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CRANIOMETRIC CHARACTERISTICS OF THE SUBGENUS *Sus* LINNAEUS, 1758 AND A SYSTEMATIC CONCLUSION

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ABSTRACT

The species *Sus scrofa* Linnaeus, 1758 differs completely from others species of the subgenus (*Sus barbatus* Muller 1838, *Sus verrucosus* Muller 1840, and *Sus celebensis* Muller 1840) in the shape of the lower canine tooth at the alveolus, and its division into two species groups differentiated by these characteristics is reasonable. The systematic status of the *Sus papuensis* Lesson and Garnot, 1926 is confirmed and it is reasonable to include it as a subspecies of *Sus scrofa.* An analysis of the differences in skull size and shape indicates distinctions between the species of the subgenus; but this morphological structure is variable and it cannot be used as a secure criterion in taxonomy. A sexual dimorphism is revealed in skull size in subgenus *Sus barbatus* while in *Sus celebensis* a sexual dimorphism is revealed in skull size and shape. The wild *Sus scrofa* was domesticated over its entire range and presently, exists in four forms - domestic cattle-shed, domestic semi-wild, feral, and wild.

Key words: skull, subgenus, *Sus barbatus, Sus celebensis*, *Sus papuensis, Sus scrofa, Sus verrucosus,* systematics, taxonomy.

INTRODUCTION

The problems associated with subgenus *Sus* L. 1758 taxonomy follow Genov (1999). In addition to *Sus scrofa*, there are other three species belonging to the subgenus *Sus*, which inhabit South-Eastern Asia: *Sus verrucosus* inhabiting Java and Beaven islands (Blouch 1993); *Sus barbatus* Muller 1838 is distributed on the continent, in West Malaysia and islands of Sumatra, Calimantan, Balabac Palavan and other small islands (Caldecott et al., 1993); *Sus celebensis* that inhabits island groups of Sulavezi, Flores, Timor and was moved to the islands of Simeulue and Nias (Macdonald 1993). Recently, the species *Sus philippensis* and *Sus cebifrons*, which inhabit the Philippine islands, were also described by Groves and Grubb (1993). Groves et al. (1997) have rediscovered *Sus bucculentus* Heude 1892 inhabiting South Vietnam, which was earlier described by Heude (1892). Hence, the number of species of that subgenus has increased from four to eight (Groves 1981, Oliver 1995, Groves et al. 1997).

To make *Sus* taxonomy clearer, cytogenetic and biochemical investigations were performed over the last twenty years. All domestic pigs, as well as *Sus verrucosus, S. barbatus, S. celebensis* and *S. salvanius* have 38 chromosomes (Bosma et al. 1984, 1991).

The aim of this study is to critically evaluate the results obtained from previous studies. In so doing, we evaluated (i) some principal craniometric taxonomic signs that were used as diagnostic tools for the determination of particular species in subgenus *Sus*, (ii) the systematic status of *Sus papuensis*, (iii) the influence of chromosome number on the taxonomy of particular species in the subgenus *Sus*. Since no other study has performed the classical biometric analysis on such a large number of specimens, first we applied these methods to the entire sample using a standardized statistical procedure; second went a step further by using a larger number of skull measurements and an array of shape indexes. The use of both kinds of variables is useful because two taxonomic units can differ in size or, if of similar size, can have different cranial shapes, i.e. different between-trait ratios. The large number of variables involved in this analysis made it necessary to use multivariate statistical methods.

MATERIALS AND METHODS

Materials

The age of the specimens was determined on the basis of the stage of growth of the third molar tooth. That molar is completely developed at the age of four years (Genov et al. 1992). After the fourth year, the size of the skull remains largely unchanged (Kozlo 1975); therefore, only specimens four years and older were included in the analyses.

