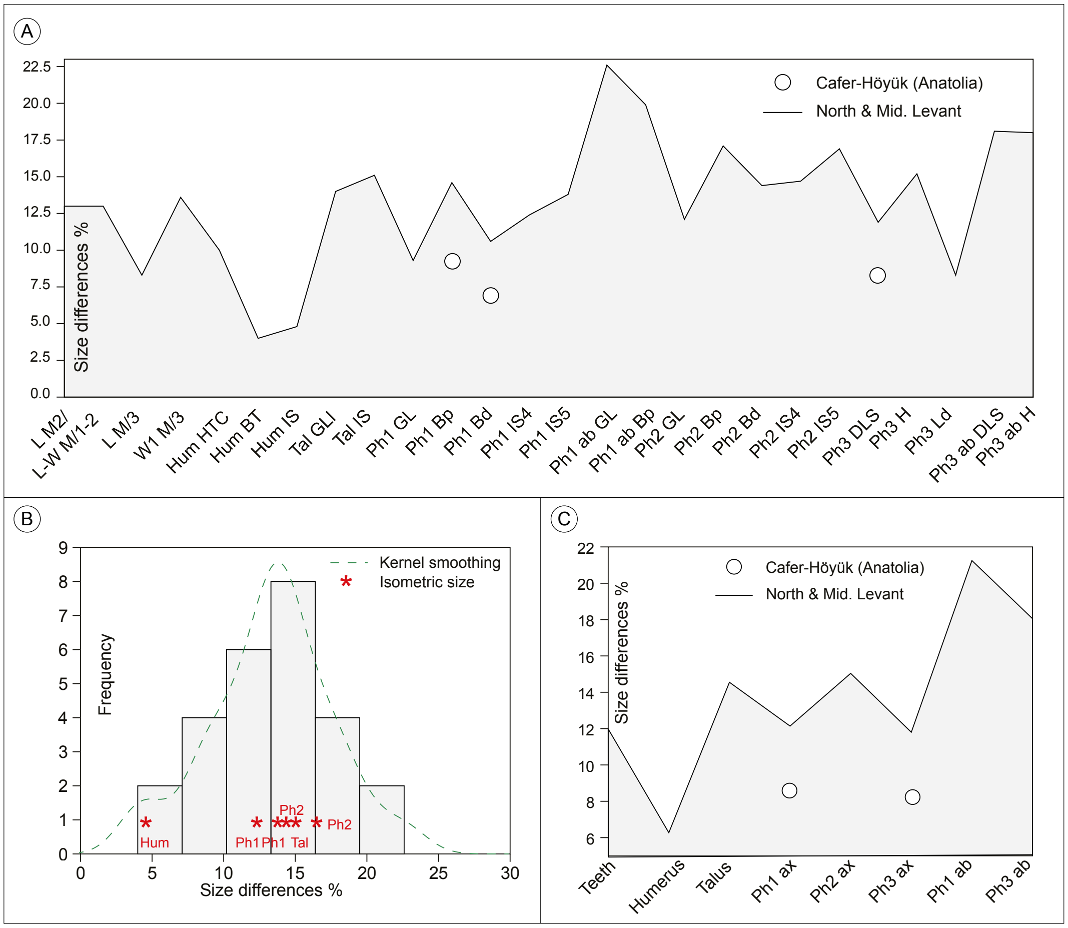
Figure 30-20 also indicates that the variations in size differences are not evenly distributed across the different skeletal parts. The teeth and humerus provided values between 4 and 13% (mean 9.5%), while estimates for the talus and axial phalanges ranged between 8.3 and 16.9% (mean 13.4%) and the differences for the 1st and 3rd abaxial phalanges fluctuated between 18 and 22.6%. The discrepancies between these three categories are highly significant, especially between the abaxial and other phalanges (fig. 30-21).

This indicates that the size reduction of the Klimonas wild boar, regarding its contemporary counterparts in the Levantine plains, did not impact the different parts of the skeleton with the same intensity. In other words, the extremities decreased significantly more in size than the head and the proximal segments of the limb (at least the anterior limb, since data are available only for the humerus); moreover, the phalanges of the abaxial fingers decreased more than the other phalanges.

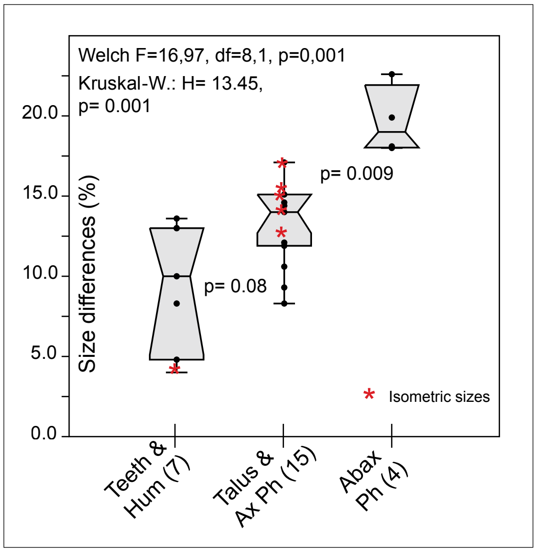
Size reduction due to insularity is never isometric for all the body parts (Sondaar 1977, Lomolino 2005). Some of these allometries result from a reduction of the locomotor apparatus, considered the second insularity syndrome (Von Vallen 1973) after body size reduction. It is reputed to result mainly from the drastic decrease of predation that releases selective pressure on an animal's capability to fly or run when escaping predation. Regarding birds, this concerns the size reduction and atrophy of wings, to an extent that they lose their capability to fly (e.g. the Mauritius Dodo).

As for mammals, especially ungulates, this mobility reduction impacts the extremities of the limbs and their adaptation to jump, run, or swim (Sondaar 1977). Within the Mediterranean area, this phenomenon is well documented e.g. in the Balearic Islands, with the spectacular reduction of the metapodials length of the extinct goat *Myotragus balearicus* (Bover and Alcover 2000). The Cyprus dwarf hippos *Phanourios minor* also provide a good illustration of this insular evolution due to predation release – the loss of an aquatic lifestyle associated with an increase in mobility over hard substrata induced reduction and "de-specialization" of the skeleton of the hands and feet. (Boekschoten and Sondaar 1966, 1972).

The abaxial fingers of suids (IInd and Vth fingers) are much reduced in regard to the axial ones (IIIrd and IVth fingers). The function of the latter mostly consists in supporting the weight of the animal when walking, running, or jumping. Conversely,



▲**Fig. 30-20** – *Synthetic presentation of the 26 size difference estimates (in %) between the measurements from Klimonas and those from continental PPN sites located in South East Anatolia (Irak: Nemrik; Turkey: Cafer-Höyük, Göbekli, Nevalı Çori), Middle Euphrates Valley (Syria: Mureybet, Jerf El Ahmar, Dja'de, Dederiyeh), Damascus (Aswad) or Lebanon (Tabarja). A, diagram of all the estimates; B, histogram and kernel densities of the frequency distribution of estimates, including for the six isometric size estimates; C, mean estimates for the different anatomic regions, from the head (left) to the terminal phalanges (right). CAD T. Cucchi, CNRS.* • *Présentation synthétique des 26 estimations de la différence de taille (en %) entre les mesures des Klimonas et celles des sites PPN continentaux situés dans le sud-est de l'Anatolie (Irak : Nemrik ; Turquie : Cafer-Höyük, Göbekli, Nevalı Çori), la vallée du moyen Euphrate (Syrie : Mureybet, Jerf El Ahmar, Dja'de, Dederiyeh), la région de Damas (Aswad) ou le Liban (Tabarja). A, diagramme de toutes les estimations ; B, histogramme et densités de kernel de la distribution de fréquence des estimations, avec mention des six estimations de taille isométrique ; C, moyenne des estimations pour les différentes régions anatomiques, de la tête (à gauche) aux phalanges terminales (à droite). DAO T. Cucchi, CNRS.*



◀**Fig. 30-21** – *Comparison of the size difference estimates between Klimonas and the Levantine PPN sites (except Cafer Höyük). The estimates are grouped according to three anatomic categories: head and proximal part of the anterior limb, distal part of the limbs (talus and phalanges of hands and feet) and abaxial phalanges of both anterior and posterior limbs. CAD T. Cucchi, CNRS.* • *Comparaison des estimations des différences de taille entre Klimonas et les sites PPN du Levant (sauf Cafer Höyük). Les estimations sont regroupées selon trois catégories anatomiques : tête et partie proximale du membre antérieur, partie distale des membres (astragale et phalanges des mains et des pieds) et phalanges abaxiales des membres antérieur et postérieur. DAO T. Cucchi, CNRS.*

because they are 30 to 40% shorter than the other fingers, the abaxial fingers are generally not in contact with the ground when the animal runs on hard substrata. Hunters call them dewclaws and know that they enter in contact with the soil (and thus imprint it) only when the latter is sandy, muddy, or snowy. Their function is therefore to avoid that the legs of the wild boar sink too deeply into the soft ground and contributes to optimising the flight of the wild boar on any kind of ground and thus to escape predators. The absence of any large predators (except small human groups) in Cyprus during the 11–10th millennia cal BC, together with mostly hard ground on this dry Mediterranean island, are likely to have contributed to the release of selective pressure on well-developed abaxial fingers.

The Cypriot wild boar was not only marked by the Van Vallen insularity syndrome of size reduction for large mammals but also underwent an evolutive adaptation of its locomotor apparatus.

The observation that both the axial and abaxial third phalanges from Akrotiri were of intermediate size, between those of the PPN continental and the Klimonas wild boars (fig. 30-19), indicates that the Cypriot wild boar's insular adaptation was reached no later than five centuries after the introduction of *Sus scrofa* in Cyprus. It is possible that the Cypriot wild boar reached morphological stabilisation sometime during the 10th millennium and then stopped evolving, which is a classical phenomenon on islands (Millien 2006). One can also envisage that, starting from the 9th millennium, the suid populations were, at least locally, submitted to new emergent predation pressures because of the intensification of dogs and human hunters on the island. The rapid evolution of the ecological context due to anthropisation during the 9th and the 8th millennia may have further modified the evolutive trajectory of the Cyprus wild boar.

1.6.1.4. Other possible marks of insularity and possible continental origins

Apart from the smaller isometric size, the Log Shape Ratio analyses of the humerus and the talus found slight shape differences between the Cyprus wild boar and its relatives from the Levantine plains (mostly Mureybet and Tabarja). For the humerus (fig. 30-12, B), the distal end of the Cypriot wild boar is more robust. This difference is weak because of the small sample size but is not due to an allometric adjustment. For the talus (fig. 30-15), we found greater shape variability and gracility of the bone shape, this time partly due to allometric effects. Such phenotypic change, especially the more significant variability of the talus shape, could be explained as the consequence of increased intraspecific competition (Blondel 1976).

Concerning the first and second axial phalanges, despite their size reduction, we did not observe any shape difference between the large datasets of Klimonas and the specimens from the Levantine plains (fig. 30-18). This confirms the strong morphological proximity of the Cyprus lineage and the middle and north Levant already found for the humerus and the talus.

However, analyses of the phalanges also pointed out that the shape of the phalanges from Cafer Höyük, located on the southeast Anatolian plateaus in the Upper Euphrates Basin, was significantly different from those of the wild boar of both Cyprus and the Levantine plains. Their isometric size is only 8% smaller than at Klimonas (versus 13% for the Levantine plains; fig. 30-20) and their diaphysis breadth is allometrically smaller than their length and distal width, in comparison to all our other reference datasets. This observation suggests that the Cypriot populations cannot come from Cafer. Of course, we have no evidence that Cafer can be considered representative of all the PPN wild boar populations of southeast Anatolia, liable to be opposed for this criterion to the populations of the middle and north Levantine plains.

1.6.5. Domestication and further evolution of the Cypriot wild boar

After 25 years of excavation and archaeozoological analyses, we have collected 7489 measurements from 2439 *Sus scrofa* specimens within a 4 km² area and the two millennia covered by the sites of Klimonas and Shillourokambos (see tab. 30-1 and Vigne 2011c, 2021b). Their analysis provides well-sustained answers to the questions that we addressed at the beginning of this chapter.

1.6.5.1. Were the Shillourokambos wild boars the descendants of those from Klimonas?

To address this question, we concentrated our attention on the shape markers that are not or are poorly connected, with size. Indeed, size and allometric morphological variations generally result from modifications to environmental conditions, including human pressures, domestication, and husbandry. Therefore, among the many observations we made above, the criteria one should consider here are the shape ratios of the distal humerus, the talus and the first and second phalanges. None showed any significant differences between Klimonas and Shillourokambos or between the different phases of Shillourokambos (fig. 30-16 and 30-18; see also Vigne 2015), except for the humerus.

For the latter, a second morphotype that differed from that of Klimonas and of the early phases of Shillourokambos appeared during the middle phases (ca. 7600–7500 cal BC). The relative occurrence of the two morphotypes fluctuated during the second half of the 8th millennium (fig. 30-13 and Vigne 2021b). However, the increase in the dataset provided evidence showing that this “second morphotypes” is an allometric adjustment resulting from the significant size decrease induced by domestication during the 8th millennium (see below). Consequently, there are no shape differences between Klimonas and Shillourokambos, or within the different phases of the latter, which is also true for the humerus.

The absence of any shape modification in the Cypriot *Sus scrofa* during these two millennia contrasts with the shape differences that we observed with the same approach above, between Cyprus and the PPN continental sites and even between Cafer and the sites of the Levantine plains. If any new lineage of suids were introduced from the continent to Cyprus during the 8th millennium, as we previously proposed (Vigne *et al.* 2011c), the slight differences we found between the Klimonas wild boars and their North Levantine relatives could have appeared in our analyses. This homogeneous morphological trajectory pleads in favour of the continuity of the same *Sus scrofa* lineage from the 11th millennium (Akrotiri) to the end of the 8th millennium (and maybe the 7th at Khirokitia) without any input of the recently domesticated pig lineages from the continent.

Of course, we shall question this preliminary conclusion below in light of the GMM observations.

1.6.5.2. Size fluctuations as a marker of domestication and pig husbandry

Much evidence was collected at Shillourokambos demonstrating that (i) pigs were domesticated at the turn of the 9th–8th millennia; (ii) their husbandry increased in intensity between 8000 and 7600 cal BC (early phases B and C) and became the main herding activity by middle phase A2; and (iii) it slightly decreased during the last centuries of the 8th millennium (middle B phase). This decline in pig husbandry is most likely a consequence of the rise of sheep and goat herding: skeletal size decrease, teeth anomalies, mortality profiles, prenatal and perinatal mortalities, and pathologies (Vigne 2011c, 2021b). In this chapter, the additional data from Klimonas provides new references and perspectives, allowing us to revisit, refine, and deepen these results. We can now divide this story into two main phases.

<u>From 8800 to 7700 cal BC.</u> The suids of early phases A and B of Shillourokambos (between 8500 and 7700) were morphologically like those of Klimonas, with, however, a noticeable increase in the size of some skeletal parts. It is not visible on the phalanges, visible but not significant for the length of the lower cheek teeth (and for the isometric size of the distal humerus and talus) and statistically significant for the length of some upper molars. This suggests an important environmental change over these 11 centuries. The climatic warm-up can be discarded since it occurred earlier and would have induced a size decrease. The age profiles testify that rearing began by at least ca. 8000–7800 cal BC (early phase B). However, this new event cannot explain the relatively continuous trend, especially between Klimonas and the early phases A and B of Shillourokambos. One explanation could be the increase of hunting pressure due to the intensification of human presence on the island. The latter was probably boosted by the necessity to protect the cereal fields against wild boar damage. We observed the same slight increase in size for the Mesopotamian fallow deer during the 8–7th millennia and interpreted it as the consequence of hunting pressure (Vigne *et al*. 2016).

<u>From 7700 to 7000 cal BC.</u> This phase starts with a noticeable decrease in the size of the upper cheek teeth, the scapula and radius, the distal extremity of the humerus, and the astragalus. Some of these decreases are only tendencies, others are statistically significant (humerus, talus). Some of them are rapid (humerus: 1–2 centuries, between middle phases A1 and A2), others are slower (talus: 3–4 centuries, between early phases C and middle phase B). They are sometimes accompanied with a drastic increase in size variability (talus: middle phase A1). For the humerus, the size decrease induced an allometric shape change that we cannot interpret as a consequence of introducing a new lineage from the continent. As the age profiles leave no doubt that suid rearing began around ca. 8000 cal BC at the latest, this size decrease can be interpreted either as a belated consequence of domestication or as the consequence of intensified pig rearing since middle phases A1 and A2 are the periods when pig husbandry was the primary animal production of Shillourokambos (Vigne and Carrère 2011). This rearing process preceded the size decrease which occurred 500 years earlier than that evidenced for goats at Shillourokambos and Khirokitia (Vigne *et al*. 2017b).

During the last centuries of the Shillourokambos settlement, pig husbandry decreased. At that time, astragalus and humerus measurements increased in size while the second morphotype observed on the humerus declined. A sudden size increase along with a return to an ancestral morphotype of domestic pigs is unlikely, especially when rearing is still attested on the site by the presence of perinatal bones. We consider that this is due more to the resurgence of wild boar hunting and the consecutive increase of larger bones in the food refuse, leading to a rise in average bone size and the proportion of the humerus ancestral morphotype.