Measurements were taken on 649 skulls [387 males skulls (upper and lower jaws) and 262 female skulls)] of the species *Sus scrofa*; four skulls of the first generation male hybrids (*Sus scrofa* x *Sus scrofa domestica* = F1); three skulls of male and four of female specimens of the second generation hybrids (*Sus scrofa* x F1); seven skulls of male specimens of European domestic pig; seven skulls of male specimens of the semi-wild Indonesian domestic pig (*Sus celebensis domesticus* x *Sus celebensis*); 11 skulls of male specimens of the species *Sus papuensis*; 11 skulls of male and eight skulls of female specimens of the species *Sus celebensis*; 17 skulls of male specimens of the species *Sus verrucosus*; 16 skulls of males and 10 of female specimens of the species *Sus barbatus*. Thus, we measured 476 crania of male and 284 of female specimens of the subgenus *Sus*.

To specify the shape of the lower canine tooth at the alveolus, the measurements of its walls for the following species and subspecies of the wild boar were done: *Sus* *barbatus* - 10, *Sus celebensis* - 8, *Sus papuensis* - 9, *Sus verrucosus* - 12, *Sus scrofa attila* - 20, *Sus scrofa majori* - 22 and *Sus scrofa vittatus* - 12.

Methods

The wild boar skulls were measured using a pair of calipers (accuracy 0.01 mm and a ruler - 1 mm); 31 sizes were found, (see Genov 1999). Furthermore, to compare not only the skull size of specific groups, but also their shape, the following indices were used for each variable, for a total of 22 indices, (see Genov 1999).

Statistical procedures include Factorial Analysis, Discriminant Analysis, and Cluster Analysis (see Genov 1999).

RESULTS

Analyses and verification of normal distribution and a correlation of data

The measurements revealed that only very few of the parameters (31 for male, 30 for female specimens, and 22 indexes as well) have a normal distribution in both data collections (i.e., the right side of the average value is symmetrical to the left). The first analysis of the species, cross-breeds, wild-grown, and domestic pig of the subgenus *Sus* (476) male specimens showed that only the following parameters have a normal distribution: W3, W8, W12, W13, W15, W20, W22, W26 and indexes B - 1:11, G - 1:22, P - 15:16, R - 19:20, S - 24:26, T - 24:27, or 25,8% of the first group and 27.3% of the second. For female specimens (n = 284) we have W3, W6, W8, W12, W13, W16, W20, W22; A - 1:10, B - 1:11, C - 1:12, E - 1:15, F - 1:16, G - 1:22, V - 28:29, Z - 29:31, i.e., 27.6% and 36.4% respectively.

The second analysis of a correlation between the variables and their indexes indicated that there was a high degree of correlation for both sexes, i.e., 95.0% for male specimen variables and 89.7% variable indexes, for 88.1% indexes and for female specimens 98.6%, 73.5% and 69.0% respectively.

Size and proportion of the walls at the alveolus of the lower canine tooth of male specimens of different subspecies of **Sus scrofa** *and between the species of the subgenus* **Sus**

Measurements of the average size of the walls of the lower canine tooth show that the subspecies of *Sus scrofa,* as well as the subspecies of *Sus papuensis*, have smaller sizes of the front wall compared to the back wall. The opposite is true for the species *Sus verrucosus*, *celebensis* and *barbatus* (Table 1). The above characteristic defines the form of the cross-section of this tooth near its border with the tendon and, in the past, it was used to divide the subgenus into the groups indicated, above. If we compare the indexes obtained between the walls of the tooth of different species, in two of the cases (1 - proportion of back to front walls, and 2 - proportion of front wall to inner wall) then the above two species groups of the subgenus clearly emerge. In the third case, *Sus papuensis* differs from the others, and occupies an intermediate position. On the other hand, it is interesting to note that the comparison is made at the level of subspecies of *Sus scrofa* and of other species a following transition can be observed. The species *Sus papuensis* and *Sus scrofa vittatus* do not show any statistical difference in the proportions of back to front and back to inner walls, yet both forms differ from *Sus scrofa attila* (Table 2).

TABLE 1
The average size of the walls of the lower canine tooth of the subspecies of *Sus scrofa* and of the species of subgenus *Sus*.

Species and subspecies	N	Back		Inner		Front	
		X	±	X	±	X	±
Sus scrofa	55	159.0	3.2	122.2	1.6	210.7	3.6
Sus scrofa majori	22	155.3	5.6	118.7	2.2	210.7	6.2
Sus scrofa attila	20	171.6	4.4	123.2	2.5	222.4	5.5
Sus scrofa vittatus	13	145.8	4.3	126.8	3.6	192.8	4.7
Sus papuensis	9	158.8	10.8	132.4	5.1	200.8	10.9
Sus celebensis	8	114.9	5.1	154.3	7.0	174.5	8.0
Sus verrucosus	10	133.6	3.9	171.8	4.1	203.6	4.9
Sus barbatus	12	148.8	7.4	194.7	9.2	226.1	9.9

TABLE 2
Differences in the subspecies of *Sus scrofa* and the species of the subgenus *Sus* depending on the proportions between the particular walls of the lower canine tooth:
1 - back: inner walls, 2 - Inner: front, 3 - Back: front.

Species and subspecies	N	1	2	3	1	2	3
Sus scrofa	55	*	*	*	-	-	-
Sus scrofa attila	20	-	-	-	*	*	*
Sus scrofa majori	22	-	-	-	**	*	*
Sus scrofa vittatus	13	-	-	-	**	*	*
Sus papuensis	9	*	*	*	*	*	*
Sus celebensis	8	*	*	*	*	*	*
Sus verrucosus	12	*	*	*	*	*	*
Sus barbatus	10	*	*	*	*	*	*

Discriminative analysis of indexes between the walls at the alveolus of the lower canine tooth of male specimens of subspecies of Sus scrofa *and the species of the subgenus* Sus

This analysis was performed to establish whether there is a difference in the form at the alveolus of the lower canine tooth of particular species and to what extent this characteristic is valid, and what is the connection between them. The results show that there is a connection between the first three species. *Sus verrucosus* manifests a larger variability. The second group is formed by the last two species. It can be observed that this characteristic clearly distinguishes those species from the first three (Table 3). As in the species *Sus scrofa*, specimens of three subspecies are included, i.e., of *S. s. majori* inhabiting the western region of the habitat, of *S. s. attila* inhabiting the central region, and of *S. s. vittatus* inhabiting the east region, and areas in the neighborhood of the species *Sus papuensis,* a discriminative analysis of the above subspecies was made. The purpose was to determine whether a relationship exists between them. The results showed that the last two forms are closer to each other than to the first two species: 44.4% of the specimens of the species *Sus papuensis* come under the subspecies *S. s. vittatus* and 25.0% of the specimens of this subspecies were allocated to the species. Even though specimens of the first two sub species occur in all investigated taxonomies, these results lead to the conclusion that the species *Sus papuensis* belongs to the group «*scrofa*» even though *Sus papuensis* has no common ground with the subspecies of the species *Sus scrofa.* (Table 4).

TABLE 3
Discriminative distribution of the species of the subgenus *Sus* depending on the size of the walls at the alveolus of the lower canine tooth.

	1		2		3		4		5		
Species	N	%	N	%	N	%	N	%	N	%	N
1. *Sus barbatus*	8	80.0	1	10.0	1	10.0	-	-	-	-	10
2. *Sus celebensis*	1	12.5	6	75.0	1	12.5	-	-	-	-	8
3. *Sus verrucosus*	2	16.7	2	16.7	8	66.6	-	-	-	-	12
4. *Sus papuensis*	-	-	-	-	-	-	8	88.9	1	11.1	9
5. *Sus scrofa*	-	-	-	-	-	-	11	20.4	43	79.6	54

TABLE 4
Discriminative distribution of the species *Sus papuensis* and subspecies *S. s. majori, attila* and *vittatus*, depending on the size of the walls at the alveolus of the lower canine tooth