The comparisons we made with Khirokitia indicate that suids further decreased in size between the end of the 8th and the second half of the 7th millennium, probably because of intensified pig rearing. Whereas it seems that the domestic pigs of Shillourokambos are the locally domesticated small Cypriot wild boar, it is more difficult to decide if the Khirokitia suids are of the same lineage or not.

2. GEOMETRIC MORPHOMETRICS

2.1. OBJECTIVES, MATERIAL AND METHOD

To test and specify the different observations made from linear measurements, we developed a geometrical morphometric approach to the dental forms and calcaneus of the Klimonas and Shillourokambos series. Taxonomic resolution of the dental forms at an intraspecific scale (Cucchi *et al*. 2011, 2014, 2020, 2021) allowed us to disentangle the respective components of insularity and domestication at the emergence of the insular form of the Cypriot wild boar. Their phylogenetic signal demonstrated in mammals (Caumul and Polly 2005, Cucchi *et al*. 2017, 2019, Hulme-Beaman *et al*. 2018) enabled us to explore the origin of Cyprus PPN suids by comparing their degree of similarity with different populations of Levantine PPN suids. Finally, the ecophenotypic plasticity of the calcaneum allowed us to detect morphofunctional changes related to the anthropogenic control of Cyprus PPN suid mobility. Recent work has shown that this bone, which is strongly involved in the locomotor behaviour of mammals (Bassarova *et al*. 2009, Ginot *et al*. 2016), can detect the lifetime captivity of a wild ungulate (Harbers *et al*. 2020). Finally, concerning the characterisation of the status of suids, either wild or reared, throughout the 9th and 8th millennia (Vigne 2021 and chap. 29), the combination of these phenotypic markers enabled us to partly answer the question of local domestication

A

Modern samples			
Origin	Taxa	N M/2	N M/3
Corsica	Domestic pig	32	18
	Wild boar	19	5
	Wild Crossed	7	3
Sardinia	Wild boar	9	9
Syria	Wild boar	3	1
Turkey	Wild boar	10	6
Northern Africa	Wild boar	6	5
	TOTAL	**86**	**47**

B

Archaeological samples					
Site	Period	Date cal BC	Code	N M/2	N M/3
Hallan Çemi	PPNA	10,500-8,800	HLC	4	8
Çayönü	PPNA		CAY-PPNA	5	8
Göbekli	PPNA		GOB	1	1
Ain Ghazal	PPNA		AGT	2	1
Çayönü	PPNA		CAY-PPNB	20	17
Nevali Çori	PPNB	8,800-5,700/7,200	NVC	4	5
Tell Halula	PPNB		HAL	9	6
Gürcütepe	PPNB		GUR	1	1
Domuztepe	PN	7,000/6,200-3,300	DOM	2	8
Çayönü			CAY-PN	4	4
Araguina	Middle Neolithic	4,300-3,300	COR-ARA	2	0
Terrina IV	Late Neolithic	3,300-2,500	COR-TER	5	5
Klimonas	PPNA	8,800	KLI	33	26
Shillourokambos middle A	Late PPNB	7,600-7,000	SHI-A	25	12
Shillourokambos middle B	Late PPNB		SHI-B	2	5
			TOTAL	**119**	**104**

Tab. 30-5 – *Modern and archaeological samples for molar geometric morphometrics.* • *Échantillons de référence modernes et archéologiques utilisés pour l'analyse de morphométrie géométrique des molaires.*

or the transfer of domestic suids from the mainland with the new wave of PPNB settlement between 8500 and 7000 BC.

For comparative analysis of the dental forms, we collected images of the second (M/2) and third (M/3) lower suid molars from current and archaeological populations (tab 30-5). The present populations include continental wild boar populations from across the Mediterranean Basin and insular populations of *Sus scrofa* from Corsica (hunted wild boar, traditionally bred southern breed pigs and hunted hybrids resulting from cross-breeding between wild boar and pigs) and Sardinia (wild boar). Corsican and Sardinian suids constitute a useful comparative model to test the resolution of domestication and insularization syndromes on the dental forms because, just like the first suids from Cyprus, humans have shaped their biogeographical history. The settlement of Corsican and Sardinian wild boars' populations is considered to result from individuals being introduced to these islands by the first Neolithic settlers in a domestic or tamed form (Vigne 1988, 1992). The feralization of a part of this livestock is at the origin of the wild boar populations on these islands. Since the Neolithic, hunting and breeding activities have further shaped their evolutionary history, with the gene flow of continental wild boar and the pressure of hunting and cross-breeding with domestic pigs. The scarce genetic and paleogenetic data available show that these tame or domestic suids were introduced from the Near East (Frantz *et al*. 2019, Larson *et al*. 2007). In fact, the mitochondrial signature of southwestern asian wild boar populations has been found in archaeological samples from Sardinia and Corsica, as well as in traditional Corsican pigs (Frantz *et al*. 2019). Corsican wild boars and the traditional Corsican Nustrale pig breed could therefore share a common anthropogenic origin.

The archaeological populations came from 15 Pre-Pottery Neolithic sites in the Upper Tigris and Euphrates Valley, Cyprus (fig. 30-1) and two Corsican Neolithic sites (tab. 30-5). The latter were used as a reference for early insular domestic forms. The Cyprus PPN material includes more than 30 individuals for the Klimonas PPNA and more than 20 individuals for the middle phase A and B of Shillourokombos (tab. 30-5). The anthropogenic choices and the incrustation of the bone material from the ancient phases of Shillourokambos did not allow us to obtain an analysable dental series for geometric morphometrics.

Our archaeological corpus of calcaneus was much smaller to analyse since our morphometric approach relies on the adult calcaneus. Indeed, the morphofunctional signal is located on the bone epiphysis, where the three extensor muscles are inserted to activate the lever role of the calcaneus in the propulsion of movement (Harbers *et al*. 2020). Therefore, we were only able to analyse two individuals from Klimonas, one from the Communal building (SU 10.3) and one from the dwelling area of section B, and six individuals from Shillourokambos from the middle phase B (SU 1001-2) and the late phase (SU 1000) of sector 3 (Vigne and Carrère 2021). The reference corpus for calcaneal analysis included current and archaeological specimens from the ANR DOMEXP (http://anr-domexp.cnrs.fr/) research programme published in Harbers *et al*. (2020). The current corpus includes 28 current wild boars from different populations of western Europe and 28 Mesolithic wild boars from 5 sites in the north and south of France to cover a wide variation of the wild phenotype within pre-Neolithisation and pre-anthropisation habitats. The corpus also includes 18 extensively and industrially reared pigs and 24 experimental wild boars, captured in the wild after weaning (6 months) and reared in captivity until 2 years of age (see Harbers *et al*. 2020 for the detailed experimental protocol details).

We used geometric morphometrics to capture the morphological complexity of the two phenotypic markers and thus increase the biosystematics resolution. This approach, based on cartesian coordinates in 2 or 3 dimensions, not only allows us to precisely quantify the variation of a complex form but also to preserve and visualise its geometry during the analysis (Baylac 1993; Cucchi *et al*. 2015).

The M/2 and M/3 dental forms were analysed in 2D from images of standardised occlusal views of the molars, combining landmarks on the occlusal surface and semilandmarks along the external outline of the crown's occlusal view, following Cucchi *et al*, 2011, Evin *et al*. 2015 with some adjustments (see Cucchi *et al*. 2021 for full details) The calcaneus was analysed in 3D using a combination of landmarks and semilandmarks on anatomical curves and articulation surfaces for a complete quantification of the calcaneal form (see Harbers *et al*. 2020).

For details of the geometric morphometrics and statistical approaches see appendix 30-15 or Cucchi *et al*. (2021).

2.2. COMPARISON OF THE PPN SUID DENTAL FORMS FROM CYPRUS AND THE CONTINENT

2.2.1. Diversity of the extent insular and continental Mediterranean populations of *Sus scrofa*

Figure 30-22 displays the dental shape space of current Mediterranean *Sus scrofa* comparative material distinguishing different populations (MANOVA M/2: df = 6, F = 4.77, p < 0.001; MANOVA M/3: df = 6, F = 2.69, p <0.005). The differentiation pattern of the shape space is almost identical between the second and third lower molars, with differences linked to the disparity of the sample sizes, suggesting that their variation carries a common signal and that there are, therefore, a priori no or few interpretative discrepancies from one marker to the other.

In this dental shape space, Corsican pig populations are divergent from the Corsican and Sardinian Island boars; however, it should be noted that the Corsican hybrid populations are indistinguishable from the Corsican wild boar. The latter can be distinguished from continental wild boars but are very close morphologically to North African wild boars, suggesting a common population history. Thanks to the variation in dental shapes, it is therefore possible to disentangle differences associated with domestication from those related to the process of population settlement and insularisation.

We observed significant differences (ANOVA: df = 20, F = 12.32, p < 0.0001) in tooth size between the populations in our reference frame (fig. 30-23). The teeth of Corsican and Sardinian wild boar have a strong insular syndrome, whereas Corsican pigs have an intermediate size between insular and continental boar populations. We noted that Corsican hybrid populations have wild dental phenotypes, both in shape and size.

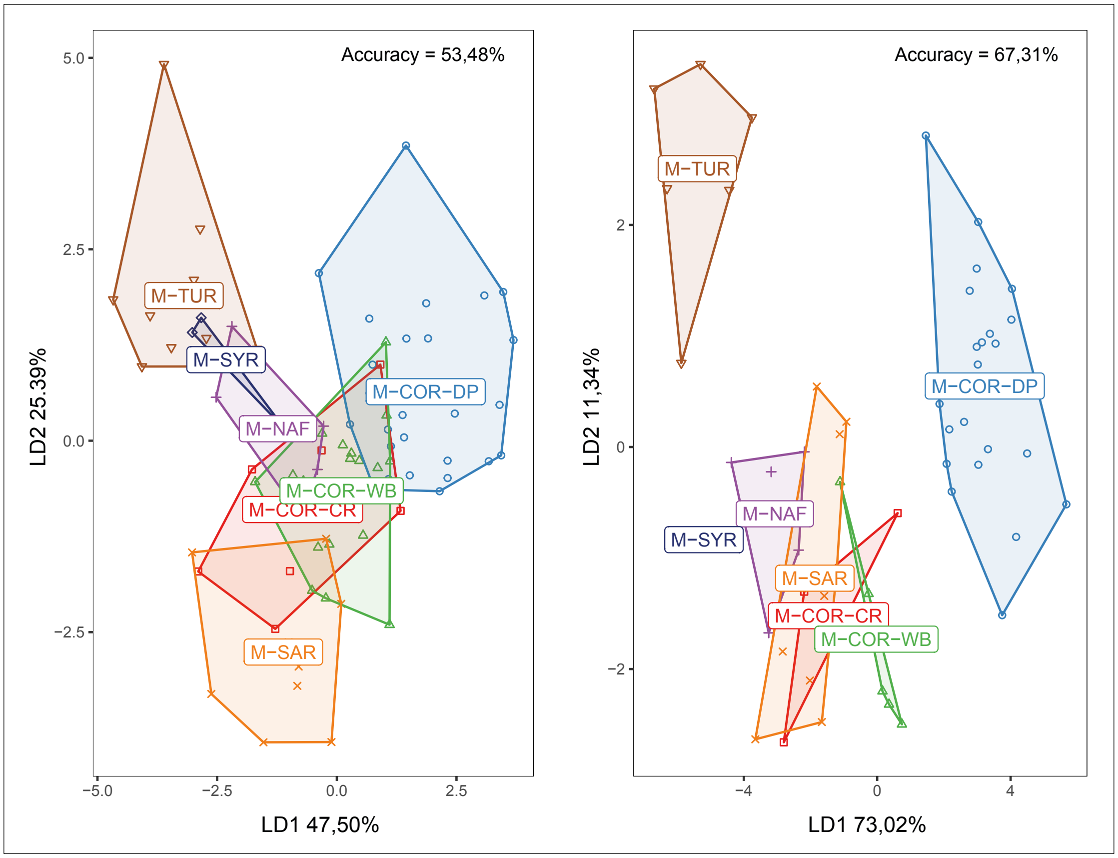


Fig. 30-22 – *Pattern of shape differentiation from the linear discriminant analyses (LDA) of the second and third lower molar for the modern Mediterranean* Sus scrofa *samples. CAD T. Cucchi, CNRS.* • *Patron de différenciation des conformations des seconde et troisième molaires inférieures issus de l'analyse linéaire discriminante pour les échantillons modernes méditerranéens de suidés. DAO T. Cucchi, CNRS.*

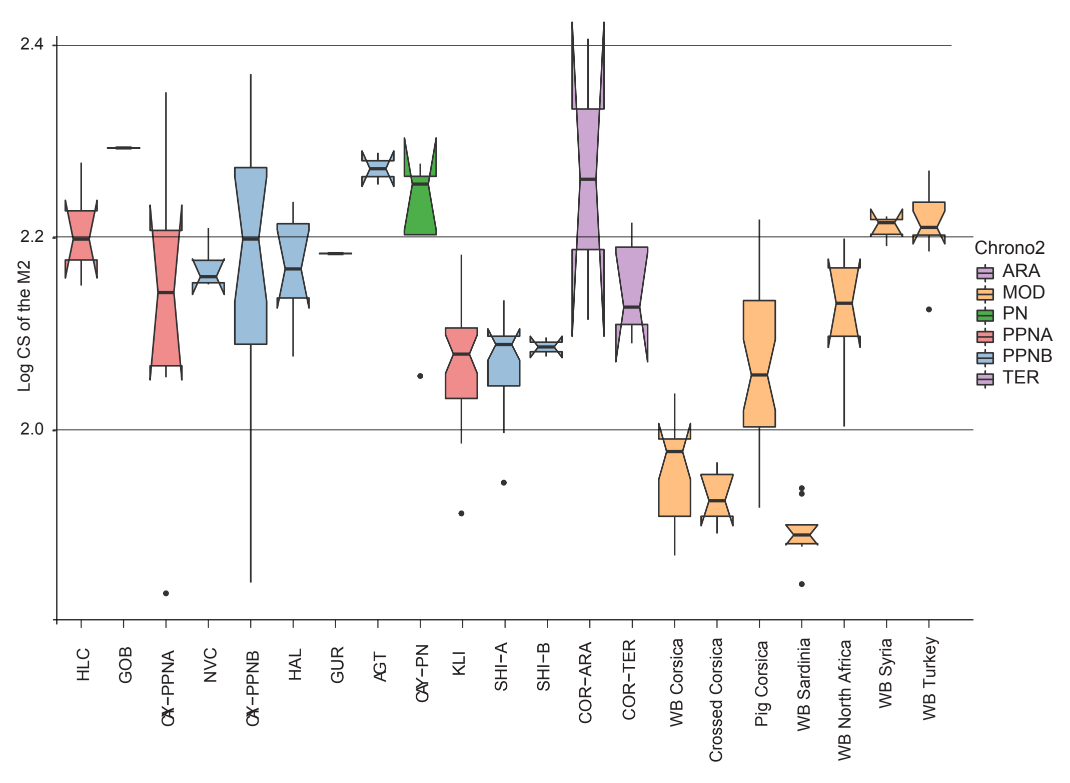


Fig. 30-23 – *Distribution of the M/2 logarithm of the centroid sizes in current and archaeological samples. CAD T. Cucchi, CNRS.* • *Distribution de la variation du logarithme des tailles centroïdes des M2 pour les échantillons actuels et archéologiques. DAO T. Cucchi, CNRS.*

This difference in centroid size between continental, insular, wild and domestic populations has a significant allometric impact (ANOVA Procrustes: df = 1, F = 4.43, $p < 0.001$) and explains nearly 8% of the dental shape variation in our modern corpus. But this allometric trend does not differ from one population to another (MANCOVA size*group: F = -0.4889, p = 0.698). These differences in size, therefore, do not prevent the differentiation between populations of suids based on their dental shape.

According to our dataset, molars size and shape variation patterns among the *Sus scrofa* populations are independently (very little allometry) influenced; therefore, we will associate these two components (size + shape) of the M/2 and M/3 forms by adding the logarithm of the centroid size to the Procrustes (shape) coordinates (Mitteroecker *et al*. 2005). This data set will provide a more complete description of the dental marker's morphological variation and a better resolution of the effects of insularisation and domestication in archaeological remains.

2.2.2. Diversity and similarity of PPN suids dental forms from Cyprus and the continent

Here, we present only the results of the analyses produced on the M/2, which will be occasionally coupled with those of the M/3 to support our interpretation.

The Klimonas and Shillourokombos suids from middle phases A and B have the same M/2 size range (fig. 30-23). Furthermore, Bayesian clustering analysis of the M/2 size variation found a typical unimodal variation suggesting that suids from Klimonas and Shillourokombos belong to an homogeneous population (appendix 30-16). Their small size is within the low variation range of the Çayönü PPNA suids, which are on average smaller than the PPNA suids from Hallam Çemi, Göbekli and the PPNB ones from Nevalı Çori and Tell Halula.

The size reduction in Cypriot PPN suids, linked to insular syndrome, is not as marked as that observed in Corsican and Sardinian populations. These populations are the smallest suids in the Mediterranean Basin and are considered as a separate subspecies, *Sus scrofa meridionalis* (Groves 2007).