Species and subspecies	1		2		3		4		
	N	%	N	%	N	%	N	%	N
1. *Sus s. majori*	9	40.9	8	36.4	3	13.6	2	9.1	22
2. *Sus s. attila*	5	25.0	13	65.0	1	5.0	1	5.0	20
3. *Sus s. vittatus*	1	8.3	1	8.3	7	58.4	3	25.0	12
4. *Sus papuensis*	-	-	-	-	4	44.4	5	55.6	9

Factor analysis of cranium parameters among the species, cross-breeds, feral, and domestic pigs of the subgenus Sus

Sexual dimorphism among specimens of different species

According to the first factor established a sexual dimorphism of the *Sus barbatus* and *Sus celebensis*. A sexual dimorphism was also observed for those species for the second factor. Remaining factors do not lead to any differences between the sexes. There is a difference between the sexes in the case of the second generation cross-breeds (F2) for the second factor.

Comparative analysis among the particular species, cross-breeds, feral and domestic pigs of the subgenus Sus*, applying the first four factors*

Based on this analysis, regardless of the sex of the specimens (for a part of the taxonomies the crania of female specimens are missing) a difference was established for cranium size and shape of the investigated taxonomies. Those results were compared with the results obtained for male specimens and no difference between them was found. For that reason, we present the results obtained from an analysis of the entire cranium material (Table 5).

For all four factors the following differences between the species were found: *Sus barbatus* - *Sus scrofa, Sus celebensis ferus, Sus papuensis* and *Sus celebensis*; *Sus scrofa domesticus* - *Sus celebensis ferus* and *Sus celebensis*. For three factors, including the size and shape (123 and 124), the follow differences between the species were found: *Sus scrofa* - *Sus scrofa domesticus, Sus papuensis* and *Sus celebensis*; *Sus scrofa ferus* - *Sus celebensis* and *Sus barbatus*; *Sus papuensis* - *Sus scrofa domesticus*. With shape only for three factors, the following differences were observed: *Sus verrucosus* - *Sus scrofa*, *Sus scrofa domesticus* and *Sus barbatus; Sus barbatus* - F2. From all species, only the species *Sus scrofa* and *Sus barbatus* differ according to the second factor. No difference was found between the species *Sus verrucosus* and F2, as well as between the species *Sus celebensis* and *Sus celebensis ferus* (Table 5).

TABLE 5
Differences between the particular species, hybrids, feral and domestic pigs, based on the factors 1-4, independently of the specimen's sex of the subgenus *Sus*.

Taxon	1	2	3	4	5	6	7	8	9	10
Sus scrofa		12	2	124	2	12	124	123	234	1234
F1	12		2	2	1	1	12	1	2	23
F2	2	2		24	2	1	1	13	-	234
Sus scrofa domesticus	124	2	24		12	1234	124	1234	234	23
Sus scrofa ferus	2	1	2	12		12	24	123	24	123
Sus celebensis ferus	12	1	1	1234	12		4	3	14	1234
Sus papuensis	124	12	1	124	24	4		13	13	1234
Sus celebensis	123	1	13	1234	123	3	13		12	1234
Sus verrucosus	234	2	-	234	24	14	13	12		234
Sus barbatus	1234	23	234	23	123	1234	1234	1234	234	

Discriminant analysis of cranium parameters of species, cross-breeds, feral, and domestic pigs of the subgenus Sus

The largest variability manifests in the species *Sus scrofa* to which the specimens of the second generation cross-breeds, the feral pig, which lives in the Malaysia Archipelago, and the species *Sus papuensis* belong. The feral pig of this archipelago *Sus celebensis ferus* also manifests a larger variability in comparison with other forms (Table 6).

Although the number crania of female specimens measured is relatively smaller, female specimens manifest a weaker variability. From 260 analyzed crania of the species *Sus scrofa*, only one is classified into the species *Sus celebensis* and vice versa for the species *Sus celebensis* only one is classified into the species *Sus scrofa.* The remaining two forms, second generation cross-breeds and the species *Sus barbatus,* do not cross with the species indicated, above.