When we project the average forms of the archaeological suid populations into the discriminating space of current wild, insular, and domestic suid dental forms (fig. 30-24), we can observe that the PPN suids from Cyprus are associated with the "insular wild boar" morphotype, whereas the continental PPN populations are outside the area of the continental Mediterranean boar-like forms. Our sampling of continental boar forms is, however, too limited to consider the phenotypic diversity of boars from the Eastern Mediterranean area.

The phenotypic relationships between the average forms of modern and archaeological populations (fig. 30-25) provides three important pieces of information:

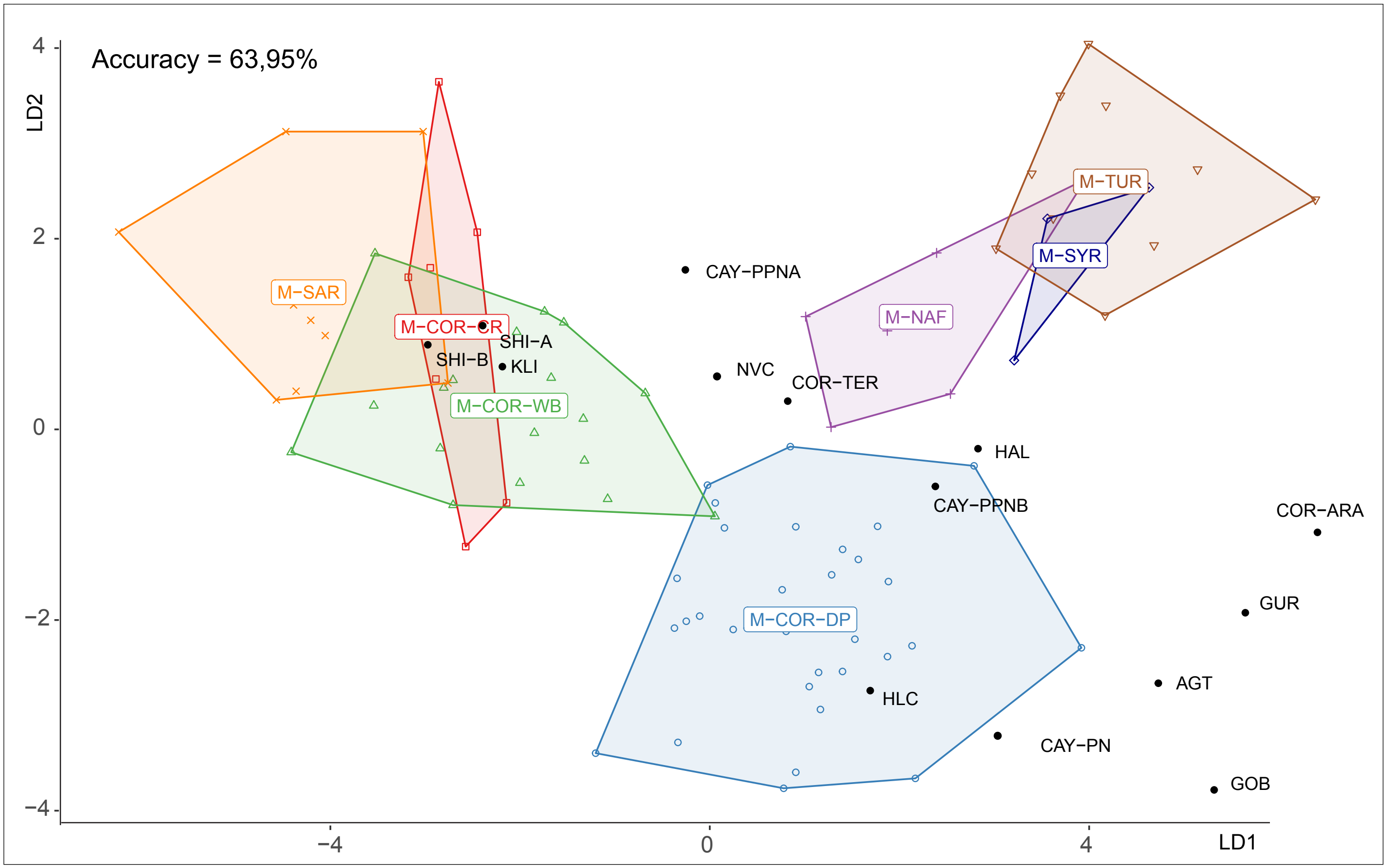


Fig. 30-24 – *Projection of the average forms of archaeological populations in the discriminating space of dental forms (M/2) computed from current wild and domestic populations of continental and insular suids. CAD T. Cucchi, CNRS.* • *Projection des formes moyennes des populations archéologiques dans l'espace discriminant des formes dentaires (M/2) des populations actuelles sauvages et domestiques des suinés du continent et insulaires. DAO T. Cucchi, CNRS.*

- The populations of Klimonas and of the middle phases A and B of Shillourokambos have a very homogeneous dental phenotype.

- This phenotype is intermediate between the wild, domestic and hybrid insular forms of Corsica and the continental PPN and present-day forms.

- M/2 and M/3 display very similar patterns, indicating that the PPN suids from Cyprus are morphologically closer to their PPNA counterparts from Çayönü and the current North African wild boar.

2.2.3. Discussion: the molar form as a marker of natural and anthropogenic evolution

The variation of modern lower M/2 and M/3 occlusal forms shows that within a suid population at the scale of the Mediterranean Basin, the dental forms can distinguish continental populations from the wild and domestic insular populations from Corsica and Sardinia. Within the insular diversity of *Sus scrofa* populations, dental form variation can also distinguish between populations living in the wild and those under anthropogenic selective pressure. The results suggest that these dental markers may allow us to address not only the degree of endemism in Cypriot PPN suids compared to their continental relatives but also whether domestic populations were introduced or not from the continent during the PPN. Although our baseline has been built up from domestic pigs of the traditional corsican breed, we cannot rule out the possibility that genetic introgression of continental breeds such as the Duroc or Large White (Richomme 2009) may have contributed to the observed divergence between wild boar and Corsican pigs. Crosses with continental breeds are frequently used to promote meat production while maintaining hardiness in extensive farming (Dupon 2019). Such a divergence is therefore potentially not observable in the contexts of early domestication.

Among the Corsican suids, crossbreeding between wild boars and pigs does not produce intermediate phenotypes, but hybrids similar in their dental form to wild boar, contrary to what has been shown in previous studies (Evin *et al*. 2015). These hybrid specimens, having been hunted, were therefore bred by a sow according to a wild lifestyle. It is therefore not surprising that in the Corsican Island context, the morphology of these hybrids is identical to that of wild boars.

These are important remarks for addressing the question of a putative introduction of domestic suids from the continent to Cyprus during the late 9th or throughout the 8th millennia.