TABLE 6
Discriminant analysis among the male specimens of the cranium parameters the species, hybrids, feral and domestic pigs of the subgenus *Sus*.

Taxon	N	1	2	3	4	5	6	7	8	9	10
Sus scrofa	388	98.2	-	0.77	-	-	0.26	0.77	-	-	-
F1	4		100	-	-	-	-	-	-	-	-
F2	3	-	-	100	-	-	-	-	-	-	-
Sus scrofa domesticus	7	-	-	-	85.7	14.3	-	-	-	-	-
Sus scrofa ferus	7	-	-	-	-	100	-	-	-	-	-
Sus celebensis ferus	13	-	-	-	-	7.7	84.6	-	7.7	-	-
Sus papuensis	11	-	-	-	-	-	-	100	-	-	-
Sus celebensis	11	-	-	-	-	-	-	-	100	-	-
Sus verrucosus	17	-	-	-	-	-	-	-		100	-
Sus barbatus	16	-	-	-	-	-	-	-	-	-	100

Cluster analysis of the species, cross-breeds, feral, and domestic pig of the subgenus Sus

Through these analyses following groups of male specimens clearly emerged. The most closely related species are *Sus celebensis* and the feral pig *Sus celebensis ferus*, which lives in the Malaysia Archipelago. In that case, the maximum closeness of propinquity degree is 0.04, followed by specimens of the species *Sus scrofa* and *Sus barbatus* as well as by the second generation cross-breeds and the domestic pig and, finally, the feral European pig and *Sus verrucosus*. After that, the larger groups were formed, which have the maximum closeness of propinquity degree greater then 1.00 (Table 7). The last group is formed by all investigated taxonomies with the maximum closeness of propinquity degree of 3.00.

For female specimens, three groups are formed. The most closely related species are those of the second generation cross-breeds and *Sus barbatus*, with the maximum closeness of propinquity degree of 0.28. Next is the group *Sus scrofa* with 1.58, and in the last position is the group *Sus celebensis*. It is interesting to note that, for both sexes, a trend of closeness of propinquity between the species *Sus scrofa* and *Sus barbatus* is apparent.

TABLE 7
Groups of species, hybrids, feral, and domestic pigs (2) for the male specimens of the subgenus *Sus* (1- the maximum closeness of propinquity degree).

N	1	2
1	0.04	*Sus celebensis ferus* + *Sus celebensis*
2	0.25	*Sus scrofa* + *Sus barbatus*
3	0.44	F2 + *Sus scrofa domesticus*
4	0.62	*Sus scrofa ferus* + *Sus verrucosus*
5	1.06	*S. s. ferus* + *S. verrucosus* + *S. papuensis*
6	1.06	F1 + F2 + *S. s. domesticus*
7	1.25	*S. scrofa* + *S. barbatus* + *S. s. ferus* + *S. verrucosus* + *S. papuensis*
8	1.40	N - 6 + N - 7

DISCUSSION

The problem of taxonomy of the subgenus Sus

In the past, the groups of species indicated, above, were divided by Nehring (1888) on the basis of the form at the alveolus of the lower canine tooth as a basic diagnostic cranium characteristic. We already mentioned this problem in interpreting the results. This characteristic shows clearly how those two groups of species are divided (Table 2). Through the first two indexes on the species level *Sus papuensis* belongs to the group «*scrofa*», but through the third index *Sus papuensis* occupies an intermediate position. When some subspecies of the species *Sus scrofa* are included in the analysis, they show a certain polymorphism for the first factor being related to the subspecies *Sus scrofa vittatus,* on the one hand, and to the species of the group «*verrucosus*» on the other, and to the subspecies *S. s. vittatus* through the third factor. Those results confirm the conclusion made by Kelm (1939), Mohr (1960), and Groves (1981) about the origin of that «species» of the above-mentioned subspecies. Its relationship to the next group can also be explained because domestic and feral pigs of the species *Sus celebensis* live there and the actual species live in the neighborhood of New Guinea islands. That is why crossings of all kinds were possible in the past and are possible today. For that reason, Schwarz (1914) put the above subspecies into that group (Groves 1981, 1983). On the other hand, it should be noted that many authors, such as Major (1883, 1897); Nehring (1888); Kelm (1939);