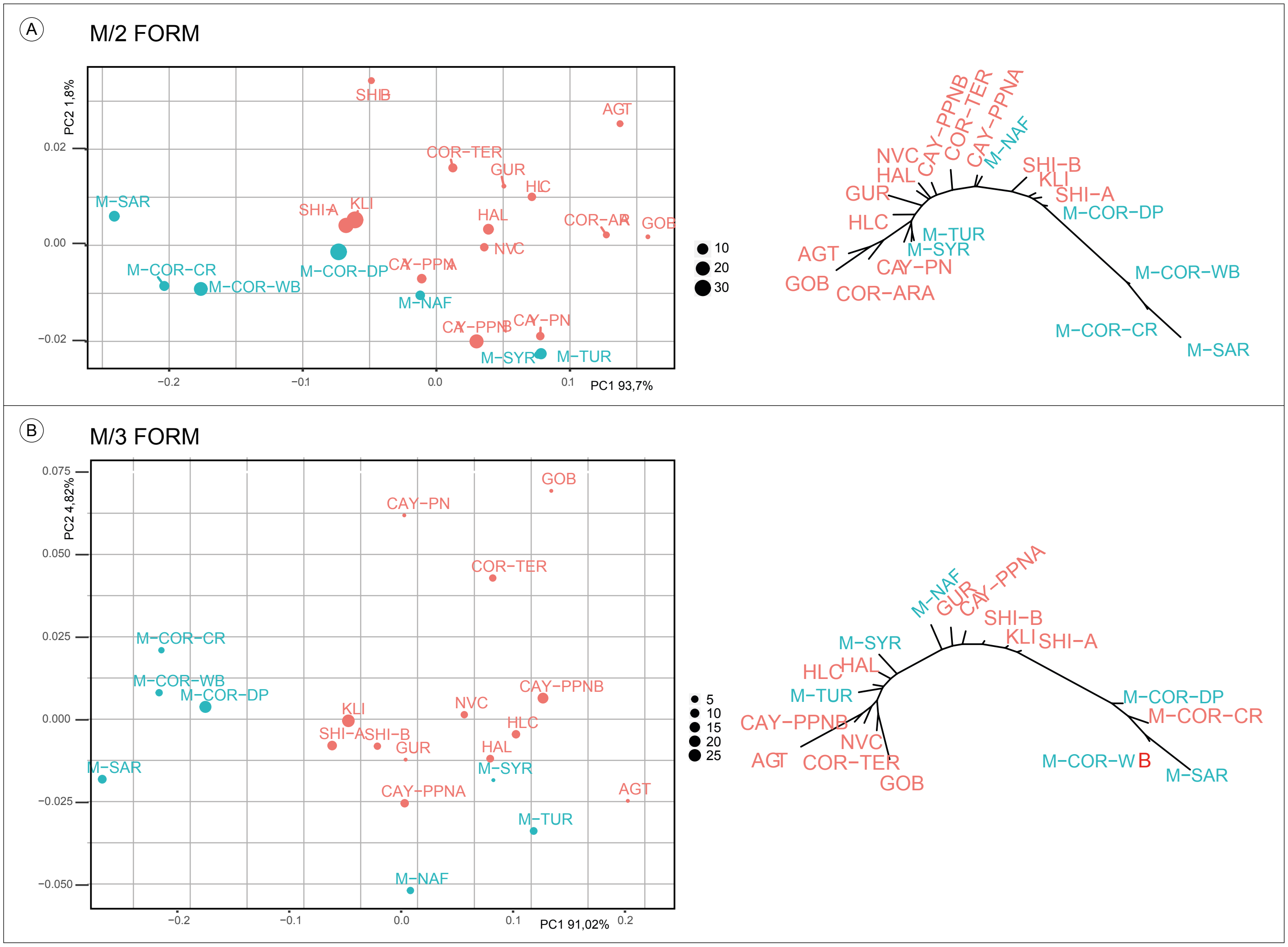


Fig. 30-25 – *Patterns of similarity and dissimilarity between the mean dental forms (M/2 and M/3) of current and archaeological samples, using principal component analysis (PCA, left) and unrooted neighbour joining trees (right). The current populations are displayed in blue and the archaeological populations in red. CAD T. Cucchi, CNRS.* • *Relations de similarité et de dissimilarité entre les formes dentaires moyennes (M2 et M3) des échantillons actuels et archéologiques à l'aide d'une ACP (à gauche) et d'arbres non enracinés calculés (à droite). Les formes moyennes issues de populations actuelles sont représentées en bleu et celles des populations archéologiques en rouge. DAO T. Cucchi, CNRS.*

2.3. CALCANEUS SIZE AND SHAPE VARIATION OF CYPRUS PPN SUIDS

The statistical prediction of Klimonas adult suids and of the middle phases of Shillourokambos in the calcaneal shape space (fig. 30-26) put them within the reaction norms of wild boars, with locomotor behaviour typical of a natural habitat. The only exception is the Shi2 individual, which has the traits of an individual with locomotor behaviour constrained by captivity. The Klimonas suids, therefore, present the anatomical characteristics of individuals with all the locomotor behaviour of wild boar living in a natural habitat, without any mobility constraints.

According to Bayesian clustering analyses, the calcanei centroid size variation of the Klimonas and Shillourokambos suids can be divided into two groups (fig. 30-27). The first group is within the range of variation of the Mesolithic boars of western Europe and the traditional domestic breeds of continental Europe. A second smaller group is within the variation of modern-day wild boar, either hunted or bred in captivity. Only one of the four small individuals displays a shape compatible with a life in captivity, which suggests that captivity is not the main component of the calcaneus size reduction. In addition, we did not observe any reduction in the size of the calcaneus linked to insularity syndrome.

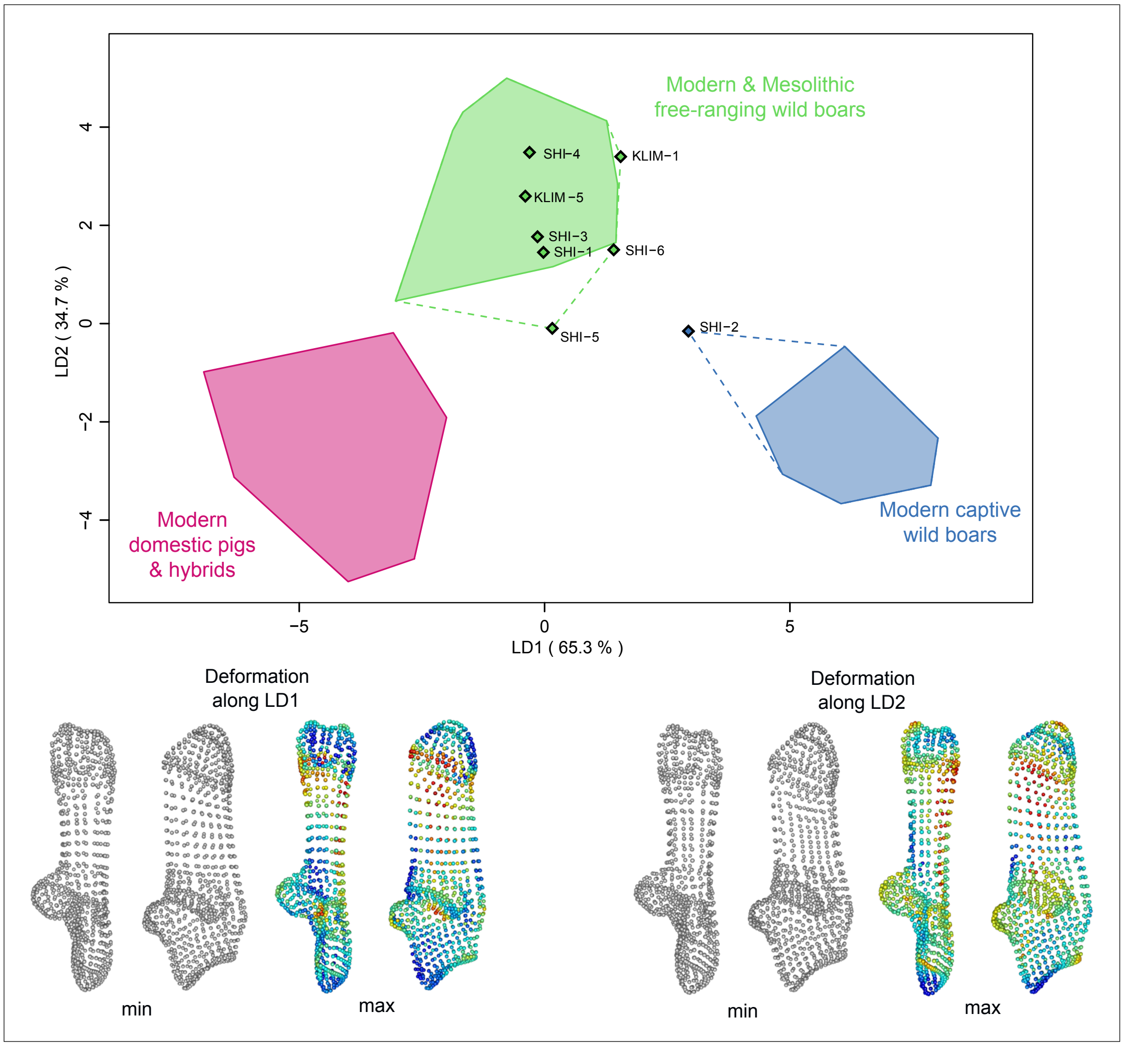


Fig. 30-26 – *Projection of Klimonas and Shillourokombos (black squares) in the discriminant shape space of the calcaneus from wild, captive and domestic* Sus scrofa. *Classification of the archaeological specimens into one of the three groups performed by the k-NN algorithm is represented by dotted lines and the fill colour of the square. CAD T. Cucchi, CNRS.* • *Projection des suinés de Klimonasq et de Shillourokambos (symbole : carré noir) dans l'espace des conformations discriminantes des* Sus scrofa *sauvages, captifs et domestiques. La classification des spécimens archéologiques à l'un des trois groupes par l'algorithme des K NN est représentée par les pointillés et la couleur de remplissage du carré. DAO T. Cucchi, CNRS.*

3. GENERAL DISCUSSION AND CONCLUSIONS

3.1. COMPLEMENTARITY OF THE TRADITIONAL, MULTIVARIATE, AND GEOMETRIC MORPHOMETRIC APPROACHES

To address the three questions listed in the introduction (particularities, origins and domestication of the small Cypriot wild boar represented at Klimonas), we applied three different and complementary approaches:

- Traditional univariate or bivariate analyses and comparisons of linear measurements allowed us to consider numerous skeleton components and, therefore, to have the most comprehensive vision of the whole body, including global size and allometries between the different parts of the body. Conversely, this approach is of low resolution because it reduces the complex morphological information to a small number of measurements without any possibility of studying the geometric relationships between them. It also fails to approach shape and size separately.

- Owing to the extraction of isometric size and Log Shape Ratios, multivariate analyses of the same linear measurements enabled us to separately study isometric size and shape, as well as the allometric relationships between them; this resolution is thus much better than the former one, but it is also based on poorly informative, unstructured, and linear measurements. In addition, it can only be applied to skeletal parts with at least four measurements, which reduces both the number of specimens taken into consideration and the anatomic scope: we could apply this protocol only to the distal humerus, the talus and the first and second phalanges, i.e. four skeletal parts;

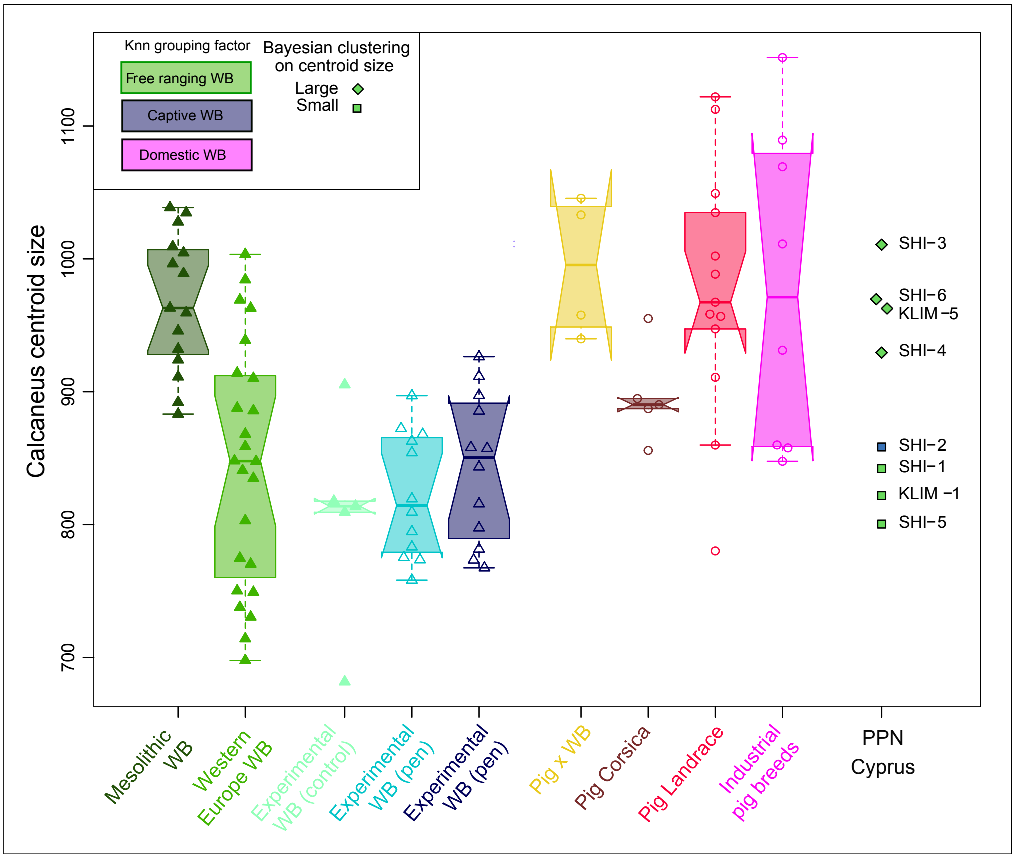


Fig. 30-27 – *Centroid size variation of the calcanei of wild, captive and domestic* Sus scrofa *compared to the PPN specimens of Cyprus, represented according to their k-NN classification as wild, domestic or captive status and according to a Bayesian classification of their size group. CAD T. Cucchi, CNRS.*

• *Variation de la taille du centroïde du calcanéum de* Sus scrofa *sauvage, captif et domestique par rapport aux spécimens PPN de Chypre. Les spécimens du PPN sont représentés selon leur classification KNN en tant que sauvages, domestiques ou captifs et selon une classification bayésienne de leur groupe de taille. DAO T. Cucchi, CNRS.*

- The geometric morphometric approach requires more time and technicity; this is why we applied it to a reduced number of anatomic parts, i.e. the molars and the calcaneus, which are, however, very informative in terms of both phylogenies and behaviour; besides, they allowed us to separate or associate study shape and size components of the form to provide a far richer morphological information than the linear measurement, with perfect preservation of the geometric relationships between the landmarks. The results are thus of a much higher resolution for the intraspecific issues that we addressed here.

Furthermore, because the protocol for recording the osteometric data for the two first approaches (i.e. measurement with a calliper) is different from that of the geometric morphometrics (3D coordinated of landmarks), the continental and insular corpus for comparisons with modern and archaeological wild boars are partly different, making these comparative approaches larger and richer. This also strengthens our results showing that the three approaches converge towards the same conclusions, which they do.

3.2. TO WHAT EXTENT CAN THE KLIMONAS SUIDS BE CONSIDERED A NEW INSULAR SUBSPECIES?

Altogether, our morphometric analyses have highlighted the morphological idiosyncrasies of the Klimonas wild boar, leading us to consider it as an endemic lineage which lived in Cyprus from ca. 10,500–10,000 to 8500–8000 cal BC, at least.

- Small size. According to 23 linear measurements and 6 isometric size estimates, the size of the Klimonas wild bar is on average 13.3% smaller than the PPN middle and north Levant wild boars. This confirms previous preliminary studies (Vigne *et al*. 2012), which we interpreted as an insular syndrome following Van Vallen (1973).

- Partial loss of locomotor capabilities. The size reduction compared to the continent was more important for the limb extremity bones, especially for the abaxial fingers (ca. -20%). This is most likely the expression of the second insular syndrome of Van Vallen (1973). Here, we propose to explain these features by (i) release of predation pressure and fast flight capabilities and (ii) by the partial functional loss of the abaxial phalanges (dewclaws) for swimming or for preventing the risk of sinking into soft ground.

- Typical insular morphology of the molars. The shape, size and form of the 2nd and 3rd lower molars significantly diverge from the PPN continental populations along an evolutionary trajectory directed towards insular wild boar phenotypes, as we have seen with the Corsico-Sardinian suids, rather than an adaptation to local ecological conditions resulting from local genetic drift.

- Possible other endemic traits. We also bring out some other small shape differences between the wild boars of Klimonas and their continental counterparts (more robust distal humerus and slender astragalus). As they are not correlated with the small size, they can be considered as possible endemic characters; however, without comparison with other island populations, we cannot conclude that they are due to insularity. Also, a slightly higher sexual dimorphism than that of modern and archaeological populations of continental wild boar may result from insularity, as an adaptation aiming to reduce the intraspecific competition between males and females.

The first three observations, and maybe the fourth, indicate that the PPN Cyprus wild boar displayed a significant degree of endemism, resulting from a rapid insular evolution. This was probably due to the small size of the founding population which, without the contribution of new continental inputs during these two millennia, accumulated genetic drift and adaptive processes. Adaptation could have been driven by a strong release of both predation (only small groups of humans) and interspecific competition (no other ungulate on Cyprus before 8500 cal BC), a consecutive widening of the ecological niche to more diverse landscapes with hard ground (including hilly and mountainous ones) and to the two rainy seasons of the dry Mediterranean climate, which already existed at that time (Hadjikoumis *et al*. 2018).

The Akrotiri dataset is very small and only concerns distal phalanges, which clearly appeared to be significantly smaller than the phalanges of the PPN Levantine wild boar (Vigne *et al*. 2009*;* Vigne 2011c). As we know that the wild boar could not have been introduced to Cyprus before 10,500 cal BC (Zazzo *et al*. 2015), this is an indication that the morphological evolution due to insularity started very quickly, as it often does in such situations (Millien, 2006, 2011, Cucchi *et al*. 2014). Nonetheless, we demonstrate that the size reduction of the abaxial phalanges increased between ca. 10,000 cal BC (Akrotiri) and 8800 cal BC (Klimonas), suggesting that the process went on during the 10th millennium, for which we have no data, and reached a kind of stasis sometime between the 10th and the 9th millennium.

Altogether, the morphological idiosyncrasy of the Klimonas wild boar associated with insular endemism and the evidence we collected on the environmental context and evolutionary processes make it possible to propose that this Cypriot lineage represents a separate subspecies, equivalent to the *S. scrofa meridionalis* of the Corso-Sardinian Islands. With reference to Circe, the goddess of metamorphosis, who temporary transformed Ulysses' crew into small pigs, we propose to name it *Sus scrofa circeus* Cucchi et al. 2021.