Kahlke (1955); Thenius (1972); Azzaroli (1975); Hemmer (1978); Groves (1981) believe the ancestor of the species *Sus scrofa* is *S. verrucosus*, which is the most primitive specimens of this genus. The Indonesian wild boar *Sus scrofa vittatus* is their first origin. Probably, this is the reason for a relationship between this subspecies and the species of the group «*verrucosus*», but we must not forget the statements by Sjarmidi and Gerard (1988), Blouch and Groves (1990), Groves and Grubb (1993) about the sympatry of this subspecies to the species of this group and its crossing with them. The division into particular groups of species becomes clearer through a discriminant analysis, where all three factors are used (Table 4). The results show the relationship between the species inside the groups. The species *Sus verrucosus* exhibits the greatest polymorphism in the group «*verrucosus*». According to the above-mentioned authors, this species is the ancestor of all of the others. Referring to another group there is no doubt about a relationship between the two taxonomies realized by the *S. s. vittatus* is living there (Table 5). The differences and similarities between particular taxonomies of the subgenus can be shown on the basis of cranium measurements by using factor analysis (Table 5). In that analysis, we included not only crania of the domestic pig and the feral pig of European and Indonesian origin, but also of the first and second generations of the cross-breeds between the domestic pig and European wild boar, i.e., conditions for this subgenus used to exist in the nature.This genus originated in the early Miocene in the East-Asian region (Matthes 1962). This genus being in efflorescence spread towards Central Asia, and from there to Europe and to the islands of south-east Asia (Hardjasasmita 1987). There is a series of wild boar remains in Europe that date to the end of the Tertiary and in the early Pliocene periods (Thenius 1972). In the tertiary form called *Sus minor* Deperet, one can include *Sus strozzi* Meneghini from the late Pleistocene, which was found originally in France and Holland (Kahlke 1955). Those animals looked to a large extent like today's *Sus verrucosus*, which lives on the island of Java (Azzaroli 1975). That species is more primitive than other species of the *genus*. The above statement originated with Hemmer (1978), who conducted comparative investigations of brain volume, and showed that the brain volume of *Sus verrucosus* is the smallest of all. The quaternary period of freezing, first in Europe, changed the living conditions of the heat-loving wild boars drastically. They migrated to the south drawing back before the frozen massifs just behind the Alps, Carpathian Mountains, and the Caucasus (Vereshchagin 1959; Lasota-Moskalewska et al. 1987). With the consecutive thaw they returned to the broad-leaved forest of the continent. Simultaneously, the boars changed their morphology and they no longer looked like those of the group «*verrucosus*»; rather, they became similar to today's wild boar. During the first intermediate period of thaw - Gunts-Mindel the species *Sus scrofa priscus* in Europe manifested itself as a species close to today's species. The origin of the species has to be searched for somewhere in the southeastern part of Asia. In that area, i.e. Sumatra and the neighboring islands, lives the subspecies *Sus scrofa vittatus*. According to Major (1897), it is the most primitive among those in the species *Sus scrofa*. That statement was confirmed by Schroter (1922), who compared crania of that subspecies with those of the *Sus scrofa scrofa* and proved that older specimens of the first subspecies had the same cranium characteristics as those of 5-6 month-old specimens of the second subspecies.