3.3. WHAT IS THE GEOGRAPHICAL ORIGIN OF THE CYPRIOT WILD BOAR

One of the consequences of this rapid evolution of island mammals is that they are so distinct from their continental ancestors that the latter are impossible to identify (Millien 2006, Cucchi *et al*. 2014). Analysis of the dental form shows that the evolutionary divergence connected to the insularisation of the Cypriot PPN suids did not reach the degree of endemism of the current Corsican suids, and that it is still possible to observe phenotypic proximities with the continental PPN populations. Indeed, the similarity of dental form patterns indicates that the PPN populations of Cyprus are closer to the PPN wild boars of Çayönü. Based on the phylogenetic signal in the dental forms (Cucchi *et al*. 2017, 2019), these results suggest northern Mesopotamia (northern Levant) and the Upper Tigris Valley as the likely location of the continental strain of these Cypriot suids. Analyses of the linear measurements of the phalanges tends to confirm this proposal, as they exclude Cafer Höyük as a possible origin of the Cypriot wild boar because of its smaller size and slender conformation of the diaphysis.

Certainly, these results should be taken with caution as our corpus for the southern Levant is limited to a single site (Ain Gazhal) and should include sites such as Ain Mallaha (Final Natufian), Jericho (PPNA), or Tell Aswad to be more convincing. Nevertheless, the Upper Tigris Valley is, to date, the region for which we have the oldest evidence of tamed suid populations (Redding and Rosenberg 1998, Peters *et al*. 2005, Price and Hongo 2019). Therefore, it seems much more likely that the Epipalaeolithic hunter-gatherer communities that introduced the wild boar to Cyprus came from a geographical area extending from the lower foothills of the eastern Taurus to the Syro-Lebanese coast. In this region, an intensification of the relationship between humans and suids via a control-type interaction model of wild populations may have existed since the end of the Younger Dryas (Vigne *et al*. 2011c).

3.4. WERE THE PPNB PIGS OF CYPRUS LOCALLY DOMESTICATED OR INTRODUCED FROM THE CONTINENT?

Our analysis of the calcaneal form of Klimonas and Shillourokambos boars compared to the shape space of Mesolithic and present-day western European boars, captive-bred boars and pigs of traditional and industrial breeds indicates that all the Klimonas specimens show a morphology typical of individuals displaying the locomotor behaviour of boars living in their natural environment (Harbers *et al*. 2020). If any further confirmation is needed, this confirms that the acquisition of these specimens for meat consumption was indeed carried out through hunting, as indicated by the sex balance and the typical mortality profiles discussed in chap. 29 (see also Vigne *et al*. 2017b).

The calcanei from the middle phase B and late phase (7400–7000 cal BC) of Shillourokambos that we were able to study all present the phenotype of individuals acquired through hunting, except for one individual whose form is typical of an individual that has grown up in captivity. This result suggests that there was indeed a practice of confinement of all or part of the herd of domestic suids at Shillourokambos. It is conceivable that the enclosure trenches of early phase B at Shillourokambos, as early as 8000–7600 cal BC (Guilaine *et al*. 2011) could have been used for pig rearing to protect crops. Convincing age-at-death evidence also pleads for an incipient suid rearing between 8000 and 7600 cal BC, and for its intensification during the middle phases, with seasonal culling typical of the dominant practice of breeding suids (Vigne 2011c, 20211b). The morphometric results obtained on the calcaneus for the following period suggest that there were two strategies for acquiring suids at the end of the occupation of Shillourokambos, one based on hunting and the other based on the seasonal slaughter of individuals reared in the vicinity of domestic spaces. The scarcity of calcaneus showing marks of captivity confirms that we could only consider adult bones, most of the reared pigs being slaughtered much younger than the hunted wild boars.

All the linear measurements and the isometric size estimates coming from the Log Shape Ratio analyses indicate that the suids covering the different phases of Shillourokambos and Khirokitia were approximately in the same size range as their counterparts from Klimonas. They are thus much smaller than the PPN continental wild boars. In more detail, we observed a slight trend in size fluctuations. The first is an increase between Klimonas and the early phases of Shillourokambos, probably due to greater hunting pressure. The second is a decrease between the end of the early and middle phases of Shillourokambos (i.e. between 7800 and 7400), likely due to the domestication process. The size is then similar to that of contemporary domestic pigs from Halula in the Middle Euphrates Valley. At the end of the middle phases (middle phase B) at Shillourokambos, the average size increased slightly, probably due to the return of hunting practices, which brought the larger bones of the local Cypriot wild boar into the village middens. This observation is congruent with the conclusions from the analysis on Shillourokambos suid mobility according to calcaneus form.

Excepting the allometric consequences of this size decrease on the morphology of the distal humerus due to domestication, we could not find any shape difference between Klimonas and all the phases of Shillourokambos based on the Log Shape Ratio analyses of the humerus, talus and phalanges. Conversely, we could find shape differences between Cyprus and the continent with the same types of measurements and procedures. This suggests that the suid lineage was very stable between 8800 (Klimonas) and 7000 BC (end of Shillourokambos), without any external (= continental) input, and that the Cypriot PPN people locally domesticated the Cypriot wild boar.

This is supported by the more powerful technique of geometric morphometrics. Indeed, the dental form homogeneity of the Klimonas and Shillourokambos *Sus scrofa* samples strongly confirms that there was no input of domestic populations coming from the continent during the transition to the early and then to the middle PPNB. Such an introduction would have induced an observable divergence between the PPNA and the PPNB dental forms of the Cypriot suids. The endemism of the Shillourokambos middle phase suids, the existence of penning in this period based on calcaneal form, the seasonal slaughtering based on age profiles and the abundance of foetal and perinatal individuals (Vigne 2021b) suggest that the PPNB villagers of Cyprus implemented herding practices inherited from their continental relatives on the local small endemic Cypriot wild boar, *Sus scrofa circeus*, present on the island since 10,500 cal BC.

We found no detectable evidence for the introduction of the early domestic pigs in Cyprus despite their occurrence in the Levant, either south (Jordan Valley), middle (Damascus area) or north (Middle and Upper Euphrates Valley; see Arbuckle 2016 for a recent overview). This may appear surprising, since we found evidence of the introduction of the early domestic lineages of goat, cattle and then sheep from the continent between 8500 and 7800 cal BC (Vigne *et al*. 2011c). The main differences are that the wild boar had been present in Cyprus for several millennia and was the only game since the PPNA. This may explain why it was easier for the PPNB Cyprus villagers to domesticate the local lineage rather than to import exotic animals and adapt them to the Cypriot climate (Hadjkoumis *et al*. 2019), exactly as they did for feral goats later, in the second half of the 8th millennium (Vigne *et al*. 2017b). Wild boar and later the feral goat, which played an important economic and symbolic role as game in the PPNB life, were locally domesticated. In contrast, species that were not part of the Cyprus bestiary were introduced as domesticated from the continent.

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KLIMONAS-Ch30-A02, https://doi.org/10.34847/nkl.dadfx028
Sus scrofa *ssp. Measurements of the upper cheek teeth of Klimonas* • Sus scrofa *ssp. Mesures des dents jugales supérieures de Klimonas*
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KLIMONAS-Ch30-A03, https://doi.org/10.34847/nkl.8a8e7urf
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KLIMONAS-Ch30-A06, https://doi.org/10.34847/nkl.8f3967b4
Sus scrofa *ssp. Measurements of the carpal bones of Klimonas* • Sus scrofa *ssp. Mesures des os du carpe de Klimonas*
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KLIMONAS-Ch30-A07, https://doi.org/10.34847/nkl.c326ri69
Sus scrofa *ssp. Measurements of the pelvis, femurs and tibiae of Klimonas* • Sus scrofa *ssp. Mesures des pelvis, fémurs et tibias de Klimonas*
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KLIMONAS-Ch30-A08, https://doi.org/10.34847/nkl.70aaqcdh
Sus scrofa *ssp. Measurements of the tarsal bones of Klimonas* • Sus scrofa *ssp. Mesures des os du tarse de Klimonas*
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Sus scrofa *ssp. Measurements of the metapodials of Klimonas* • Sus scrofa *ssp. Mesures des métapodes de Klimonas*
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KLIMONAS-Ch30-A10, https://doi.org/10.34847/nkl.dd199rua
Sus scrofa *ssp. Measurements of the first axial phalanges of Klimonas* • Sus scrofa *ssp. Mesures des premières phalanges axiales de Klimonas*
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KLIMONAS-Ch30-A11, https://doi.org/10.34847/nkl.7e45zj5j
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KLIMONAS-Ch30-A12, https://doi.org/10.34847/nkl.8148237r
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