To this point, we have assumed that the cranium and its inherited information is a reliable criterion for describing a particular species. Therefore, the species *Sus barbatus* shows the greatest differences with other species. During its phylogenetic development in the Pliocene, that species was separated from the original species *Sus verrucosus*. In that way, the species became isolated from the later-formed species, such as *Sus celebensis* and *Sus scrofa,* (Thennius 1972; Azzaroli 1975; Briedermann 1986). After *Sus scrofa*, that is the most widely distributed species (*Sus barbatus*) and it was investigated by many authors (Allen 1948; Gibson-Hill 1948; Hislop 1948, 1949; Kempre 1948; Pfeffer 1959; Diong 1973; Pfeffer and Caldecott 1986; Caldecott 1991; Caldecott *et al.* 1993). In contrast to the other two species (*Sus verrucosus* and *Sus celebensis*), which live on the islands of the Malaysia Archipelago, the species *Sus barbatus* also lives on the continent - Malay Peninsula. By using the results of the factor analysis (Table 5), we can see that this species has a different cranium size and shape compared to the species and forms of *Sus scrofa, Sus celebensis ferus, Sus scrofa ferus, Sus papuensis* and *Sus celebensis.* The difference between *Sus barbatus,* on the one hand, and the first two generations of the cross-breeds, the domestic pig, and *Sus verrucosus,* on the other hand, is only in the shape of the cranium. Other species that differ from *Sus scrofa domesticus* in all factors are *Sus celebensis* and *Sus celebensis ferus*, which means that the European domestic pig is not connected with those two forms. From the factor analysis results we can see that cross-breeds show small differences compared to the others, which is due to the mixing of the two different genetic types and, probably in this case, the variability is greater.

The results obtained by the discriminant analysis (Table 6) show a high polymorphism of male specimens for the species *Sus scrofa* and its relationship with *Sus papuensis.* According to Groves (1981), the latter species originated from *Sus scrofa.* Some of the male specimens of the species *Sus scrofa* can be related to *Sus celebensis ferus* while female specimens are related to *Sus celebensis,* and vice versa for *Sus papuensis*. That can be explained by the fact that in the south-eastern part of the area those three forms are sympatric. The cluster analysis (Table 7) shows a very high maximum closeness of propinquity degree between *Sus celebensis* and *Sus* *celebensis ferus.* That fact confirms the conclusion made by Groves (1983) regarding the origin of the second form from the first form. There is an interesting connection between the species *Sus scrofa* and *Sus barbatus* that cannot be observed using other analyses. That can be explained by their common origin. The formation of the second group consisting of the second generation cross-breeds and the domestic pig can also be explained because we have cross-breeds between the wild European boar and the domestic pig. But, how can we explain the relationship between *Sus scrofa ferus* and *Sus verrucosus*? As Briedermann (1986) emphasized, one can assume that after the wild-growing process, domestic pig regained characteristics of the wild boar, but not those of the species from which the domestic pig originated, but the characteristics of the ancestor. That can be seen from the next cluster, where *Sus papuensis* attaches to the above-mentioned species.

Based on the results of our study, we can say that there are differences between particular taxonomies in the subgenus. Future genetic investigations should answer the question of how crucial those differences are for defining them as a separate species. According to Wilson (1993), the species is a sum of the populations or subspecies whose specimens have the freedom to reproduce themselves in natural conditions. In this case, all of the species of the subgenus *Sus* have freedom to cross and to produce a productive generation (Mohr 1960, Sjarmidi and Gerard 1988, Blouch and Groves 1990, Groves and Grubb 1993).This is the first time a thorough analysis was performed to systemize the subgenus *Sus*. As a result, our conclusions are as follows:

1. The species *Sus scrofa* differs totally in the form of the canine tooth at the alveolus from the other species of the subgenus.
2. Its division into two groups of species seems justified.
3. The so-called species *Sus papuensis* should be included in the species *Sus scrofa* as a form of subspecies *Sus scrofa vittatus.*
4. The analysis of the differences in size and shape of crania to some extent shows the differences between the species of the subgenus, but this morphology structure is variable and cannot be considered a definitive taxonomic criterion.
5. The morphometric analysis performed confirms the systemization of the subgenus *Sus,* with the exception of *Sus papuensis.*
6. The taxonomy of *Sus scrofa* is clarified.
7. The sexual dimorphism of *Sus barbatus* and *Sus celebensis* is related to the size of the cranium.

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